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Space use in Wagner's gerbil *Gerbillus dasyurus* in the Negev Highlands, Israel

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Space use of *Gerbillus dasyurus* (Wagner, 1842) was studied on a 1.25-ha site during 2 months. The density was 20.8 animals per ha and 72.7% of captured individuals were sexually active adults. The observed sex ratio differed significantly from 1:1 with a male bias. An active ventral sebaceous gland was recorded in reproductively active males only. No significant correlation was found between body mass and ventral gland size. Male home ranges were larger than those of females and overlapped between one another to a greater extent. There were three clusters of capture points which indicated the occurrence of spatial associations of individuals whose home ranges broadly overlapped with one another and were almost isolated from home ranges of individuals belonging to other associations. No difference in microhabitat distribution of male captures was found, whereas that of female captures differed significantly among microhabitats, being the highest in patches with high shrub cover.

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Introduction

Wagner's gerbil *Gerbillus dasyurus* (Wagner, 1842) is one of the most interesting model species for ecological studies. It seems to be an exception from the macroecological rule that species with narrow habitat distributions usually have restricted geographical ranges, whereas species with broad habitat ranges are widespread (Brown 1995). *G. dasyurus* is the most abundant rodent species in the Negev Highlands. It occupies a wide variety of habitats (Krasnov *et al.* 1996), but has a relatively small geographic range in comparison with other *Gerbillus* species (Harrison and Bates 1991). Ecological studies require basic information on the life history of a species, whereas the biology of *G. dasyurus* is known insufficiently. Recently, we reported some basic data on the biology of this species and described patterns of its habitat distribution, reproduction, density dynamics, sex and age

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population structure, mobility, and burrow architecture (Shenbrot *et al.* 1997). However, a significant aspect of the species biology, namely spatial structure of the population, was omitted. The aim of this paper is to fill this gap and present data on home ranges in *G. dasyurus*.

Material and methods

The study was conducted at the northern rim of the Ramon erosion cirque, Negev Highlands, Israel (30°35'N, 34°45'E). The main landscape of the study area is a complex of hills with deep loess layer (up to 1 m) and wide dry riverbeds covered with shrubs of *Anabasis articulata*, *Atriplex halimus*, *Artemisia herba-alba*, *Salsola schweinfurthii* and *Noaea mucronata*. The region is characterized by hot, dry summers (mean daily air temperature in July is 34°C) and relatively cool winters (mean daily temperature in January is 12.5°C). Data were collected during October and November when mean daily temperature ranged between 14 and 29°C. The mean annual rainfall in the area is near 100 mm.

Gerbils were trapped on a 1.25-ha site (125 × 100 m) located within a valley of dry river (Upper Nahal Nizzana) that included both the main stream (about 30–40 m in width) and a wide terrace with a narrow slope. The site was divided into 500 plots (5 × 5 m each) whose corners were marked by numbered wire flags. Animals were trapped using 150 Sherman live-traps baited with millet seeds. The traps were placed in the middle of plots and relocated by turns daily to cover the entire area of the site. As a result, the trapping effort (number of trapping days) was equal for all plots. The traps were checked every morning between 07:00 and 07:30. Each captured gerbil was sexed, checked for reproductive status, weighed (to ± 0.1 g with Pesola spring scale), toe-clipped, and then released. We recorded pregnancy, lactation, perforation of the vaginal opening or the presence of vaginal plug for females, and scrotal testes for males. We determined the relative age based on body mass and reproductive status of each animal. Gerbils with body mass less then 15 g were classified as juveniles; gerbils with body mass of 16–18 g were classified as subadults; gerbils with body mass of 19–21 g were classified as subadults if they were sexually immature or as adults if they were in reproductive conditions; and gerbils with body mass greater than 21 g were regarded as adults. The length and width (to the nearest 0.5 mm) of the ventral gland was measured using a caliper. The status of the gland was classified as absent, developing or active. The gland was considered to be active if it was covered by a layer of yellow sebum, and to be developing when the contours of the gland were clearly visible but only a small amount of sebum was seen.

The number of resident animals was evaluated using capture-mark-recapture procedure. Most individuals were marked during the first 2 weeks of trapping. Only five unmarked gerbils were recorded during the last 1.5 month. These seemed to be non-resident animals passing through the study site. Most gerbils trapped in the vicinity of the site but out of its borders were unmarked.

The location, shape and size of individual home ranges were calculated using the Fixed Kernel estimation method (program Home Ranger 1.0 developed by Fred Hovey, BC Forest Service Research Branch, Revelstoke, Canada). Relative exclusiveness of use of space was determined using the index E proposed by Alho (1979):

$$E_i = \frac{1}{\sum_a N_{ia}} \sum_a \frac{N_{ia}^2}{\sum_i N_{ia}}$$

where N_{ia} is number of registrations of ith individual in ath point. In dyadic bonds, values of E range from 0.5 (shared usage of the home ranges) to 1.0 (total individualization of the home ranges). Thus, this index allows to evaluate the degree of individualization of territory and is reciprocal to the degree of overlap. Variables analyzed did not conform to the assumptions of parametric tests and could not be transformed to normality (Shapiro-Wilk's tests). Thus, non-parametric statistics were used (χ^2-test, Mann-Whitney U-test, Spearman rank order correlation and Kruskal-Wallis ANOVA by ranks). Data are presented as mean ± 1 SE.

Results

In total, 44 *G. dasyurus* were captured. The number of recaptures for 26 of them ranged between 10 and 19, so they were considered to be residents of the site. The other 18 gerbils were trapped repeatedly from one to four times, six of them were caught in the central parts of the plot, and 12 at the margins of the plot. All these individuals were regarded as non-residents. Thus, the direct evaluation of resident density was 20.8 animals per ha.

Most captured individuals (72.7%) were sexually active adults, whereas the fractions of sexually inactive adults and young animals were lower (18.2% and 9.1%, respectively). The observed sex ratio differed significantly from 1:1 with a male bias ($\chi^2 = 4.45$, $p < 0.05$). Males comprised 65.9% of all individuals. In October and November, the population was still in reproductive phase; six of 14 adult females were either pregnant or lactating and 12 of 18 adult males had scrotal testes.

Adult males and non-pregnant adult females did not differ in body mass (24.6 ± 0.60 g and 24.0 ± 0.86 g, respectively), although sexual differences in body mass of this species have been reported (Shenbrot *et al.* 1997). An active or developing ventral sebaceous gland (average size 32.5 ± 2.38 mm^2) was recorded in 12 of 18 adult males. All males possessing the active ventral gland were reproductively active and had their testicles in scrotum. No significant correlation was found between body mass and ventral gland size (Spearman rank order correlation: $r_S = -0.032$, $p = 0.922$). Neither a developing nor an active ventral gland was recorded in non-reproductive adult males, young males and all females.

Spatial distribution of the home ranges of adult resident individuals is shown on Fig. 1. The size of home ranges varied from 244 m^2 to 2128 m^2 in males and from

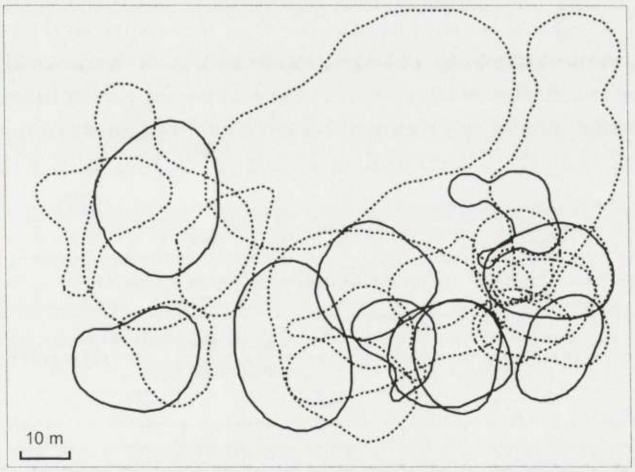

Fig. 1. Home ranges (95% contour intervals) of resident *Gerbillus dasyurus*. Solid lines indicate home ranges of females, dotted lines indicate home ranges of males.

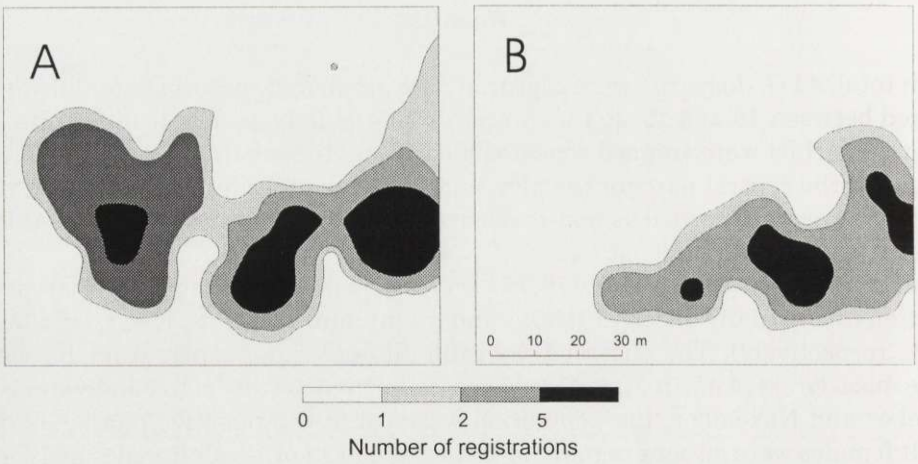

Fig. 2. Distribution of capture density of males (A) and females (B) of *Gerbillus dasyurus*.

230 m^2 to 670 m^2 in females. No correlation between body mass and home range size was found in both males and females (r_S = 0.181 and r_S = 0.01, respectively, $p > 0.5$). Mean area of home range of males was significantly larger than that of females (861.5 ± 142.2 m^2 and 423.0 ± 44.9 m^2, respectively; Mann-Whitney test: $U = 37.0$, $p < 0.05$).

Capture points of *G. dasyurus* were distributed unevenly. There were three clusters of male capture points (Fig. 2). These clusters indicate the occurrence of spatial associations of individuals whose home ranges broadly overlapped with one another and were almost isolated from home ranges of males belonging to other such associations. The distribution of female capture points also demonstrates the occurrence of three spatial associations although less expressed than those of males (Fig. 2). Thus, superimposing of the distributions of male and female capture density demonstrated the occurrence of three spatial assemblages of 6–8 individuals each. Calculations of the index of relative exclusiveness of use of space (Table 1) demonstrated that the individualization of space by males within associations

Table 1. Relative exclusiveness of space use by *G. dasyurus* within and between spatial associations. Numbers are the values of index *E* (Alho 1979). See text for explanation.

Association	Within spatial association	Between spatial associations	Mann-Whitney *U*	*p*
Male-male	0.961 ± 0.009 (n = 36)	0.997 ± 0.001 (n = 144)	1548.5	0.0002
Female-female	0.977 ± 0.008 (n = 28)	0.997 ± 0.001 (n = 62)	667.5	0.0806
Male-female	0.933 ± 0.009 (n = 74)	0.998 ± 0.001 (n = 213)	3352.5	< 0.0001
Both sexes	0.949 ± 0.006 (n = 138)	0.998 ± 0.0006 (n = 419)	15585.5	< 0.0001

Table 2. Mean number of *G. dasyurus* captures per 1 trap at different patches.

Group of animals	Patch categories			
	Covered by *Atriplex halimus*	Covered by *Anabasis articulata*	Covered by grass-like vegetation	Non-vegetated
Males (n = 192)	1.53 ± 0.16	0.88 ± 0.22	1.00 ± 0.10	0.87 ± 0.12
Females (n = 132)	1.21 ± 0.13	0.53 ± 0.15	0.15 ± 0.08	0.12 ± 0.12
All gerbils	2.74 ± 0.20	1.41 ± 0.15	1.15 ± 0.11	1.00 ± 0.00

was significantly lower than that between associations. The same was true for heterosexual dyadic bonds. However, the values of this parameter for females did not differ significantly within and between associations (Table 1). Nonetheless, relative exclusiveness of space use for both sexes within associations was significantly lower than that between associations. In addition, the home ranges of males within associations were individualized weaker than those of females ($U = 35.5$, $p < 0.05$).

The patchiness of the study site was relatively high. Patches covered by shrubs alternated with patches covered by grass-like vegetation and non-vegetated patches. Microhabitat distribution of *G. dasyurus* reflected this patchiness (Table 2). Mean number of total captures differed significantly among patches of different categories (Kruskal-Wallis test: $H = 36.55$, $p < 0.001$), being the highest in the patches covered by shrubs of *Atriplex halimus* and lower in patches with other types of vegetation. When the distributions of captures among different patches were considered separately for males and females, the difference in microhabitat distribution between sexes was found. The distribution of female captures differed significantly among patches ($H = 24.02$, $p < 0.001$). Mean number of female captures was highest in patches covered by *A. halimus* shrubs, intermediate in patches covered by *Anabasis articulata* and lowest in patches of two other types. No difference in microhabitat distribution of male captures was found ($H = 3.42$, $p = 0.33$).

Discussion

Results support the previous findings that density dynamics of *G. dasyurus* usually is correlated with the level of annual precipitation (Shenbrot *et al.* 1997). Precipitation in winter 1996–1997, prior to the study, was close to the multi-annual average (103.3 mm), and the density of the gerbils was close to the average in the study area during the last 7 years (see Shenbrot *et al.* 1997). In addition, the occurrence of males with scrotal testes and pregnant and lactating females indicates that the breeding period of *G. dasyurus* in the study area can be longer than it was thought earlier (Shenbrot *et al.* 1997).

A male bias in the observed population of *G. dasyurus* corresponds with the data reported earlier (Shenbrot *et al.* 1997). This sex ratio bias can be primary (ie at birth) or secondary (occurs thereafter). Shenbrot *et al.* (1997) observed male bias within both adult and young animals and, thus, argued that it was difficult to explain this bias by different male and female survival. Moreover, strong postnatal male bias has been observed in litters of *G. dasyurus* in the laboratory (B. R. Krasnov and I. S. Khokhlova, unpubl.).

Morphology and activity of the ventral gland are closely related to reproduction in many gerbil species. Only reproducing individuals of both sexes possess the active ventral gland in *Meriones unguiculatus* and *M. erythrourus* (Payman and Swanson 1980, Gromov 1997). In other species, for example *Gerbillus perpallidus* (Gromov 1997), *G. henleyi*, *G. gerbillus* (B. R. Krasnov and G. I. Shenbrot, unpubl.), the same relationship between ventral gland activity and reproduction has been reported for males, whereas females never have any morphological sign of a ventral gland. All reproducing males of *Tatera indica* and *Meriones meridianus* have a well developed ventral gland. The percentage of females possessing a visible ventral gland is low, while non-reproducing females do not have it (Kumari *et al.* 1981, Gromov 1997). *G. dasyurus* belongs to a group of species in which males, but not females, possess a ventral sebaceous gland that is active during the reproductive season.

Spatial distribution of home ranges and the degree of their individualization reflect particular differences in spacing strategies in individuals of different sexes. Home ranges of *G. dasyurus* weakly overlapped between females. Territorial individualization provides a female with a possibility to occupy a separate burrow for parturition, to decrease competition with other females and to increase the amount of food per female in the reproductive period. Male home ranges were larger and overlapped extensively with each other and with home ranges of 2–3 adult females. The pattern of broad overlapping of home ranges of individuals of different sexes has been considered as more typical for a promiscuous or polygynous mating system than for a monogamous system (Heske *et al.* 1995). However, the occurrence of distinct spatial associations of several males and several females permits us to suggest that the mating system in *G. dasyurus* is rather polygynous than promiscuous, but more detailed behavioral and genetic studies are required to confirm the type of mating system in this species.

Home ranges of individuals did not have distinctly expressed borders. It seems that this species lacks the behaviour of territorial defense. However, the high degree of female home range individualization suggests that there are some, yet unknown, behavioural mechanisms of home range separation (at least, during the reproductive period). The mechanisms can be either aggressive responses to other females (eg Popov and Chabovsky 1998) or active avoidance of any contacts (eg Verevkin 1985).

Males of *G. dasyurus* shared parts of their home ranges with other males. This pattern of spatial distribution can increase between-male competition. However, the large area of male home ranges can lead to the partition of the shared areas among individuals by time of activity. Different individuals use the shared areas in different periods so that the probability of the encounters decreases. A similar pattern has been reported for feral *Mus musculus* (Khokhlova and Krasnov 1986).

Furthermore, the level of individualization of territory in *G. dasyurus* is relatively high. This indicates relatively low level of contacts among individuals. Nevertheless, spatial associations of individuals seem to be a remarkable feature of the spatial use system in *G. dasyurus*. Individualization of territory within these associations was lower than between associations (at least for male-male and male-female bonds). We consider the lower territorial individualization by males within associations as an indirect evidence of regular, albeit weak, social alliances between individuals. It remains to be determined whether these alliances are constant and personalized. In addition, spatial associations of individuals seem to be formed by sexual alliances between individuals (males-females) as well as by social alliances between males. The role of females in the formation of spatial associations seems to be minimal.

No indication of any habitat preferences in *G. dasyurus* was found in earlier studies (Abramsky *et al.* 1985, Rosenzweig and Abramsky 1985). Shenbrot *et al.* (1997) noted that *G. dasyurus* mostly utilized sites with relatively high abundance of annual vegetation and shrub crown volume (suggestive of preference for highly productive and moderately covered patches) and avoided extremely dense vegetation. Surprisingly, the results of the present study clearly demonstrated distinct microhabitat preferences of females, but not of males. It seemed that females preferred to exploit areas covered by shrubs and avoided open patches. This suggests that the tendency of microhabitat selection is manifested in females of *G. dasyurus* during the reproductive period. Shrub cover provides reproducing females with necessary shelters. In addition, the sheltered by shrubs patches were the only source of green vegetation before winter rains. Fresh green vegetation is a typical dietary component of most rodent species during reproductive periods. Fresh vegetation provides animals not only with water, but also with the green plant factor, 6-methoxybenzoxazolinone (6-MBOA), which has been shown to be important for reproduction (Berger *et al.* 1987, Linn 1991). Indeed, reproducing captive *G. dasyurus* readily ate young leaves and distal parts of brunches of *A. halimus* (I. S. Khokhlova, unpubl.).

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