SOCIO-ECOLOGY OF SAHARAN GERBILS, ESPECIALLY *MERIONES LIBYCUS*

by

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Les auteurs ont étudié cinq Gerbillidés (*Meriones libycus, M. crassus, Gerbillus pyramidum, G. gerbillus* and *Psammomys obesus*) et un Dipodidé (*Jaculus jaculus*) sur le Hamada du Guir, Algérie, par piégeage et marquage, et par l'observation sur le terrain et au laboratoire.

Les rongeurs de toutes ces espèces se déplacent fréquemment sur plusieurs centaines de mètres. Les femelles de *M. libycus* restent, d'habitude, dans une seule daya, mais les mâles circulent plus loin.

Ce système social est caractéristique des Gerbillidés :

1) chaque adulte reste normalement seul,

2) les mâles ont des domaines étendus qui se recouvrent souvent,

3) les femelles habitent des domaines relativement petits et exclusifs.

Néanmoins, la sociabilité de ces quelques espèces est assez variable. L'agressivité extrême du *Psammomys* peut être expliquée par ses ressources alimentaires qui sont facilement défendables.

"Socio-ecology" (Crook, 1970) is that study of social systems which is primarily concerned with their adaptive significance. The main approach is comparative : one attempts to explain variations in social behaviour as adaptations to ecological differences. Increasing interest in this problem has inspired recent comparative field studies of several mammalian taxa (e.g. Jarman, 1974; Barash, 1974; Clark, 1974).

The gerbils (Rodentia, Myomorpha; alternatively considered family Gerbillidae, e.g. by Petter, 1961, or subfamily Gerbillinae of Cricetidae, e.g. by Walker, 1964, or of Muridae, e.g. by Ellerman, 1940) are a group of some 11 to 14 genera. They are the dominant rodents in the Great Palaearctic Desert, and occur in adjacent semi-arid and savannah habitats. In the northwest Sahara, eight species representing four genera occur in the vicinity of Beni-Abbes, Algeria (30° 7′ N lat, 2° 11′ W long). Their taxonomic status has been determined by Petter (1961), who also described the habitats typical of each species. There is thus an excellent foundation for a study of comparative socio-ecology. The social structure and ecology of one species, *Psammomys obesus*, has now been described in some detail (Daly & Daly, 1973, 1974 , 1975).

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The objectives of this study were :
1) to supplement Petter's habitat descriptions with quantitative data ;
2) to infer social organisation from trapping data (which afford information about sex and species differences in ranging and the degree of range overlap, whether prolonged associations occur, dispersal of juveniles, etc.);
3) to seek influences of ecological differences upon social organisation.

One species, *Meriones libycus*, proved sufficiently diurnal and observable to be made the object of a more intensive study, similar to our previous study of *P. obesus*.

STUDY AREA

The vicinity of Beni-Abbes has been described by Petter (1961) to whom readers are referred for greater detail. The Hamada Guir is a vast stony plain lying to the southwest of the Wadi Saoura. The study area (Fig. 1) comprised about 10 km^2 on a protrusion of the hamada into the canyon of the Saoura.

Where soil has accumulated in slight depressions in the hamada, two sorts of concentrations of vegetation occur. "Graras" are elongated gullies perhaps 1 km or more in length, and generally less than 1 m in depth and less than 30 m in width. "Dayas" are depressions up to several hundred meters in diameter, often the terminal drainage points of graras.

With the exception of a single *Acacia Seyal* tree, all plant life on the study area consisted of perennial shrubs up to 2.5 m in height and 110 m in diameter, and much smaller annuals. In the centre of the lushest dayas, up to 30% of the ground is covered by perennials. The perennial cover over the whole area is less than 1%.

In early Nov., at the outset of the study, 40 mm of rain fell on the study area, the first large storm after 6 years during which the mean annual rainfall had been 20 mm. Further rains of 18 and 12 mm occurred in Mar. After the Nov. storm, there was a major "asheb", a rapid growth and completion of the life cycles of various small annuals, from about Dec. to Mar. At the height of the asheb, the ground cover of annuals was about equal to that of perennials : up to 40% in the densest areas, and less than 1% overall.

Important perennial species are listed in Table 1. Species composition often varies dramatically from one daya to another, but most on the study area contained a mixture of the common species in Table 1. A few dayas near the road were dominated by *Salsola foetida*, which was absent elsewhere.

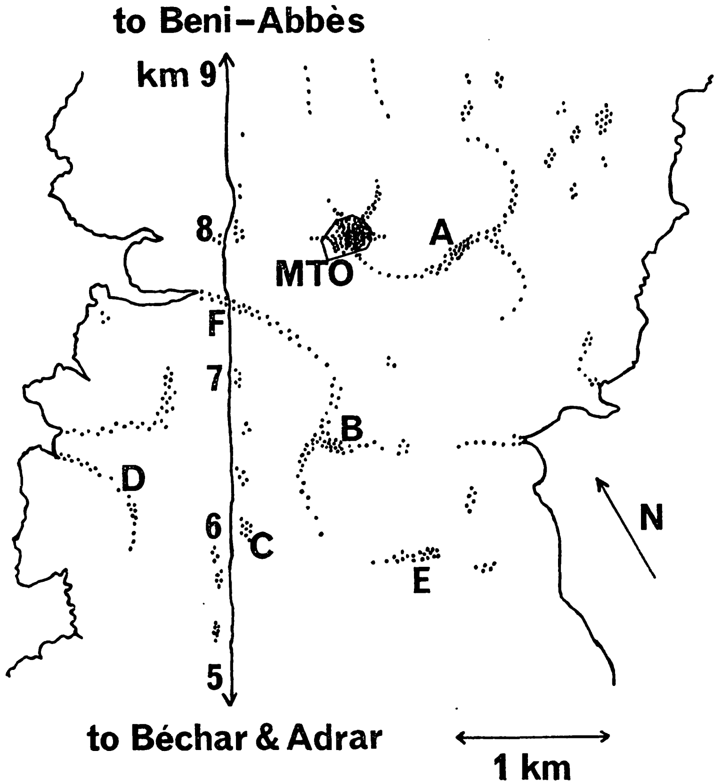

Fig. 1. — Map of the study area.

The vegetation is heavily exploited by domestic goats, sheep and camels. In 1967, the meteorological service (MTO) enclosed a daya of about 9.3 ha with a two-strand barbed- wire fence, thus excluding domestic ungulates. Plant and rodent densities are therefore maximal in the MTO daya (Figs. 1, 3, 4), and the study of *Meriones libycus* by direct observation was conducted there.

METHODS

Trapping.

Trapping was conducted on the study area on 43 nights between 12/11/73 and 2/1/74, on 35 nights between 10/2 and 25/3, and on 6 nights from 17/4 to 22/4.

Traps were baited with bread and dates. Open wire cage-traps and enclosed Longworths traps were originally set out in pairs. After 288 trap-pair-nights, 59 rodents had been captured in cage traps and 2 in Longworths. The latter were then discarded.

In other trials elsewhere, Longworths set alone were usually avoided by gerbils, but they were effective for mice *(Mus musculus)* in Beni-Abbes.

20 to 25 cage-traps were set nightly, and were visited 2 or 3 times. In cold weather in Dec., they were picked up before midnight. Otherwise they were left until near dawn. All vegetated areas and open burrows were trapped. Traps were moved nightly. Trapping was concentrated in the areas where rodents were most numerous (in particular the MTO daya, daya A, and grara B), but no area was left untrapped for more than 10 days during the trapping periods.

Trapped animals were identified by species and sex, marked by the amputation of one or two toes, weighed, and released on the spot. *Meriones libycus* and *Psammomys obesus* were also marked for visual identification by cutting away small patches of fur, revealing the darker underfur in distinctive patterns and loci.

Ziziphus experiment.

A systematic trapping experiment was conducted at *Ziziphus lotus* bushes. At each of the 31 bushes on the study area, 5 traps were left open for two successive nights in Dec., and again in Mar. They were visited three times per night.

Observation.

Marked *M. libycus* were directly observed with binoculars, mainly at the MTO daya. This daya was mapped in detail and all bushes named according to a rectangular co-ordinate system. (All bushes on the study area outside the MTO daya were named and located on a larger map if rodents were trapped there.) Observed animals were identified and located, and then were usually followed for as long as possible, with the observer recording their route and behaviour. Most observations were made between mid-afternoon and dark.

Vegetation sampling.

Vegetation was sampled around each capture site (CS). Along orthogonal axes meeting at the CS, the ground was scratched at 5, 10, 15 and 20 m from the CS in each of the 4 directions. 16 lines, perpendicular to the axes and centred at the scratches, were then sampled. One of us walked slowly along each line fixating a point on the horizon, and lowered a hand-held vertical metal rod of 3 mm diameter with each step of about 60 cm. The other recorded whether the rod intersected a plant, and if so, the plant species and the maximum height of the intersection according to intervals marked on the rod (0-10 cm, 10-25, 25-60, > 60). 25 points were sampled on each of the 16 lines, a total of 400 around each CS.

Plant species identifications follow Ozenda (1958).

RESULTS

Rodents present and habitat selection

Rodents present on the study area are listed in Table 1. These included 5 species of gerbils and a jerboa, *Jaculus jaculus* (Dipodidae). For numbers trapped, see Table 3.

		M.libycus	M.crassus	G.pyramidum	G.gerbillus	P.obesus	J.jaculus
Total number of captures		272	80	48	12	8	27
Capture site bushes (% of total captures for that rodent species)							
	Ziziphus Lotus	60	30	38	83	0	15
	Launaea arborescens	24	4	25	0	0	4
	Zilla macroptera	7	14	7	8	0	0
	Pergularia tomentosa	7	0	15	0	0	0
	Antirrhinum ramosissimum	0	3	0	8	0	0
	Salsola foetida	0	3	0	0	75	4
	No bush	3	48	17	0	25	78
Cover around capture sites (each plant species as % of total plants around CSs for that rodent species). Perennials only.							
Scrophulariaceae	Antirrhinum ramosissimum	36.4	15.0	31.4	18.9	0.7	33.6
Cruciferae	Zilla macroptera	10.3	9.4	13.7	8.4	5.6	12.8
Compositae	Launaea arborescens	17.8	10.0	20.6	14.0	1.4	7.2
	Anvillea radiata	9.2	6.7	5.2	5.6	0.7	7.2
	Rhanterium adpressum	4.1	0.0	3.5	20.3	0.0	4.0
	Bubonium graveolens	0.3	5.0	1.0	1.4	0.0	2.4
Leguminosae	Psoralea plicata	1.1	1.7	0.4	0.0	0.0	0.8
	Crotalaria Saharae	0.2	0.0	0.0	0.0	0.0	0.0
	Acacia Seyal	0.0	0.0	0.6	0.0	0.0	0.0
	Lotus Jolyi	0.0	0.0	0.1	0.0	0.0	0.0
Umbelliferae	Pituranthos Battandieri	3.3	0.0	3.9	1.4	0.0	0.0
Caryophyllaceae	Gymnocarpos decander	0.9	1.7	1.4	0.7	0.0	0.0
Rhamnaceae	Ziziphus Lotus	0.7	0.0	1.4	6.3	0.0	2.4
Asclepiadaceae	Pergularia tomentosa	0.3	1.7	2.4	0.0	0.0	0.0
Cistaceae	Helianthemum Lippii	1.9	0.0	1.4	0.0	0.0	0.8
Resedaceae	Randonia africana	0.7	1.1	1.1	0.7	0.0	0.0
Cucurbitaceae	Colocynthis vulgaris	0.1	0.0	0.4	0.0	0.0	0.0
Graminae	Aristida pungens	0.1	0.0	0.1	0.0	0.0	0.0
Chenopodiaceae	Salsola foetida	0.0	37.8	0.0	0.0	91.7	22.4

TABLE 1. — Plant species in the vicinity of capture sites of each rodent species.

Gerbillus gerbillus was trapped in only two dayas and in a grara at the hamada edge. These were the three sandiest sites on the study area, all with small dunes. This confirms Petter's (1961) characterisation of the species as "exclusively psammophile". However, ♀ 1 traversed at least 500 m of bare stony hamada in travelling 1260 m between the two sandy dayas.

Psammomys obesus CSs were all in dayas dominated by *Salsola foetida* (see Table 1), of the family Chenopodiaceae with which this gerbil is always associated (Daly & Daly, 1973). These dayas were of a distinctive species composition : cover at *P. obesus* CSs varied from 9 to 16%, with *S. foetida* comprising 82 to 97% thereof. These bushes were desiccated : most had no green growth at all, and there was never more than 20 g on any bush. It was clear from tracks and debris that *P. obesus* were eating whatever plants were available, especially new leaves of an annual, *Diplotaxis Pitardiana* (Cruciferae). The two gerbils (one female and one male) moved frequently and independently between dayas, totally cropping *S. foetida* as it grew (see "Ranging" below).

Employees of the research centre told us that *P. obesus* had appeared in these hamada dayas six years earlier, after the last flood of the Saoura, and had been present ever since, while the *S. foetida* steadily declined during successive dry years. There were certainly but two remaining during our study. They were present throughout the six months, and the female littered in the second week of March.

Plant species at the CSs of the other gerbil species are summarized in Table 1. Habitat differentiation is more clearly related to the quantity of vegetation around the CSs, as shown in Fig. 2. Plant height was not a useful measure for differentiating CSs.

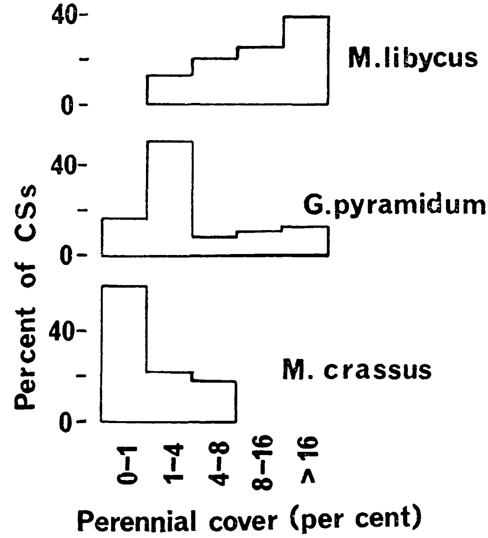

Fig. 2. — Cover by perennial bushes (% of ground covered) around capture sites of gerbil species.

To test differences in perennial cover, only the first CS for each individual rodent was considered. Directional (one-tailed) tests were used to compare species, using predictions from Petter's (1961) habitat descriptions. No prediction was possible between *M. crassus* and *J. jaculus* since both were described as occupying bare hamada ; they are therefore compared with two-tailed tests. CS cover and test results are summarized in Table 2.

Petter's account is in general confirmed : *M. crassus* occupied open hamada, *M. libycus* the dayas, and *G. pyramidum* was taken mainly in the former in Dec., and mainly in the latter in Feb. and Mar. Jerboas were usually trapped in the most open terrain of all.

A further three species of gerbils may be found in the area. *Gerbillus campestris* were trapped in a deep rocky ravine descending from the hamada edge, the very habitat described by Petter (1961). *G. nanus* were numerous in the MTO daya in 1968 (Mermod, 1969), but we only encountered the species in the wet wadi bottom of the Saoura, again the habitat described by Petter. Their disappearance from the hamada is probably attributable to the succession of dry years from a)

	M.libycus	G.pyramidum	M.crassus	J.jaculus
Bush	33	14	19	2
No Bush	0	3	14	8

M.l. - G.p.	Exact 1-tail $p = .035$
G.p. - M.c.	$\chi^2 = 2.1$, 1-tail $p < .10$
M.c. - J.j.	$\chi^2 = 3.0$, 2-tail $p < .10$

b)

	M.libycus	G.pyramidum	M.crassus	J.jaculus
Mdn cover (%)	11.25	1.75	0.75	0.00

M.l. - G.p.	$U = 99$;	$N = 33,17$;	1-tail $p < .0001$
G.p. - M.c.	$U = 162.5$;	$N = 17,33$;	1-tail $p < .01$
M.c. - J.j.	$U = 103.5$;	$N = 33,10$;	2-tail $p < .08$

TABLE 2. — Capture sites of the four most common rodent species, compared on : a) presence of a bush at the burrow, and b) perennial ground cover around the burrow.

1968 to 1973. *Pachyuromys duprasi* were taken on the hamada by both Petter and Mermod, but we never trapped one in two winters (Nov.-Apr., '72-3 & '73-4) despite widespread and deliberate search. We cannot certainly conclude *P. duprasi's* disappearance from the region, for Mermod caught several only after letting traps stand for more than a month, and he suggested that this species is uniquely wary. However, *P. duprasi*'s gait is distinctive (Petter, 1961), and Mermod had already surmised its presence from its tracks, which we never found.

Ziziphus experiment.

Petter concluded from distribution in the field and from the results of staged encounters between captive gerbils, that *M. crassus* is excluded from the dayas by the active aggression of *M. libycus.* However, it seemed to us that *M. crassus* actively selected open habitat even where free from *M. libycus*' aggression. The "*Ziziphus* experiment" permitted a test of this by comparison of two areas, each containing burrowed *Z. lotus* bushes and only one of the two *Meriones* species. In the MTO daya, there were eight *Z. lotus* bushes and no *M. crassus.* In the long grara west of the road (D in Fig. 1), there were six *Z. lotus* and no *M. libycus.* The number of *Meriones* trapped at each bush was correlated with the perennial cover around each.

For Dec., *M. libycus* captures correlate positively with cover ($r = .70$), and *M. crassus* captures correlate negatively ($r = -.39$). Neither coefficient is significantly different from zero, but they differ significantly from each other ($\chi^2_{1df} = 3.01$, directional $p < .05$, test after Hays, 1963, p. 532). This suggests that there is a real species difference in habitat selection independent of direct confrontational competition. Of course, competition from *M. libycus* is very likely a more ultimate cause of *M. crassus*' preference for less vegetated sites, either through individual experience of previous confrontations or by exerting a selection pressure for such preference.

In Mar., *M. libycus* were present in both areas, so the same comparison could not be made. However, captures remained consistent with the hypothesis of differential habitat selection : in the long grara, two *M. libycus* were captured at the *Z. lotus* bush with the most surrounding cover, two *M. crassus* at that with least, and neither species at the four intermediate bushes.

It should perhaps be noted that there are large differences in the habitats favoured by different geographical populations of these widespread species, and in particular that *M. crassus* elsewhere chooses vegetated sites (Petter, 1961).

Ranging

Table 3 presents the maximum spontaneous displacements recorded for each rodent species recaptured on the study area. These data indicate that every species moves about over distances of at least several hundred meters. This is clear despite the paucity of data for certain species, and despite the necessary limitation of the study area's

		No. of animals marked	No. recaptured	Total no. of recaptures	Maximum RL
Meriones libycus	♀	15	13	142	2280 m
	♂	13	16	97	2420
Meriones crassus	♀	15	9	31	960
	♂	18	8	15	1870
Gerbillus pyramidum	♀	6	4	13	910
	♂	11	7	19	4500
Gerbillus gerbillus	♀	2	1	5	1260
	♂	2	2	3	0
Psammomys obesus	♀	1	1	5	470
	♂	1	1	1	470
Jaculus jaculus (Dipodidae)	♀	5	2	4	1020
	♂	5	5	13	2420

TABLE 3. — Rodents trapped on the study area, and maximum range lengths. (RL = linear distance between most distant capture sites of an individual.) 84 nights trapping (c. 2000 trap-nights) between 12-11-73 and 22-4-74.

magnitude. A more extensive trapping programme must surely yield still larger ranges. In fact, a single trapping instance north of the study area affords the Figure of 4500 m for a *G. pyramidum* male.

Moreover, these large distances are not merely traversed, but represent familiar ranges. This is confirmed by records for particular individuals of several species :

1. *Meriones libycus*. The clearest case is afforded by male 3, who made at least seven round trips between the MTO daya and daya A, a distance of 1 km (Fig. 1). Other males similarly ranged widely. The only female to move outside the vicinity of a single daya shifted permanently rather than retracing (see "Behaviour of *M. libycus*" below).

2. *M. crassus*. Female 5 was trapped five times over 3 1/2 months within a range of 200 m along a single grara; she was once trapped 960 m away, but had returned to her usual burrow and was retrapped there less than 2 hr later. Several males were captured at widely disparate sites, but recaptures were few, and clear evidence of regular retracing was not obtained. Such evidence *was* obtained by Petter (1968).

3. *Gerbillus pyramidum*. Male 2, originally marked west of the road in Dec., made at least two round trips between the MTO daya and daya B, a distance of 1360 m, in Feb. and Mar. Evidence of retracing by females was not obtained.

4. *Psammomys obesus*. The male and female, present throughout the study, moved frequently among several dayas along the roadside over a range length of 470 m. Sightings supplementing the trappings indicated that they were seldom in the same daya simultaneously.

Petter (1961) estimated much smaller ranges on the basis of tracks and direct observation of released gerbils of many species. However, in a later study of *M. crassus* (Petter, 1968), he found spontaneous displacements of up to 3800 m, apparently within a known range. Mermod (1970) recorded spontaneous moves of 550, 800, and 2500 m in *G. gerbillus* and imagined they were atypical cases of "nomadism". Our data show that large movements are commonplace in these gerbils' lives. Russian scientists have recorded many instances of large displacements by gerbils (Naumov, 1963). Recently, by means of radioactive tracers, spontaneous movements of up to 17.5 km have been recorded in the great gerbil *Rhombomys opimus* (Lobachev, 1973).

Range magnitude must of course vary with resource dispersion, both inter- and intra-specifically. For example, the ranges of both the *Psammomys*, exploiting very sparse resources in the present study, greatly exceeded the largest range recorded in any of more than 100 marked animals in two seasons at the oasis of Ouarourout (Daly & Daly, 1974, 1975).

Sex differences.

Table 4 compares the ranging behaviour of the sexes in the three most frequently trapped species. Range length (RL) is the linear

	♀♀			♂♂				
	Mdn RL	N	Mean N captures	Mdn RL	N	Mean N captures	Mann-Whitney U	1-tailed p
M. libycus	183 m	10	14.7	516 m	11	9.3	35	<.05
M. crassus	400	9	4.4	1500	5	3.4	11	<.08
G. pyramidum	169	4	4.3	361	6	4.0	6	<.13

TABLE 4. — Comparisons of ranging by sex.

distance between the two most distant CSs of an individual. Included are all adults retrapped at an interval of at least a week.

As in *P. obesus* (Daly & Daly, 1975), males range more widely than females in these species, although statistical reliability diminishes where data are few. A factor introducing bias in the direction of relatively inflated female ranges is the greater recapture frequency for females within each species. Ranging of *M. libycus* is treated in more detail below.

Behaviour of *M. libycus*

In the MTO daya and elsewhere, *M. libycus* inhabited multi-entranced burrows directly under large bushes. Most time was spent under cover, but the gerbils were often in plain view at the edges of such bushes, foraging, eating, grooming, or sitting quietly.

Moves between bushes were frequently observed. An animal might ramble over a route of 100 m or more in a few minutes, pausing briefly at many bushes to investigate, eat, sand-bathe, scratch, scent-mark, etc., and seldom or never enter a burrow. Encounters between gerbils were sometimes observed on such rambles, and are summarized under "Interactions" below.

Diurnal activity was especially frequent in late afternoon, but could be observed throughout the day in winter. By March, it had become rare. Tracks and trapping indicated a high degree of nocturnal activity throughout the study.

Ranging and dispersion of females.

Ten adult females were trapped and marked on the entire study area during the first trapping period (Nov. and Dec.). Nine were still present in Mar., and alterations of range were mostly slight. Particular females inhabited dayas A (♀ 1), B (♀ 2), and C (♀ 9) throughout the study (See Fig. 1). A smaller female was present with ♀ 9 in daya C for a week in Dec., then disappeared.

Five females (numbered 3 to 7) inhabited the MTO daya. Fig. 3 shows their ranges during two 38-day periods. The polygon maps the surrounding fence. (The lower barbed-wire strand was 50 cm high,

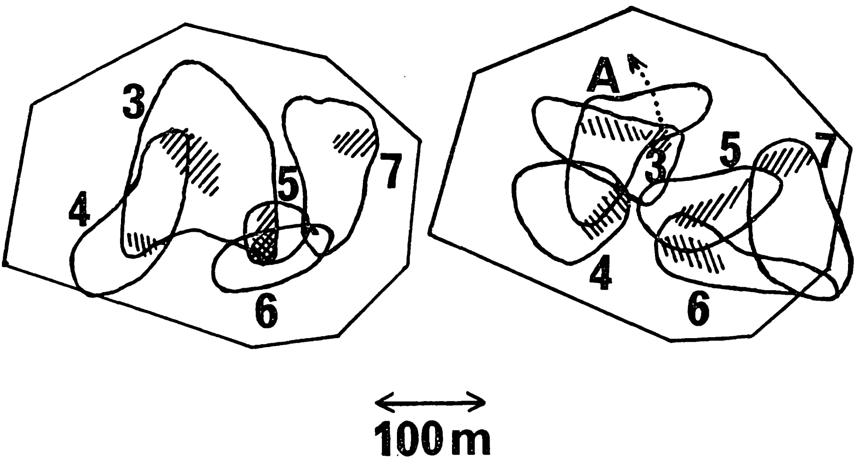

Fig. 3. — Female ranges in the MTO daya ; left : Nov. 21-Dec. 28 ; right : Feb. 10-Mar. 20.

and of no importance to the gerbils). Irregular shapes enclose all areas in which each female was ever detected. Cross-hatched areas are those intensively used. Individuals were observed on a mean of 11.2 days in the first period, 12.0 in the second. Considerable stability of range is apparent.

The tenth , ♀ A, inhabited daya E (Fig. 1) from Nov. 12 to Feb. 13, was in daya A on Feb. 17 and 20, and in the MTO daya from Feb. 25 on. After ♀ A's arrival, ♀ 3 was not seen in her former range, but was trapped on Mar. 1 at a bush at the edge of her earlier range (indicated by arrow in Fig. 3), and then disappeared. At this time, ♀ A was the smaller animal (102 vs 128 gm).

Fig. 3 indicates that ♀ ranges showed a degree of overlap even in the core areas. In particular, ♀♀ 5 and 6 were both intensive users of one large *Z. lotus* bush, and ♀♀ 3 and 4 each visited the other's principle bush. Despite circumstantial evidence that ♀ A displaced ♀ 3, signs of rigorous territorial exclusion were lacking.

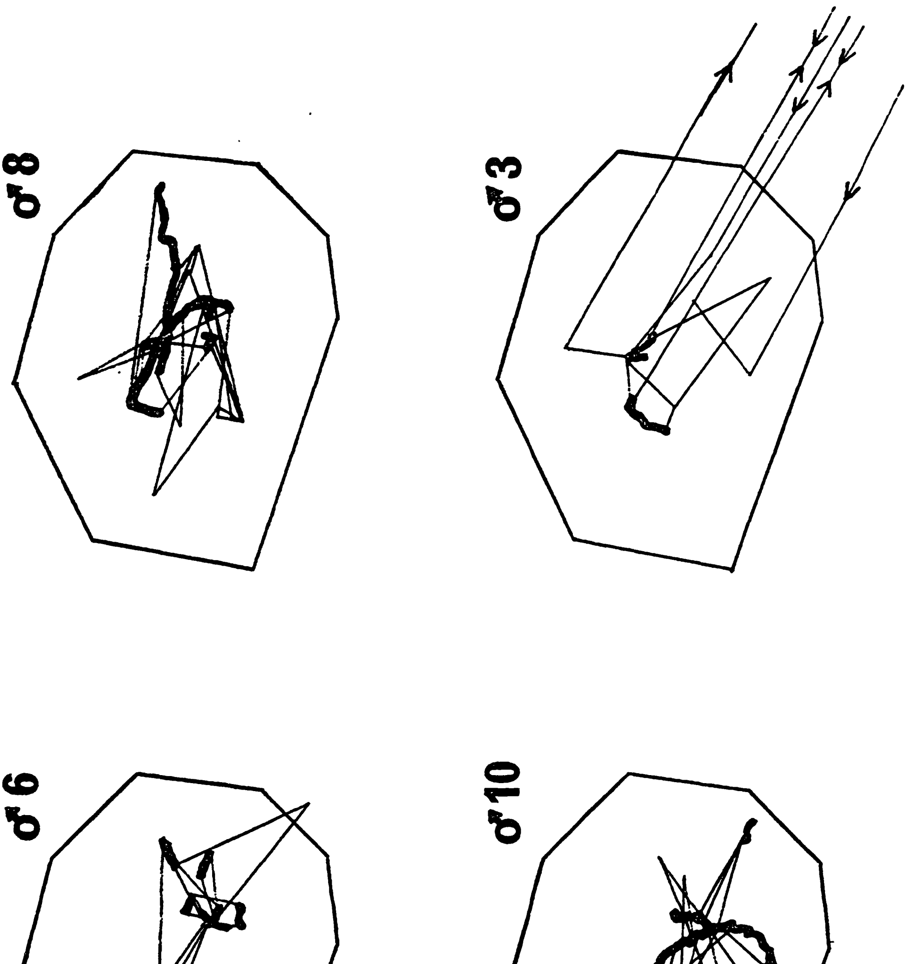

Fig. 4. — Male ranges in the MTO daya in Feb. & Mar. Thin lines connect sites where seen successively. Thick lines represent movements directly observed.

Ranging and dispersion of males.

Males did not often confine their activities to single dayas, but instead visited several. Nine adult males were marked on the study area in the first period, and a tenth in January. All ten were trapped in the MTO daya at one time or another. Four of these were also trapped in other dayas on the study area, and prlonged absences suggested that others ranged outside the study area. Only ♂ 8, the largest and apparently most dominant (see "Interactions" below) was present in a single daya, the MTO, throughout the study.

Within the MTO, males did not exhibit the delimited and largely separate ranges typical of females, although ♂ 8 confined his activities to a few central bushes in Nov. and Dec. Fig. 4 shows the ranging of four males who were frequently present in the MTO in the second period. Several bushes within the core areas of particular females were visited by all four males.

Seasonal changes and reproduction.

Table 5 separates the ranges observed in two 44-day periods. Included are all adults observed over at least a week's interval. Data are total RLs over each 44-day period (see "Ranging" above), and Mean Weekly RLs (Daly & Daly, 1975), based on all weeks in which an animal was seen on at least two days. One-tailed tests were

	♀♀		♂♂		
RL over 44 days:	Mdn RL	N	Mdn RL	N	
Nov.15 - Dec.28	111 m	9	159 m	8	U = 22, p > .10
Feb.10 - Mar.25	140	9	1420	5	U = 7, p < .05
	T = 13, p > .10		U = 6, p < .05		
Mean Weekly RL:	Mdn MWRL	N	Mdn MWRL	N	
Nov.15 - Dec.28	32 m	8	63 m	8	U = 20.5, p > .10
Feb.10 - Mar.25	60	9	188	5	U = 1, p < .001
	T = 4, p < .05		U = 7, p < .05		

TABLE 5. — Ranging by *M. libycus* during two study periods. (U and T are the Mann-Whitney and Wilcoxon statistics respectively ; see text for fuller explanation.)

used on the predictions of greater male RLs (usual in small mammal studies), and greater ranging in the breeding season (i.. e. the second period, see below).

Only in the second period are RLs significantly greater for males than females. Only in males is the increase in the second period significant. (The Wilcoxon Signed-Rank Test is used to compare periods for females, because the same nine were present in both periods. In males, only three were present in both periods; testing by the Mann-

Whitney Test is a conservative procedure which ignores the partial correlation).

When short-term ranging is compared by the MWRL measure, the sex difference is again significant only in the second period, but both sexes show increased ranging from the first to the second period.

Seasonal breeding, beginning after the first period, can be inferred from the following evidence. Testicular sacs of fully adult males were inconspicuous in Dec. and prominent by Feb. Juveniles appeared on different parts of the study area in late Mar. and Apr., and could be ascribed Feb. birthdates on the basis of external measurements (mainly tail length, which is the most convenient growth measure for age estimation in gerbils; see Petter, 1961, Daly & Daly, 1975). Sudden weight drops of 20 gm indicated that ♀ 5 littered between Feb. 20 and 23, and ♀ 2 between Mar. 2 and 5. We did not see copulation, but it was observed in the MTO daya in late Jan. by G. Ågren.

One female bred earlier. Five like-sized pups (4 males, one female) were trapped in late Feb. within a ten-m radius within the range of ♀ 3. Age was estimated at 8-10 wk (tails 100-110 mm), suggesting a conception date of about Nov. 30. Between Nov. 21 and 23, five different males were trapped at the home bush of ♀ 3, then the largest female. From Dec. 9 to 12, ♀ 3 was daily observed on long rambles of up to 140 m; this behaviour is apparently associated with advanced pregnancy, and was not observed in other females until Feb.

♀ 3 thus bred soon after a major rainfall, but well before the resultant "asheb". Pups of this litter still weighed less than 40 gm at tail lengths of 100 mm; later pups were more than twice as heavy when the same tail and body lengths were reached. While the first pups were reared, there was still little fresh greenery and no new seed crop.

In American desert rodents, there is evidence of opportunistic breeding in response to the growth of annuals following rain (Beatley, 1969 ; Kenagy, 1973). That gerbils show similar opportunism seems likely. It is conceivable that some animals may come into reproductive condition in direct response to the rainfall.

Table 6 shows adult weight changes during the study, based on the first and last trapping instance for each individual within each

	First period (Nov. 15 – Dec. 28)				Interim				Second period (Feb. 10 – Mar. 25)			
	Mean change	N	t	p.	Mean change	N	t	p	Mean change	N	t	p
♀♀	+14.1 g	9	7.50	<.001	+14.7 g	9	3.75	<.01	+7.4 g	9	1.68	>.1
♂♂	+14.9	8	3.77	<.01	+11.8	5	2.10	>.1	−7.2	5	3.17	<.05
♀ vs ♂			0.19				0.43				2.33	<.05

TABLE 6. — Weight changes in adult *M. libycus* over the study.

period. Both sexes gained weight during the first period ; only females gained significantly between periods ; and, in the second, there was a significant sex difference, with males losing weight while females continued to gain.

Juvenile dispersal and survival.

A few observations of juveniles were collected. On Mar. 1, pups of the first litter were trapped at scattered points up to 96 m apart, all within ♀ 3's former range. Only one male was seen after Mar. 7 : ♂ 12 had emigrated 1 km to F (Fig. 1) by Mar. 20, when testicular descent was evident (c. 3 months old), and had returned to the MTO daya, a full-sized adult, by Apr. 19.

Eight later juveniles were trapped, including two 6-wks-old females together at a *Z. lotus* bush in the MTO daya, and three 8-wks-old males, each faithful to a different *Z. lotus* bush in daya A for two successive days. These few records suggest a process of juvenile dispersal similar to that in *P. obesus* (Daly & Daly, 1975) : a gradual separation of littermates within their mother's range, followed by longer emigrations and sexual maturity at about three months of age.

Interactions and scent-marking.

In observations at the MTO daya, only 19 direct interactions between identifiable adults were seen. In 21 other cases, two adults were seen together at one bush without interacting. These 40 cases are summarized in Table 7.

	Total cases.	One soon leaves with no direct interaction.	Remain at one bush with no direct interaction.	Remain at one bush with direct interaction.	Chase (Chaser 1st, chasee 2nd).
♀ – ♂	24	6	5	9 (7 cases : ♂ mostly following ♀. 2 cases : ♀ mostly approaching ♂; ♂ sidle at ♀.)	4 (♂8 ♀A, ♀A ♂10, ♀5 ♂10, ♂8 ♀5)
♀ – ♀	3	2		1 (Sitting 20 cm apart with occasional orienting to other.)	
♂ – ♂	13	7	1	1 (Each sniff, sidle and vocalize at other.)	4 (♂8 ♂3 twice, ♂8 ♂10, ♂8 ♂6)

TABLE 7. — Summary of cases where two *M. libycus* adults were seen at a single bush.

The rarity of observed interactions was surprising. Visual contact with active animals exceeded 30 observer-hrs in Feb. and Mar. Gerbils of both sexes, especially males, were often followed for 10 to 30 min over complex routes through dozens of bushes.

These rambles were not predominantly foraging trips. Although feeding bouts were frequent, they were usually limited to a single leaf, shoot, flower, or seed before the gerbil moved on. Other frequent activities were investigatory sniffing, grooming, very brief digging and sand-bathing bouts, and above all else, locomotion.

Rambles probably function to maintain familiarity with both the physical and social environments. Scent-marking may play a role in this regard. Marking by means of one to three discrete ventral rubs was sometimes seen, and digging little pits and sand-bathing in them was frequent. Of 16 cases of ventral marking by known animals, 11 were performed by males (5 animals) and 5 by females (4 animals). Most marking occurred during rambles and was performed either on a stone or on the lip of a small depression the animal had just dug.

In only one case did an animal who had recently chased another mark, and then only after moving 60 m from the site of the chase. In another case, a male chased a female whom he encountered soon after marking. One male and female each marked several times around the same vicinity while associating with one another ; she was within two days of parturition and behaving subreceptively. During another association only the female marked.

Once, a male paused to mark at a bush during a ramble, whereupon another male emerged immediately after the first left, marked a few cm away, and left in the same direction. This and other observations suggested a time-sharing function similar to that which has been suggested for cats (Leyhausen, 1971). On three occasions, two males were seen to ramble over identical routes for some 6 to 16 bushes, 30 to 60 min apart. The animals did not appear to be scent-tracking, nor did they mark.

Comparative social behaviour and socio-ecology

Repertoire.

The social behaviour repertoire of several gerbils has been described, and some variations in form can be discerned, though little is known about causation, and less about function. The presence, frequency, and degree of stereotypy of particular acts often varies between species. This cannot be readily correlated with the varying degrees of sociability indicated by mutual tolerance (see below).

Sexual behaviour has been described in detail for *P. obesus* (Daly & Daly, 1975), and *Meriones persicus* (Eibl-Eibesfeldt, 1951), and, more briefly, for several other species. Large species differences in the form of sexual behaviour (as occur in hamsters, for example, Daly, 1975), have not been observed, but the degree of familiarity necessary for mating apparently varies (see "Pairing" below).

In fighting, an upright posture is most common. This may soon give way to leaping, rolling and biting from several orientations, but at least in certain species, a prolonged ritualized upright struggle may resolve the fight without any biting (*Tatera indica*, Bland, 1969 ; *P. obesus*, Daly & Daly, 1975 ; *Gerbillus dasyurus*, Fiedler, 1973).

"Sidling" is a sideways approach to another animal, which occurs in both homo- and heterosexual encounters (though rarely performed by females). Nyby, Thiessen & Wallace (1970) described it as preliminary to fighting in *M. unguiculatus*. Several field observations of *M. libycus* (Table 7) and *P. obesus* suggest that sidling normally averts a fight. Its form suggests a motivational conflict between approach with the rear legs and avoidance with the head. The exact topography varies among species. An unusually high intensity sidle in *P. obesus* is illustrated in Daly & Daly (1975), Fig. 1. We have not seen prolonged, stereotyped sidling in *Gerbillus*.

Rapid forepaw digging occurs in social encounters both in sidling and in direct orientations. It is common in *P. obesus* and *M. crassus*, rare in *M. libycus*. Fiedler (1973) considers it a ritualized threat. In *P. obesus*, it occurs in the sexual approach of receptive females.

Audible foot-thumping occurs in many species, including all seven we have trapped. Species are often discriminable by distinctive rhythms (Fiedler, 1973, and own observations). Foot-thumping can be caused by a variety of aversive states, including the cessation of reward (Routtenberg & Kramis, 1967). Suggested functions include communication of alarm (many authors), territorial claim (Fiedler, 1973), and an unspecified role in mating (Eibl-Eibesfeldt, 1951). All are speculative.

Vocalizations may occur in sexual, agonistic, and mother-pup interactions. No comparative descriptions are yet possible. Vocalizations communicating alarm have been noted in *Rhombomys opimus* and *Meriones libycus syrius* (Petter, 1961 and personal communication).

Scent-marking with a mid-ventral gland occurs in many (perhaps all) gerbils (Sokolov & Skurat, 1966). A great deal is known of its causation in *M. unguiculatus* (reviewed by Thiessen, 1973), but nothing of its functions. Chin gland marking is also widespread. Glands at the corners of the mouth are prolongedly investigated during highly stereotyped interactions in several *Meriones* and *Gerbillus*.

Dispersion and sociability.

We have enough field information to describe a system of dispersion and sociability common to most gerbils, as follows :

1. Females occupy relatively small home ranges which do not overlap extensively, and sometimes not at all.

2. Males, especially when large and reproductively active, occupy relatively large home ranges. Overlap is extensive or even total.
3. Adults occupy separate burrows. Tolerance of conspecifics is low. The only cohabiting groups are mothers with young and undispersed littermates, who remain together for some time after the mother has left.

This description applies to *M. libycus* (this study), *P. obesus* (Daly & Daly, 1974, 1975), and *Taterillus pygargus* (Poulet, 1972), and is consistent with the less complete information available for *M. hurrianae* (Fitzwater & Prakash, 1969), *M. crassus* (Petter, 1968, and this study), *G. pyramidum* (this study and unpublished observations), and *G. nanus* (Kirchshofer, 1958).

An apparent exception is *Tatera indica*. Prakash (1962) has claimed they are "invariably" found in pairs, and, more recently, that burrows contain "3-10 individuals" (Prakash & Jain, 1971). Other *Tatera* and *Taterillus congicus* seem always to be in family groups (Petter, personal communication). Study of marked animals of these species should be particularly interesting.

Species vary in social tolerance (that is, in whether social encounters without antagonism occur, see below). This need not imply departures from the system outlined above. Small groups of cohabiting *Meriones (M. persicus* and *M. vinogradovi*, Petter, 1961 ; *M. unguiculatus*, Leont'ev, 1962*)* apparently result from prolonged associations of littermates through their first winter.

Social living cannot be assumed from observations of laboratory strains. After initial high mortality (and genetic selection ?), a laboratory colony highly tolerant of paired or group maintenance was soon established with *M. tamariscinus*, known to live solitarily in the wild (A. Zahavi, personal communication). Wild-caught *M. libycus*, known to dwell solitarily, could be maintained in amicable pairs, but males were likely to mutilate pups, behaviour obviously subject to rapid counter-selection.

Whether the extensive Asian colonies of *Rhombomys opimus* (see "Sociability and resources" below) fit the three-point system above is not yet known.

Pairing.

"Pair formation" may be important in gerbils. Investigation is needed.

In domesticated *M. unguiculatus*, mating seems to require a familiarization period seldom necessary in laboratory rodents, and some owners claim that particular pairs may or may not prove compatible. However, a group-living female may mate with several males in rapid succession (Gallup & Waite, 1970).

In captive *P. obesus*, copulation can occur within a minute of introduction, whereas in *M. libycus* and *M. crassus*, couples had to be left together, whereupon conception occurred within ten days. These comparisons are inconclusive due to possible seasonality effects, but they suggest that oestrous cycling may be more dependent on stimulation from males in *Meriones* than in *Psammomys*. *Psammomys* is more anti-social than *Meriones* species, and couples will not remain together at a bush nearly so long as in *M. libycus*.

In the laboratory, pairs of *P. obesus* could not be left together without severe fighting. Four pairs of each of *M. libycus* and *M. crassus* were established in cages containing two tin cans as nest sites. In all *M. libycus*, the male and female slept together after the first day and groomed each other occasionally, but ate separately. In all *M. crassus*, pairs fought occasionally and always slept apart, the females dominated the males, and the latter finally only emerged when the females were in their cans.

In the wild, "pairing" may occur in any of these species under particular conditions of scattered resources, but an enduring relationship is not necessarily a close one. The *Psammomys* "pair" on the study area did not, in fact, cohabit. In *M. crassus*, a male at least occasionally remained in the vicinity of a single female's burrow for two successive nights. In *M. libycus*, more persistent proximity was sometimes seen. ♂ 3 visited ♀ 1 at daya A for stretches of up to a week, and they were often seen together. In the MTO daya, ♂ 6 once closely attended ♀ 5 for three consecutive days.

Despite much study and speculation about gerbil scent-marking, the possibility that the primary function may be intersexual has been neglected. In *M. unguiculatus*, ventral gland secretions permit individual identification (Dagg & Windsor, 1971; Halpin, 1974), and familiarity with a particular male may facilitate female receptivity, although experimental evidence for this is wanting. A female strategy which selects as mates those males best able to maintain their presence, and thus their familiarity to the female, seems clearly adaptive.

Sociability and resources.

Both the field and laboratory observations described above and in Daly & Daly (1975) indicate the following ranking on the degree of sociability : *M. libycus, M. crassus, P. obesus*. This is not directly related to the usual densities at which these animals live : on this measure, the ranking is *P. obesus, M. libycus, M. crassus* (Petter, 1961, and own observations). These different rankings may be explicable by ecological differences.

An economically defendable resource has been proposed as the fundamental requisite for the evolution of a territorial system (Brown, 1964). *Psammomys* alone among Saharan gerbils exploits a clearly visible, spatially confined food : Chenopod leaves. Females inhabit functional territories that correspond to a requisite quantity of food Daly & Daly, 1974), and exhibit greater exclusivity of range than *Meriones* despite higher densities.

That *M. crassus* is less socially tolerant than *M. libycus* may be attributable to the more extreme desert conditions inhabited by the former. Very sparse resources necessitate well-spaced foraging.

M. libycus may be considered more opportunistic, invading any vegetated areas, sometimes even inhabited oases. A greater sociability might seem to complement such opportunism. However, *G. pyramidum* is more catholic in habitat selection than *G. gerbillus*, but is more disturbed by group maintenance in captivity (Petter, 1951, and own observations).

Rhombomys opimus is an herbivorous central Asian gerbil. Several reports suggest a more complex social structure in this species. Lobachev (1974), for example, describes "family groups" within "parcellas" within "elementary populations" within "local populations" within "geographical populations". Most of these levels probably reflect resource discontinuities, and it is not clear whether there is any difference in social structure from the usual gerbil groups of mother and pups ("family group") and a male visiting several females ("parcella"). Higher units apparently represent levels of decreasing gene interchange, but are unlikely to comprise socially meaningful membership groups.

Yazgulyev (1974) reports considerable synchrony of activities in *R. opimus* colonies, and changing activity patterns as a function of population density. Petter (1961) reports that alarm vocalizations evoke immediate unanimous flight. These vocalizations are apparently only heard where the gerbils are numerous.

The seemingly more advanced social behaviour of *R. opimus* has a parallel in North American prairie dogs (*Cynomys*, Sciuridae). Clark (1974) describes increasing complexity from the ancestral genus *Spermophilus* through the subgenus *Leucocrossuromys* to the subgenus *Cynomys*, and relates this to the more stable and predictable herbaceous resources exploited by *Cynomys*. *Rhombomys* occupies a very similar niche, and a 10-year study at the Turkmenian Plague Control Centre showed a more stable population and more stable resources for *R. opimus* than for *M. libycus erythrourus* (Vasil'ev, Efimov & Zarkhidze, 1964).

Resource stability and social complexity seem complementary in steppe-dwelling *Cynomys* and *Rhombomys*, yet this relationship need not hold in desert. Here, Chenopod leaves provide a more predictable resource than seeds and permit more regular breeding (Kenagy, 1973), but this has not given rise to complex sociability in *Psammomys*. It remains possible that sociability varies within species as a function of population density, and study of *Psammomys* and *Meriones* populations over a range of densities would be valuable.

A different correlate of sociability in rodents has been advanced by Barash (1974), who found that marmot (*Marmota*, Sciuridae) sociability increases with shorter growing seasons and concomitant more prolonged development. Although dramatic species differences in developmental speed either to weaning or to sexual maturity have not been found in gerbils, Barash's analysis may explain some variations among them. Most *Meriones* species for which socially meaningful "colonial" membership groups have been proposed (*M. persicus*, Eibl-Eibesfeldt, 1951 ; Petter, 1961 ; *M. vinogradovi*, Petter, 1961 ; Fiedler, 1973 ; *M. unguiculatus*, Nyby, Thiessen & Wallace, 1970) occupy areas of seasonal snow cover (but not *M. libycus syrius*, Petter, personal communication). Whether these species are truly relatively sociable is a question for future research.

Thus, particular proposed correlates of sociability provide highly plausible explanations of variation within certain taxa, but may prove inapplicable elsewhere. The prediction of contrasts in social behaviour from a knowledge of resource characteristics is likely to improve with further field studies and development of theory.

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SUMMARY

The socio-ecology of gerbils on the Hamada Guir was investigated, with special attention to the behaviour of *Meriones libycus*, by trapping and observation of marked animals, as well as by observations in captivity.

Habitats of different species overlap, but are highly discriminable by the amount of perennial cover. All species trapped (5 gerbils and 1 jerboa) move frequently over ranges of at least several hundred m. In *M. libycus*, females usually remain in one daya for many months, while males range more widely.

Although social tolerance varies among species, gerbils are generally solitary as adults, with males traversing large, overlapping ranges, and females occupying smaller, more exclusive ones. *Psammomys obesus* is the most aggressively solitary of the species studied, probably because it exploits the most economically defendable food resource.

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