

# Flexible Social Structure of a Desert Rodent, *Rhombomys Opimus*: Philopatry, Kinship, and Ecological Constraints

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**ABSTRACT:** We tested hypotheses based on philopatry, kinship, and ecological constraints to explain sociality in a semifossorial desert rodent, the great gerbil, *Rhombomys opimus*. Data were collected in the field in Uzbekistan in the spring and fall of 1996 and 1998–2004. Population densities fluctuated dramatically with high turnover in both males and females to reveal that dispersal and social structure were density dependent. Fewer gerbils dispersed at higher densities and members of family groups dispersed together. A majority of females lived in groups at high densities, but as population densities declined, proportionally more females were solitary. DNA analysis revealed that group-living females were genetically similar, whereas solitary females visited by the same male, as well as adult males and females in the same family group, were usually not genetically similar. Reproductive success as measured by the number of emergent pups and survival of juveniles during the summer drought was not related to group size or whether females were philopatric. A majority of females in family groups reproduced, and all females engaged in cooperative behaviors. We accepted three hypotheses to explain fluctuations in group formation in the great gerbil: variation in food abundance and distribution, habitat saturation, and kinship. We conclude that great gerbils are facultatively social. Flexible social behavior may be adaptive in unpredictable desert conditions. Females live solitarily under conditions of limited food and high mortality that disrupt social behavior and group formation and share territories with female kin under favorable conditions for survival and reproduction when kin groups can be maintained. Males adjust to the distribution of females.

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Why do some mammals live in groups while many others are solitary? A central focus of behavioral theory is to understand the underlying causes of cooperative behavior and formation of social groups (Alexander, 1974; Krause and Ruxton, 2002). Because group living may impose reproductive and survival costs on group members, evolution of social living requires that the fitness benefits to individual members outweigh the costs (Emlen, 1994; Hatchwell and Komdeur, 2000; Koenig et al., 1992; Wrangham and Rubenstein, 1986). Hypotheses for group formation in rodents are often based on how group living functions to overcome environmental constraints (Ebensperger, 2001; Faulkes et al., 1997; Solomon, 2003). Specifically, group-living rodents benefit from more efficient defense of resources (Slobodchikoff, 1984), decreased predation risk (Blumstein and Armitage, 1997; Klump and Shalter, 1984), improved care of young (Armitage, 1981), and more tolerant interactions in stressful conditions (Ganem and Nevo, 1996). The rodents may overcome environmental constraints through cooperative digging of burrows (Ebensperger and Bozinovic, 2000), more efficient harvesting of food (Ebensperger and Cofre', 2001; Faulkes et al., 1997), and enhanced thermoregulation via communal nesting (Hayes, 2000). Multiple factors are probably involved (Ebensperger, 2001; Solomon, 2003).

Retention in the natal group (philopatry) is a major factor leading to the formation of social groups in many birds and mammals (Emlen, 1995; Koenig et al., 1992; Solomon, 2003). Ecological constraints such as habitat saturation, environmental harshness, and unpredictable conditions limit the likelihood that a dispersing individual will successfully establish and reproduce in a new territory (Emlen, 1982). By remaining in the natal area, an individual might inherit a high-quality territory and gain fitness through social interactions with kin (Emlen, 1994; Koenig and Pitelka, 1981; Koenig et al., 1992). Richness of resources and the temporal and spatial dispersion of food and shelter often determine dispersal and group formation (Johnson et al., 2002). Individuals are more likely to remain in the natal area and cooperate when food and space become limited at high population densities (Getz et al., 1992; Wolff, 1992) and ecological constraints impose a high dispersal cost (Emlen, 1997; Hatchwell and Komdeur, 2000).

Few species, with the exception of fossorial mole-rats, of desert rodent seem to live in large, cooperative social groups (Randall, 1994, in press). One desert-adapted rodent, the great gerbil, *Rhombomys opimus*, is also an exception with a social structure similar to the "egalitarian polygynous harems" found in some ground-dwelling squirrels (Michener, 1983). The great gerbil is one of the few social gerbils in a group of primarily solitary species (Goltzman et al., 1977; Gromov, 2000; Pavlinov et al., 1990). Social groups consist of a male with one to six females. Behavioral interactions are amicable and cohesive among group members but agonistic toward nonmembers, and males do not dominate females. Group members cooperatively defend territories, harvest herbaceous food, and give alarm calls and footdrum in response to predators (Karpov and Korneev, 1979; Kutcheruk et al., 1972; Naumov and Lobachev, 1975; Randall and Rogovin, 2002; Randall et al., 2000; Tchabovsky et al., 2001). The resident male actively scent marks the burrow area with urine, feces, and ventral gland secretion and chases away other males. Litters are produced in spring, and females may continue to produce litters into the fall depending on precipitation and availability of food. Pups from different litters

readily interact soon after emergence from the burrow, and offspring can remain in the natal territory after the age of maturation. Great gerbils are predominantly folivorous rodents that require a large amount of low-calorie food. Earlier studies reported yearly population fluctuations with changes in climate, feeding resources, and habitat structure (Karpov and Korneev, 1979; Kutcheruk et al., 1972; Mokrousov, 1978; Naumov, 1965, 1967; Naumov and Lobachev, 1975; Naumov et al., 1972). They described population cycles of 4–6 years with extremely high and low densities about 10–11 years apart depending on the region (Dubiansky and Dubianskaya, 1977; Mokrousov, 1978; Naumov et al., 1972).

Our goal was to test hypotheses based on theories about group formation to understand why great gerbils form social groups, when so many gerbils and other semifossorial desert rodents meet the challenges of an unpredictable desert environment through a solitary lifestyle (Randall, 1994, in press). Although the physiology and ecology of desert rodents are well known (Genoways and Brown, 1993; Shenbrot et al., 1999; Randall, in press), there is still much to be learned about behavioral adaptations to the challenges of desert conditions. Knowledge of the factors involved in formation of social groups in environments in which population densities fluctuate in response to changing environmental conditions should facilitate an understanding of the complexity and diversity of factors involved in the evolution of social traits in mammals.

No single factor can account for the origin of social behavior or the evolution of cooperative interactions (La Galliard et al., 2005; Perrin and Lehmann, 2001). Our analyses, therefore, have focused on four main factors known to influence group formation in rodents: resource availability, dispersal and philopatry, kinship, and predation (Ebensperger, 2001; Hayes, 2000; Solomon, 2003) (see Table 1). Although given separately, these factors are not mutually exclusive and are interrelated. Philopatry is related to abundant resources and high survival so that as population densities and competition increase the cost of dispersal becomes high and animals remain in the natal territory (Emlen, 1994; Hatchwell and Komdeur, 2000; Wrangham and Rubenstein, 1986). Habitat saturation, an outcome of high population densities, leads to increased philopatry and formation of kin groups (Kokko and Lundberg, 2001; Waser, 1988). Kinship often, but not always, plays an important role in shaping social interactions in rodents and the evolution of social behavior (Lacey and Wiczorek, 2004; Matocq and Lacey, 2004). Group-living females may gain higher fitness through greater reproductive success than solitary females (Mappes et al., 1995; McGuire et al., 2002), and in cases of a reproductive skew, nonreproductive females should become “helpers” (Emlen, 1997). Finally, group living often provides diurnal rodents with better predator defenses (Blumstein and Armitage, 1997). We did not test predator defense hypotheses in this study, but evidence from prior studies shows that the alarm system employed by great gerbils probably plays a role in avoiding predation (Randall and Rogovin, 2002; Randall et al., 2000; Rogovin et al., 2004).

## METHODS

## Study sites

We studied *R. opimus* on a ecological reserve (Ecocentre Dzeiran) in the southern Kyzylkum desert 30 km south of Bukhara in western Uzbekistan (64°36'–64°43' N and 39°35'–39°40' E) beginning in the spring of 1996 and continuing from 1998 to 2004. We collected data in spring from 25 March to 19 May 1996, 26 March to 30 May 1998, 23 March to 12 June 1999, 29 March to 16 May 2000, 31 March to 15 May 2001, 20 March to 22 May 2002, 15 March to 27 May 2003, and 19 March to 26 May 2004. Data were also collected in the fall from 24 September to 7 October 1996, 28 September to 12 October 1998, 12–31 October 1999, 16 October to 4 November 2000, 12–31 October 2001, 8–31 October 2002, 8–31 October 2003, and 16–28 October 2004.

Vegetation varied from open desert to scrubby woodland. The gerbils occupied a variety of habitats from Haloxylon wood (*Haloxylon aphyllum*) on stabilized sand dunes to sandy and sandy-loam plain covered in spring by ephemeral annuals and perennial shrubs (*Calligonum caput-medusae*, *Calligonum microcarpum*, *Astragalus villosissimus*, *Ammothamnus lehmannii*, *Convolvulus hamadae*). Settlements (clusters of gerbil colonies) were also associated with the borders of saline depressions with plant communities dominated by annual and perennial succulents in the family Chaenopodiaceae (*Climacoptera*, *Horaninovia*, *Salsola*, *Suaeda*). The region is characterized by extremely hot and dry summers and relatively cold winters. Late winter and spring precipitation strongly influences growth and abundance of nonsucculent plants that are the main food sources in spring, whereas succulents become the main resource in summer and fall. Haloxylon trees represent a food source available throughout the year, but their role increases in the summer, fall, and winter periods when there is a shortage of other food (Moshkin et al., 2003; Rogovin et al., 2003a).

Each year in the spring and fall, we located and numbered gerbil colonies. Each colony was defined as an isolated system of interconnecting burrows within which at least 90% of a family group's activity occurred during the breeding season. The

**Table 1**  
**Hypotheses for group formation in the great gerbil**

Factors affecting group formation	Hypotheses	Results	Data
1. Resource availability	Abundant food resources increase survival and decrease dispersal, affecting size and composition of gerbil groups	Accepted	Tables 2 and 4, Figure 2
2. Dispersal and philopatry	As population densities increase, burrow sites are limited and philopatry increases	Accepted	Table 3, Figure 4
Sex-biased dispersal	Males are less philopatric than females	Accepted	Figures 1, 3, and 4
Natal area fidelity	Young that remain in or near natal area have higher survival	Rejected for males	Figure 3
3. Kinship	Females in groups with a resident male are related	Accepted	Table 5
	Solitary females sharing same male are unrelated	Accepted	Table 5
	Higher individual female reproductive success in larger than smaller groups	Rejected	Figure 5
	Female helpers	Rejected	Figure 6
	Indirect fitness benefits in cooperative female groups	Suggested	Table 5
4. Predation	Better predator defenses <sup>a</sup> ; individuals in groups are less vigilant than solitary individuals <sup>b</sup>	Suggested, not tested in this study	See references below

<sup>a</sup> Randall and Rogovin (2002); Randall et al. (2000); Rogovin et al. (2004a); Tchabovsky et al. (2001).

<sup>b</sup> Tchabovsky et al. (2001).

study site varied across years as we expanded the area, so there would be enough subjects for behavioral observations and tests and for adequate records of reproduction, survival, and dispersal. The first year (1996), we worked in three separate areas of approximately 30 ha. When we returned in 1998, we discovered that two of the three areas had few gerbils. We therefore continued to study gerbils on only one of the areas from 1996, consisting of about 20 ha, and established another area of 23 ha 1 km away. These two areas corresponded to the central parts of two settlements of gerbils separated by unfavorable habitat, and we continued to mark and study gerbils in this 43-ha area for the remainder of the study. We increased the study area by 5 ha in 1999, 5 ha in 2000, and 3 ha in 2001. By 2002, we were observing and marking gerbils on a 73-ha area. We also scanned an additional 32 ha biweekly for marked migrants to estimate distances of dispersal. There was only one case when a subadult male emigrated from one site to the other, and we observed only four marked gerbils out of the marking area during the entire study.

We used convex polygons to estimate distances between colony centers and the size of each colony to define the area of burrows in use by a family group in a current season. We first mapped the study areas with a compass, a tapeline, and an unpublished map of vegetation of the Bioserve made in 1980 by G.I. Shenbrot. In the spring of 2001, we corrected the map with the distribution of gerbil colonies with a global positioning system (GARMIN-12). Maps of gerbil colonies included occupied and unoccupied burrow systems in a current season on a scale of 1:2000 within the study area. We were able to estimate areas occupied by gerbils from our map since the beginning of our study because we had marked active burrows with flags and because gerbils rarely establish new burrows and use and modernize old systems.

## Animals

After we identified individual social groups, we trapped gerbils in 30 x 15 x 15-cm livetraps made of wire mesh, which were baited with a mixture of rolled oats, sunflower seeds, carrots, greens, and peanut butter. We marked adults and pups in each group in both ears with numbered tags (Monel no. 1) and took a small section of the ear to store in 95% alcohol for DNA analysis. We also clipped light brown guard hairs of adult gerbils to expose dark patterns in the underhairs for individual identification at a distance. These marks included distinctive spots and stripes on the back, shoulders, hips, hind legs, and rump of the gerbils. Pups of similar size that emerged from the burrow together were assumed to be part of the same litter and were given a uniform visual mark (one spot or stripe) as well as numbered ear tags. (There were too many pups of small body size to give them individually distinctive marks.) We documented the number of juveniles in each litter by trapping and visual observation until we were satisfied that all juveniles in a litter had emerged from the burrow and been counted. During the spring season from 1996 to 2004, we trapped and marked 167 adult males, 352 adult females, and 1211 newborn juveniles after emergence from natal burrows. We also monitored females for reproductive status. We estimated the phase of female receptivity by the

appearance of the vagina and observation of breeding behavior. When nonreceptive the vagina is closed. Pregnancy was determined by a continuous weight gain and palpation of the abdomen. Females in late pregnancy that did not exit the burrow for 1–2 days and then showed signs of lactation with extended nipples were assumed to have given birth and have a litter of pups in the burrow.

### Measurements of feeding resources

We estimated abundance of food plants available in spring and during periods of food shortage (summer and fall) within the areas used by social groups in a year of peak density (1999). We measured legume shrubs (*Astragalus*, *Ammothamnus*) in the spring and succulent annual and perennial shrubs in the fall by random selection of two points at the center and two at the periphery of gerbil colonies. At each of the four points, we counted and measured shrubs of each species within a 5-m-radius circle and averaged the values. Heights and diameters for a random sample of 20 individuals of each species were also measured within the 5-m circles to calculate crown volumes. Data for analysis were represented as mean crown volumes ( $\text{cm}^3$ ) of legume and succulent shrubs. For *Haloxylon* trees, the total number of trees and their diameters and heights were estimated within each colony area, and the data were represented as crown volumes in a circle of 5-m radius.

We counted the number of annual (ephemeral) plant species within a 25 x 25–cm frame in the area of each colony by throwing the frame six times (three times at random at the central part and three times at random at the periphery). Data for analysis were represented as the number of individuals per square meter of grass (family Poaceae) and herbs (all other ephemeral plants). For more complete information see Rogovin et al. (2003a).

Each spring since 1998, we estimated productivity of ephemeral vegetation in a set of 10 permanent plots of 0.1-ha size at the periphery of colonies by randomly throwing a 25 x 25–cm frame six times in each plot and counting plant species within the frame. Heights of plant species (cm) were measured (10–15 random measures for each species) as they reached maximum height. We multiplied the mean height of plants by the number of individuals of each species and used a sum of all species to characterize the productivity within each colony. To characterize between-year variation in productivity of ephemeral plants, mean values were used for each year and expressed as a percentage of the maximum (100%).

### Behavioral observations

We observed gerbils in their respective social groups during periods of daily activity in the morning from approximately 0800 to 1200 h and again in the evening from 1700 to 1900 h. (Duration and amount of activity depended on temperature.) We watched the gerbils with binoculars from a distance of approximately 40 m to estimate the total group size, group composition, range of adult and juvenile activity,

and behavior. Continuous observations of family groups helped us to determine dates of pup emergence and their number.

We observed females with pups and females without pups in nine family groups in 2003 to compare cooperative behavior in mothers and nonmothers. We identified one female with newly emergent pups in a group of two to three females and then proceeded to quantify cooperative behavior of a focal female with no emergent pups and the behavior of the identified mother of the newly emergent pups. Behaviors included (1) frequency of any physical contact with the pups, such as nose to nose or nose to body, females climbing over the top of pups or pups moving under the female, and moving pups from one burrow to another; (2) frequency of carrying green vegetation into the burrow; and (3) frequency of alarm calls (see Randall and Rogovin, 2002). On average, we collected 5.5 h of continuous behavioral data on each mother and 2.5 h on each nonmother. Because of different periods of observation, data were standardized by hour of observation.

### Measurements of dispersal and survival

We measured the survival of gerbils from the date of emergence from the natal burrow in spring to the next fall and defined this measurement as the first season of survival. The second season of survival was from the fall to the next spring, and the third season was from spring to the fall again. We measured survival in each year from 1998 to 2001 so that we had 2–5 years of data after the birth of an animal.

Gerbils begin to disperse from natal colonies in summer; thus, the first measurement of dispersal for juveniles each year was in the fall after the spring of birth. We measured dispersal as the distance from the center of the natal colony to the center of the new area, using the map described above. We considered the gerbils dispersed from the natal colony if the distance between centers of colonies used in different seasons exceeded  $D_{\max 1}/2 + D_{\max 2}/2$ , where  $D_{\max 1}$  is the long diameter of colony 1 and  $D_{\max 2}$  is the long diameter of the second colony, colony 2.

We accounted for dispersed and nondispersed gerbils in the fall and the next spring at 1 year of age. Because many gerbils disappeared during the first year of life and the exchange between settlements in the study area separated by unfavorable habitat seemed extremely low (we found only one case), we assumed that the gerbils no longer trapped or observed had died. At the same time, gerbils found within the borders of the study area were classified as survived. Thus, to compare survival and breeding success of philopatric and dispersed gerbils, we use the following definitions: (1) “gerbils survived” were those found alive in the population in the fall and still alive the following spring at 1 year of age, (2) “gerbils disappeared” were those found alive in the population in the fall but not found in the population the next spring and presumed dead, (3) “gerbils dispersed” were those found alive at 1 year of age and had emigrated from the natal colony during the year since emergence from the burrow, and (4) “resident gerbils” were those found alive at 1 year of age in the natal colony but not in another colony (defined as philopatric). We recognize that our numbers may be somewhat compromised because in the “disappeared” category we were unable to determine the exact movements of the

animals and do not know whether individuals dispersed sometime between fall and spring before they disappeared from the study site. Therefore, these data are our best estimate of survival and reproduction of gerbils during the first year of life.

To answer the question whether gerbil survival at colonies (residency) related to habitat variables representing feeding resources, we analyzed gerbil residency in 1999 and from the fall of 1999 to the spring of 2000. Because 1999 was a year of highest density, availability of resources would likely influence survival and dispersal decisions. Survival at a colony was estimated as the percentage of marked gerbils found inhabiting the colony in a current season out of the number of gerbils marked at the colony in a previous season of the fieldwork.

## DNA analysis

We used multilocus minisatellite “DNA fingerprinting” (Jeffreys et al., 1985) developed for several species of reptiles, birds, and mammals (Marfori et al., 1997; Parker et al., 1999; Peare and Parker, 1996) to analyze genetic relationships from ear samples collected in 1996 (18 adult males, 28 adult females, and 20 pups), 1998 (19 adult males, 45 adult females, and 95 pups), and 2001 (10 adult males, 25 adult females, and 105 pups). We used Jeffreys’ probe 33.15 (Jeffreys et al., 1985) with *Hinf*I digested DNA to determine the proportion of DNA fragments shared between individuals (band sharing [BS]) as an index of genetic similarity that correlates with genetic relatedness (Lynch, 1988, 1990; Wetton et al., 1987). We identified parents of pups when possible by identifying pairs of adults that completely accounted for the bands present in offspring lanes in addition to satisfying BS criteria.

Background BS was calculated from 68 dyads of individual gerbils randomly selected from different colonies that were not next to each other and in which no adult males were thought to have sired pups in both colonies.

## Statistical analyses

Parametric statistical tests were used when data met requirements for a normal distribution. These tests included analyses for differences between means with a two-tailed Student’s *t* test for independent groups and one-way ANOVA for multigroup comparisons. In cases where data could not be normalized by log transformations, we used nonparametric Mann-Whitney *U* tests for two independent group comparison, Wilcoxon signed-rank test for paired comparisons and Kruskal-Wallis for one-way multigroup comparisons. To compare differences in frequency distributions, we used chi-square tests with a Yate’s correction. Statistical tests were performed with SYSTAT 10.0 and SPSS. All values are given as mean  $\pm$  SE.

A stepwise linear regression model was used to build regression equations of how gerbil survival at colonies related to habitat variables representing feeding resources in years of high population density (1999–2000). Independent variables included crown volumes estimated within a 5-m-radius circle for (1) legume shrubs, (2) perennial succulent shrubs and annual succulents vegetating in summer and fall, (3)



Haloxylon trees, (4) abundance of annual grasses (family Poaceae, number of individuals per square meter), and (5) abundance of annual herbs (number of individuals per square meter). Data were log transformed,  $X_i = \log_{10}(x_i + 1)$ .

To elucidate the role of climatic and vegetative conditions in determining between-year variation of population density, we calculated Spearman rank correlations between a set of generalized characteristics of climate, vegetation, and population variables (percentage of colonies occupied, mean group size, and number of pups per female) (see Table 2). Climate data are from a meteorological station 25 km north.

## RESULTS

### Population fluctuations

Population densities and group sizes fluctuated during the years of the study. Breeding was very high, and population densities increased to 94% saturation of burrows in the study area in 1999 followed by a catastrophic mortality beginning in 2000 that led to very low population densities from 2001 to 2003 (Table 3). Population densities and group sizes, including adults and emerged juveniles, were highest in 1998–1999 because of a favorable year for breeding in 1998 and a rather warm winter with an early spring that facilitated reproduction in the spring of 1999 (Tables 2 and 3). A drought began from mid-April in 2000 and continued into 2001 that included a cold winter with limited precipitation. Limited rains in early spring of 2001 followed by very hot and dry weather did not improve conditions for ephemeral plants and nonsucculent perennials required for successful breeding in the spring and survival during the summer drought. These conditions were associated with very high gerbil mortality and decline in population densities. A relatively mild winter in 2001–2002 favored the beginning of population recovery. Although the drought broke in the spring of 2002 and breeding was good, juvenile survival was low, probably a result of the intense cold rains in March–April. The cold rains were associated with a rapid decrease in daily temperatures coinciding with the late stage of lactation in females and with mass emergence of juveniles. A similar condition was probably the reason for fewer groups and smaller litter sizes in 2003 (Table 3).

A high rate of turnover was characteristic of both males and females in the population, with a maximum life span of 2.5 years in females. Only 9.7% of females and 3.6% of males survived for 1 year after birth (Figure 1A). Survival among females was significantly higher than among males from the spring of birth to the fall ( $v^2 = 4.03$ ,  $df = 1$ ,  $p = .045$ ), as well as from the fall of the first year of life to the next spring ( $v^2 = 6.13$ ,  $df = 1$ ,  $p = .013$ ).

### Resource availability

Habitat saturation, measured in percentage of colonies occupied, was negatively correlated with temperature and positively correlated with precipitation and

vegetation productivity (Table 2). Mean number of pups per female per colony correlated positively with winter temperatures, precipitation, and duration of green food (nonsucculents) and negatively with the number of hot days in April–May, which reflects the beginning of a drought season. Group sizes, however, were only strongly and significantly correlated with winter precipitation (Table 2).

A regression analysis revealed that the availability of perennial plants had a significant effect on juvenile survival from the spring to the fall of 1999, mostly via succulent vegetation available in summer and fall and to a lesser extent via perennial legumes and Haloxylon vegetation but not via annual ephemeral plants. From the fall of 1999 to the spring of 2000, survival of gerbils at colonies was also determined by succulent plants in 1999, but only for adult gerbils (at the age of .1 year) (Table 4).

### Group composition

The social structure of great gerbils fluctuated by year according to population densities (Figure 2). We found a trend for difference in the number of females in family groups by year (Kruskal-Wallis test  $H = 11.26$ ,  $df = 6$ ,  $p = .08$ ). Significantly more females lived together in groups during the highest density years (1998–1999,  $1.82 \pm 0.144$ ) than the lowest density years (2001–2002,  $1.2 \pm 0.08$ ) (Mann-Whitney U test,  $z = 1466$ ,  $n_1 = 67$ ,  $n_2 = 34$ ,  $p = .005$ ). As population densities declined, proportionally fewer females lived in groups and more females were solitary (Figure 2). Males became more mobile and traveled between solitary females. The percentage of solitary females in the higher density years (1996–2000) was 4–8.5% compared with 21.5–50% of females living alone in the lower density years (2000–2003). In the highest density year (1999), there were 16 female groups consisting of two to six females. In contrast, in 2002, the lowest density year, there were no groups of more than two females. After a few cases of late reproduction in 2002 and a favorable winter, the number of groups in 2003 with two to three females increased to 10. Equal proportions of single females, females paired with one male, and female groups occurred in 2004.

**Table 2**  
**Mean  $\pm$  SE daily temperature in degree celsius, sum of precipitation in millimeter, approximate weeks annual and nonsucculent perennial plants were available and relative productivity of annual vegetation**

Years	1996	1998	1999	2000	2001	2002	2003	2004	% colonies occupied <sup>a,b</sup>	Group size <sup>a,b</sup>	Pups per female <sup>a,c</sup>
Temperature <sup>d</sup> (January–February)	0.69 $\pm$ 0.74	1.09 $\pm$ 0.61	5.61 $\pm$ 0.66	3.44 $\pm$ 0.44	1.31 $\pm$ 0.78	5.72 $\pm$ 0.64	4.26 $\pm$ 0.42	6.59 $\pm$ 0.43	-0.09	-0.04	0.57
Temperature <sup>d</sup> (March–May)	15.5 $\pm$ 0.82	16.05 $\pm$ 0.80	15.33 $\pm$ 0.74	18.06 $\pm$ 0.77	19.01 $\pm$ 0.78	16.68 $\pm$ 0.58	14.69 $\pm$ 0.75	17.0 $\pm$ 0.73	-0.71	-0.18	-0.21
Days in April–May with mean daily temperatures $>20^{\circ}\text{C}$	35	38	29	49	45	24	28	32	-0.42	-0.14	-0.64
Precipitation <sup>d</sup> (January–February)	19.8	60.7	55.8	34.6	26.1	32.8	22.5	40	0.49	0.82**	0.36
Precipitation <sup>d</sup> (March–May)	22.9	69.3	36.7	11.5	49.2	95.6	72.2	44	0.31	0.07	0.32
Vegetation (number of weeks)	—	8	8	6	7	9	9	10	0.50	0.09	0.53
Vegetation productivity (%)	—	78	61	44	35	78	95	100	0.58	0.04	0.27

Correlations (Spearman  $R$ ) are given for relationships between environmental variables and percent colonies occupied, mean group size, and mean pups per female.

<sup>a</sup> Correlation with conditions of previous year 1998–2003,  $n = 6$ .

<sup>b</sup> Data from Table 3.

<sup>c</sup> Data from Table 6.

<sup>d</sup> Data from meteorological station 25 km north.

\*\* $p < .05$ .

**Table 3**

Number of marked males, females living solitary, females paired with one male or in female groups, and juveniles of *Rhombomys opimus*; maximum active colonies per hectare and mean active colonies per hectare (ha in parentheses); percentage of active colonies of total identified on the study site; and mean group sizes (*n* in parentheses) in the spring of 1996 and 1998–2004

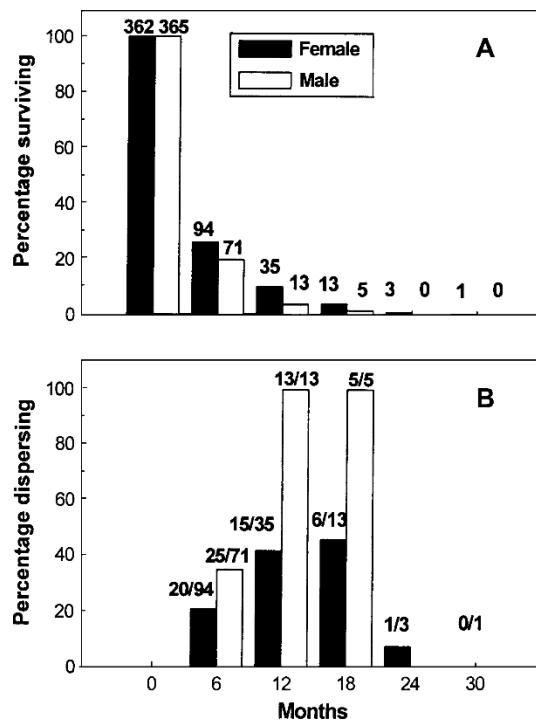
Year	Adult males	Adult females			Juveniles	Maximum active colonies per hectare	Mean active per hectare	% Active colonies <sup>a</sup>	Mean group size <sup>b</sup>
		Solitary	Pair	Group					
1996 <sup>c</sup>	25	3	15	23	27	2	0.5 (30)	41 (23/56)	3.9 ± 0.4 (17)
1998 <sup>d</sup>	20	4	8	35	96	4	0.6 (20)	46 (29/63)	13.4 ± 2.2 (11)
1999	38	3	22	49	400	4	1.3 (43)	94 (59/63)	13.0 ± 1.8 (41)
2000	20	11	7	33	129	4	0.5 (53)	40 (25/63)	7.6 ± 1.3 (28)
2001	12	10	6	11	102	1	0.2 (56)	11 (7/63)	7.8 ± 1.0 (20)
2002	11	7	5	2	128	1	0.2 (73)	13 (8/63)	11.3 ± 1.3 (13)
2003	15	13	7	29	119	2	0.4 (73)	27 (17/63)	7.3 ± 0.9 (27)
2004	26	15	15	19	210	3	0.5 (73)	37 (23/63)	9.6 ± 1.1 (28)

<sup>a</sup> Active colonies were within 30 ha in 1996 and within 43 ha since 1998.

<sup>b</sup> Adults and all emerged juveniles during spring breeding season.

<sup>c</sup> Pups emerged from burrow too late for accurate estimate.

<sup>d</sup> Juveniles were marked on only one of two study sites, whereas adults were marked at both sites.



**Figure 1**

Survival (A) and dispersal (B) of male and female gerbils marked as juveniles in spring (month 0) after emergence from the burrow and measured for survival and dispersal in the fall after birth (6 months) with continuous measurements in spring and fall for 2.5 years. *n* is given above bars.

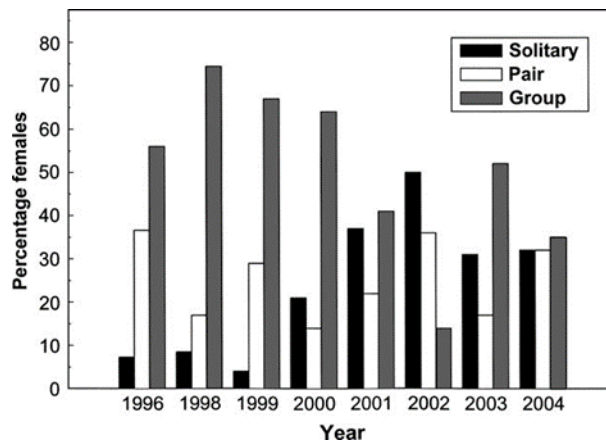
**Table 4**

**Results of stepwise linear regression of great gerbils' survival from spring to fall and from fall to spring at colonies on habitat variables representing feeding resources at peak population density and the beginning of density decline<sup>a</sup>**

Season	Age	Equation	n	R <sup>2</sup>	F	df	p
Spring to fall of 1999	Juveniles	SurJuv = 0.04 + 1.39SUC <sup>****</sup> + 0.61LEG <sup>**</sup> + 0.41SUCT <sup>**</sup>	33	0.39	6.19	3,29	.002
	Juveniles emerged before April 15	SurJuv = -0.28 + 1.24SUC <sup>**</sup>	24	0.34	5.46	1,21	.012
Fall of 1999 to spring of 2000	Adults	SurAd = 0.32 <sup>*****</sup> + 1.16SUC <sup>*</sup>	40	0.08	3.31	1,38	.076
	Juveniles born 1999	SurJuv NS	34	0.05	1.54	1,32	.222
	Adults	SurAd = 0.14 <sup>*</sup> + 1.64SUC <sup>***</sup> - 0.62LEG <sup>**</sup>	33	0.39	9.68	2,30	.001

<sup>a</sup> SurJuv = survival of juveniles; SurAd = survival of adults; LEG = crown volume of legume shrubs (cm<sup>3</sup>); SUC = crown volume of annual succulents vegetating in summer and fall and of perennial succulent shrubs (cm<sup>3</sup>); SUCT = crown volume of *Haloxylon* trees (m<sup>3</sup>).

\*  $p < .1$ ; \*\*  $p < .05$ ; \*\*\*  $p < .01$ ; \*\*\*\*  $p < .001$ ; \*\*\*\*\*  $p < .0001$ .



**Figure 2**

Comparison of percentage of solitary females, females paired with a single male, or females in groups of two to six iyears of higher (1996, 1998–1999), lower (2000–2002), and recovering densities (2003–2004). n in Table 3.

### Philopatry and dispersal

Proportionally more males than females dispersed from the natal colony in the first year of life (from spring of birth to the next spring) ( $v^2 = 10.49$ ,  $df = 1$ ,  $p = .0012$ ), whereas from spring of birth to the fall, the difference was not significant ( $v^2 = 3.29$ ,  $df = 1$ ,  $p = .069$ ). In total, within 1 year after birth, 42.8% of females and 100% of males changed colonies at least once (Figure 1B).

Comparison of resident and dispersed male gerbils that were found in the population in the spring after birth at 1 year of age with males present in the fall but not the following spring showed better survival of males that dispersed from the natal colony between the spring of birth and the fall ( $v^2 = 15.79$ ,  $df = 1$ ,  $p = .0001$ ). Thirteen of 71 males born in the spring and still alive in the fall survived to reach 1 year of age the following spring. All 13 (100%) of these surviving males had dispersed into new colonies by fall. Of the 58 males that disappeared and presumably did not survive from the fall to the next spring, 20 males (34%) were observed dispersed from the

natal colony in the fall. Such a difference was not pronounced for females. Of 94 females born in the spring and alive in the fall, 35 lived to the next spring and 59 disappeared. Of the 35 females that lived for 1 year, 15 females (43%) dispersed from the natal colony in the fall, whereas 13 of the 59 females (22%) that disappeared from the fall to the next spring were found dispersed from the natal colony in the fall ( $v^2 = 3.61$ ,  $df = 1$ ,  $p = .57$ ).

When we compared the relationship between survival at the next spring after birth (1 year old) and the distance dispersed from the natal colony in the fall of the year of birth for males and females, we found no significant difference in the distance dispersed of females that survived compared with females that disappeared (Mann-Whitney U test,  $z = 518$ ,  $n_1 = 14$ ,  $n_2 = 14$ ,  $p = .413$ ). Surviving females moved a significantly shorter distance than surviving males ( $z = 319$ ,  $n_1 = 14$ ,  $n_2 = 13$ ,  $p = .004$ ) (Figure 3). Dispersing males that survived, however, traveled significantly longer distances than dispersing males that disappeared ( $z = 204.5$ ,  $n_1 = 13$ ,  $n_2 = 20$ ,  $p = .001$ ). Dispersal from the natal colony depended on the population density (Figure 4). There was a significant difference in the frequency distribution of philopatric and dispersed males between the year of peak density (1999) compared with the years before (1998) and after (2000) the peak (1998 and 2000 considered together:  $v^2 = 7.53$ ,  $df = 1$ ,  $p = .006$ ). The most pronounced difference was between 1999 and 2000, in which a significantly higher proportion of males dispersed in 2000 compared with 1999 ( $v^2 = 10.14$ ,  $df = 1$ ,  $p = .002$ ). Females

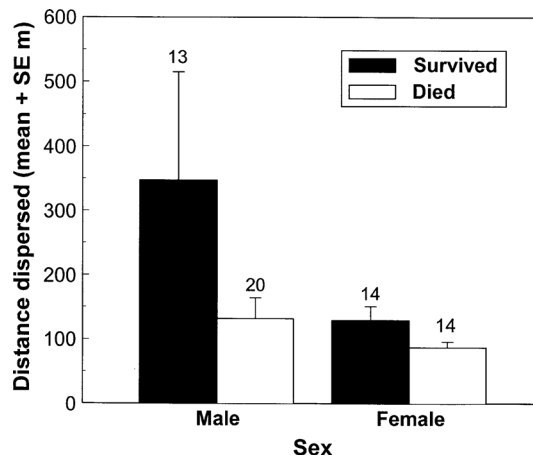


Figure 3

Distance (m) dispersed of male and female gerbils born in spring that were dispersed by the fall and still in the population the next spring (survived) compared with gerbils dispersed in the fall and not found in the population the next spring (disappeared). n is given above bars.

did not demonstrate significant differences in frequency distribution of philopatric and dispersed individuals between the year of peak density and the two neighboring years of lower density ( $v^2 = 0.02$ ,  $df = 1$ ,  $p = .899$ ). Percentage of philopatric females decreased after 2000 and then increased again in the recovering population as densities increased (Figure 4).

In many cases, gerbils moved together into new colonies, and there were times when we observed an entire family group change colonies. Of 31 juvenile females and 27 juvenile males that dispersed from their natal colonies in the fall of different years, 48.4% (15) of females and 63% (17) of males were associated with one or more members of their natal group in the new colony. Even among adults that changed colonies from spring to fall, 6 of 10 (60%) adult females and 6 of 11 (54.6%) adult males were found associated with family members. Taking into account the high mortality during the summer drought, these data demonstrate the possible high frequency of dispersal by social groups from natal colonies. New social groups also may contain nonrelatives. Of the same dispersed gerbils described above, 61.3% (19) of the 31 juvenile females and 51.9% (14) of the juvenile males were found associated with gerbils that originated from colonies other than the natal colony. Of the 10 adult females and 11 adult males that dispersed, six females and six males were found in groups that contained at least one gerbil from another colony.

Availability of food during periods of drought also influenced dispersal. We compared dispersal in colonies with green vegetation available in the summer and fall (annual and shrubby perennial succulents) with colonies without such resources in 1999, the year of highest density and lowest dis-

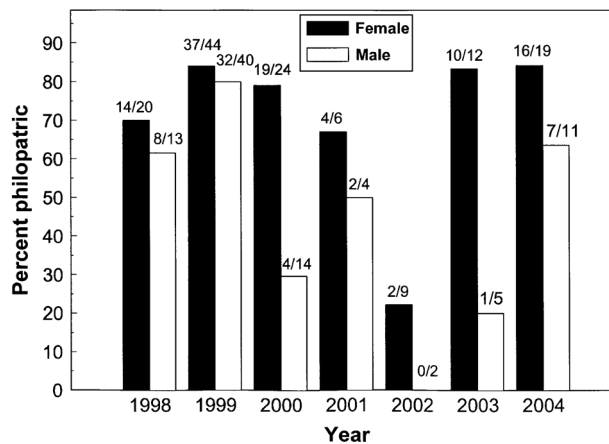


Figure 4

Percentage of males and females remaining in the natal area in the fall after the summer drought in years of high (1998–2000), low (2001–2002), and recovering (2003–2004) population densities. Number at the top of bars represents the number of philopatric gerbils in the fall divided by the total number surviving from spring to fall.

persal, and found no significant difference. Dispersal from spring to the fall was observed at 33% of 15 colonies without green succulent plants compared with 16.7% of 24 colonies with succulents ( $v^2 = 0.66$ ,  $df = 1$ ,  $p = .417$ ). When we examined the more stable and abundant resource, the Haloxylon trees, we found a significant difference. The dispersal from spring to fall in 1999 occurred at 34.6% of 26 colonies without Haloxylon trees compared with 0 of 13 colonies with Haloxylon trees ( $v^2 = 4.06$ ,  $df = 1$ ,  $p = .043$ ).

**Table 5**

**Mean  $\pm$  SE bands shared by females and males and females in family groups and solitary females that shared the same male in years in which DNA was analyzed<sup>a</sup>**

Family groups	1996	1998	2001
Females	0.54 $\pm$ 0.17 (6)	0.584 $\pm$ 0.03 (14)	0.71 $\pm$ 0.04 (3)
Male-female	0.35 $\pm$ 0.03 (14)	0.40 $\pm$ 0.03 (19)	0.40 $\pm$ 0.06 (11)
Solitary females	0.295 $\pm$ 0.065 (2)	0.381 $\pm$ 0.007 (2)	0.309 $\pm$ 0.068 (5)

<sup>a</sup> Background BS = 0.264  $\pm$  0.099 calculated from 68 random dyads ( $n$  in parentheses).

## Kinship and social relationships

DNA analysis of female relationships revealed that adult females living together had genetically similar band values expected of close relatives in this population (Table 5). Females in groups shared an average of 0.596  $\pm$  0.13 ( $n = 25$ ) bands compared with 0.264  $\pm$  0.10 bands derived from background BS estimates of 68 random pairings (normal approximation to the Mann-Whitney U test:  $z = 7.05$ ,  $n_1 = 25$ ,  $n_2 = 68$ ,  $p = .0001$ ) (Zar, 1999).

Based on the background BS estimate, the expected proportion of bands shared between first-order relatives was predicted to be 0.606 (Georges et al., 1988; Parker et al., 1998; Rabenold et al., 1991).

Solitary females sharing the same male had significantly lower band values (0.322  $\pm$  0.039,  $n = 9$ ) than females in groups (0.596  $\pm$  0.13) (Mann-Whitney U test,  $z = 223.5$ ,  $n_1 = 9$ ,  $n_2 = 25$ ,  $p = .0001$ ). Only five females in 23 family groups had BS coefficients of  $\geq 0.5$  (ranging from 0.38 to 0.49), suggesting that they were not as closely related as other females in the family groups. We found no difference in the number of bands shared by females in groups across years ( $F_{2,23} = 1.91$ ,  $p = .172$ ) (Table 5).

Males and females that lived together were usually not genetically similar (Table 5), but there were some cases in which males were genetically similar to one or more females in the group. In 1996, one male and female pair with BS value of 0.58 did not reproduce. In 1998, males and females had BS values resembling those of first-order relatives in 7 of 43 comparisons (bands shared  $\geq 0.6$ ). In 2001, there were two highly inbred groups: a male and three females had an average BS value of 0.6  $\pm$  0.087 and a male and two females shared an average of 0.61  $\pm$  0.066 bands. Both of these groups successfully produced pups. Despite this variation in the number of bands shared, there was no significant difference in bands shared among male-female pairs across years ( $F_{2,41} = 0.719$ ,  $p = .493$ ).



**Table 6**

Number of emergent pups per female<sup>a</sup> during spring reproduction in years of high (1998–1999), declining (2000), low (2001–2002), and recovering (2003–2004) population densities

Years	1998	1999	2000	2001	2002	2003	2004
Number of females	22	69	43	27	16	37	40
Mean $\pm$ SE pups per female	5.4 $\pm$ 0.5	6.5 $\pm$ 0.8	3.8 $\pm$ 0.4	5.1 $\pm$ 0.9	8.3 $\pm$ 0.9	4.0 $\pm$ 0.6	5.7 $\pm$ 0.7
Median	5	7	4	4	9	4	5.5
Range	2.5–8	0–18	0–7.7	0–17	3–14	0–9	0–13.5

<sup>a</sup> Number of emergent pups per female was estimated as number of pups emerged at the colony per number of females in the colony.

## Reproductive success of females

The number of emergent pups per female varied by year (Kruskal-Wallis test  $H = 25.68$ ,  $df = 5$ ,  $p = .0001$ ). Females had more pups in the year of highest density (1999) compared with the next year (2000) when the population was crashing (Table 6). Reproduction remained low in 2000 and 2001 but increased in 2002 when the population began to recover.

Group size did not seem to influence the reproductive success of females. When comparing reproductive success by group composition (solitary female, female and male pair, and female groups) in all years combined, we found no statistical difference in the number of emergent pups per female (Kruskal-Wallis test  $H = 1.02$ ,  $df = 2$ ,  $p = .60$ ) or in the survival of pups (Kruskal-Wallis test  $H = 3.74$ ,  $df = 2$ ,  $p = .154$ ) (Figure 5). Because we were concerned about the effect of year on reproduction in females in the different groups and were unable to compare the interaction between group size and year in our nonparametric test, we examined the number of emergent pups and pup survival in the three groups in separate tests in each year. We found no significant differences in these comparisons ( $p > .05$ ).

We also found no differences in reproductive success between philopatric females and females dispersed from the natal colonies. The number of juveniles produced by 1-year-old females from 1999 to 2001 did not differ significantly between philopatric females reproducing in the natal area (2.81  $\pm$  0.67 juveniles per female) and dispersed females (5.13  $\pm$  1.32 juveniles per female) (Mann-Whitney U test,  $z = 98$ ,  $n_1 = 21$ ,  $n_2 = 13$ ,  $p = .172$ ). We found similar results for the number of litters in philopatric (0.64  $\pm$  0.14) and dispersed females (0.92  $\pm$  0.21) ( $z = 113$ ,  $n_1 = 22$ ,  $n_2 = 13$ ,  $p = .31$ ).

Based on evidence of pregnancy and lactation, about 10.5% females did not reproduce, but there was no relationship between nonreproduction and group sizes. The majority of females in all groups, ranging from single females to females in a group of six, showed evidence of breeding.

Although we could estimate that some females did not reproduce in some adult groups, we could not conclusively discriminate mothers from nonmothers by observations of behavioral interactions among females and pups because pups interacted with all females. Because females in groups appeared to be highly related, we were unable to determine conclusively which of the females were

mothers in many cases and which might be acting as helpers from our DNA fingerprints. Females in groups also showed similar frequencies of cooperative behavior (Figure 6). Comparison of a mother with one litter of newly emergent pups and a female in the social group without emergent pups revealed no differences in social behavior. Identified mothers (n = 9) and presumed nonmothers (n = 9) participated equally in contact with pups (Wilcoxon signed-rank test:  $z = 0.78$ ,  $p = .859$ ), food storage ( $z = 0.065$ ,  $p = .515$ ), and alarm calling ( $z = 1.13$ ,  $p = .260$ ).

## DISCUSSION

### Environmental constraints and resource availability

Breeding and survival in the great gerbil seem to depend more on environmental conditions than group size per se. We found that the population density and the size and structure of social groups varied yearly in response to changing conditions of precipitation and temperature. Years with sufficient winter precipitation seemed to produce enough vegetation to facilitate spring breeding and larger family groups. A 2-year drought caused a shortage of spring, nonsucculent

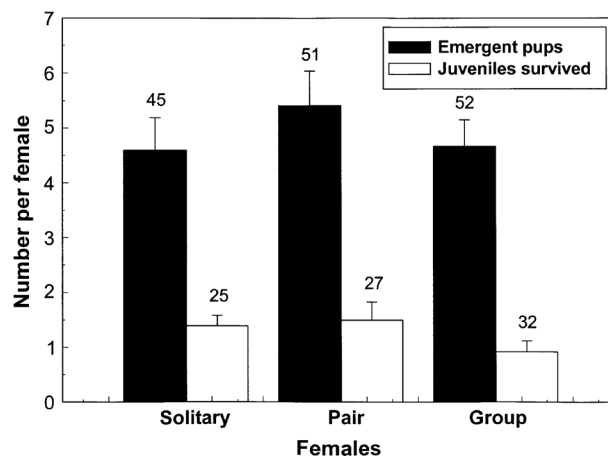


Figure 5  
Number (mean  $\pm$  SE) of emergent pups per female per colony and the number of juveniles surviving from the spring to fall for solitary females, females paired with a male, and females in groups of two to six with a resident male. n is given above bars.

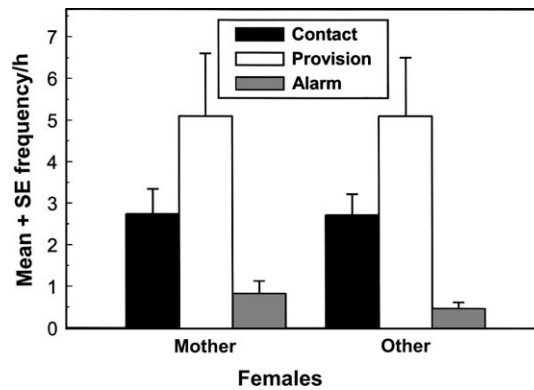


Figure 6

Comparison of contact frequency with pups, number of times taking food into the burrow (provision), and frequency of alarm calls of a female in a family group with newly emergent pups (mother, n = 9) and another female in the group with no pups (other, n = 9).

vegetation and was associated with periods of high mortality during which population densities became very low and group sizes small. The availability of succulents was also a factor in the survival of both adults and juveniles during hot summers.

The great gerbil is similar to other desert rodents (North American kangaroo rats and mice, African and Asian jerboas, Australian murid rodents, and other gerbil species in Africa, Asia, and the Middle East) that limit reproduction to periods of rainfall and the subsequent growth of green vegetation (see reviews in Randall, 1993, 1994; Shenbrot et al., 1999). In general, a wide variety of desert rodents breed toward the end of the rainy season and in the months afterward, regardless of when rainfall occurs. Reproduction is suppressed by a dry diet and then stimulated when rains occur and green vegetation becomes plentiful, causing a relatively fast rate of recovery of population numbers.

### Philopatry and dispersal

As population densities increase, habitats may become more and more saturated so that territories become limited, dispersal decreases, and group sizes increase (Komdeur et al., 1995; Wolff, 1994). Great gerbils are similar to many other social mammals in that males are more likely to disperse than females (Devillard et al., 2004; Dobson, 1982; Greenwood, 1980), while females remained at or near their natal site to form related groups of breeding females (Solomon, 2003). The percentage of gerbils that remained in the natal area after the summer drought was high in both sexes when population densities were high, leading to larger group sizes, but in the lower density years, the proportion of philopatric females was greater than the proportion of philopatric males. Females were still found in the natal territory 1 year after birth, while all males had either dispersed or disappeared from our study area.

Male great gerbils that dispersed had higher survival than those which remained in or near the natal territory, which suggested that both survival and increased mating opportunities may drive dispersal in the males. Advantages to male dispersal include

decreased competition (Moore and Ali, 1984; Perrin and Mazalov, 2000) and inbreeding avoidance (Pusey and Wolf, 1996). Social interactions within large family groups may be a source of stress for adult males (Rogovin et al., 2003b). A dispersing male gerbil either joined a female or a group of females, usually at moderate to high population densities, or moved among single females when a larger proportion of females lived solitarily at lower densities. DNA analysis revealed that males did not appear closely related to females in family groups, suggesting that male-biased dispersal may reduce inbreeding (Pusey and Wolf, 1996). Some adult males, however, must sometimes remain in the family group because we found that about 20% of males in the spring were genetically similar to females in their family groups. If males live longer than 1 year and remain in the same territory, it is likely that some of the females in the group will be their daughters.

Although philopatry usually coincides with the long-lasting use of natal areas, whole groups or parts of groups could emigrate together and thus retain the social relationships already established. Group dispersal is seldom considered in dispersal studies. In great gerbils, the occurrence of solitary adults may not mean that they originally dispersed from the natal colony separately and independently. In years with high mortality, gerbils might have dispersed with other family members and then been left as solitary females when the other females died and males dispersed. We found that about half of the males and females that left their natal colonies between spring and fall were living with one or more members of their natal group in a new colony in the fall, but by the next spring, many of these relationships no longer existed, especially in years with high mortality. It may be that great gerbils disperse together because of strong social relationships that develop early in life (Bekoff, 1977). The causes for movement and change of burrows are unknown but could include parasites, depletion of local feeding resources, or predation. We believe that predators were a factor because we observed entire family groups ( $n = 4$ ) escape to unoccupied burrows in response to a marbled pole cat (*Vormela peregusna*) entering the occupied burrow.

### Kinship and reproductive success

Our long-term monitoring of individual gerbils supports the hypothesis that female great gerbils form kin groups, especially at higher population densities. This hypothesis is strongly supported by the result of DNA analysis, which revealed the genetic similarity of group-living females and the genetic differences of solitary females. Female gerbils mainly live with female relatives, but solitary females do not come together to form groups, even when they share the same male. The apparent preference for females to live with relatives suggests that some indirect fitness benefits from group living and cooperative social interactions are gained by females (Hamilton, 1964). On the other hand, group living could be a by-product of avoiding costs of dispersal. We were unable to test directly the inclusive fitness hypothesis because of lack of sufficient data on breeding success of kin and their descendants, but we did find that females in groups exhibited cooperative behaviors associated with food acquisition (Faulkes et al., 1997), communal care of young (Emlen, 1994;

Gittleman, 1985), and defense against predators (Blumstein and Armitage, 1997; Klump and Shalter, 1984).

Do female gerbils gain a reproductive advantage by living in groups of relatives as found in other rodents (Mappes et al., 1995; McGuire et al., 2002)? When we examined individual breeding success of females in groups of different sizes, we found no evidence that group living increases the current reproductive success of females (Table 1). An examination of the number of emergent pups and survival of juveniles after the summer drought when we would expect high mortality revealed no differences among solitary females, single females paired with a male, and polygynous female groups. Furthermore, we found no statistical difference when we compared the number of juveniles and litters of philopatric and dispersed females.

Because great gerbils form matrilineal groups through retention of females in the natal group and some females in the group may not reproduce, it seems possible that nonreproductive females would take the role of helpers (Emlen, 1997). The decision to help, however, does not automatically follow from the decision to stay in the natal territory (Emlen, 1982; Kokko et al., 2001). A reproductive skew of a dominant female with helpers does not seem present in the great gerbil (Jarvis et al., 1994; Reeve et al., 1998). There is no apparent division of social behavior, and all females give alarm calls, carry food into the burrow, and interact with pups (Randall et al., 2000, and results from this study). Rather than a dominant female breeder and nonreproductive helpers, all members of the family group seem capable of breeding and engaging in parental care. Furthermore, all females in a group share a common territory and are unrestricted in their access to resources. Because solitary females and females in groups seem to have equal breeding success, there would be little incentive for females to remain in a group as a subordinate and give up reproduction. If there is a reproductive skew in the great gerbil, it would be low and possibly transitory (Allainé, 2000).

## Predation

Increased protection from predators via alarm calls has been demonstrated in numerous species of group-living mammals ranging from rodents to primates (Blumstein and Armitage, 1997; Blumstein and Daniel, 2004; Manser et al., 2001; Seyfarth et al., 1980; Zuberbühler, 2000). In addition to avoiding predatory attacks, group members benefit by devoting less time to vigilance and more time to feeding and storing food as group size increases and there are more animals to watch for predators (Bertram, 1978; Elgar, 1989; Lima and Dill, 1990; Quenette, 1990). Great gerbils are prey of a diverse group of terrestrial and aerial predators, including snakes, the desert monitor lizard (*Varanus griseus caspius*), pole cats, buzzards, and harriers. Although not tested in this study, group living probably provides great gerbils an enhanced ability to detect and escape from these predators (Randall et al., 2000; Rogovin et al., 2004a). The gerbils have a well-developed system of alarm signals to communicate response urgency (Randall and Rogovin, 2002; Randall et al., 2000), and solitary female gerbils spend more time vigilant when foraging than females in groups (Tchabovsky et al., 2001).

## Sociality in semifossorial desert rodents

The best reproductive strategy for great gerbils may be the flexibility to modify group size as environmental conditions dictate, especially because both solitary and group-living females seem to have almost equal reproductive success. Rodents are known to display flexible social systems that vary in response to changing environmental conditions (Austad, 1984; Lott, 1991; Schradin and Pillay, 2005; Travis et al., 1995), and mammalian social behavior can reflect mixed strategies that facilitate responses to environmental uncertainty (Flaxman, 2000; Haccou and Iwassa, 1995). Flexible group sizes may be a general response to arid conditions in social desert rodents (Randall, 1994, in press). The Mongolian gerbil (*Meriones unguiculatus*) forms larger groups and attains higher population densities where vegetation is more abundant and predictable compared with smaller groups in more arid regions with little herbaceous growth (Ågren et al., 1989a,b; Xia et al., 1982). Social groups of the Indian gerbil (*Tatera indica*) are much larger where resources are plentiful (Idris and Prakash, 1985), and the striped mouse (*Rhabdomys pumilio*) from the Karoo in South Africa exhibits a flexible social structure and forms communal breeding groups with helpers in regions with permanent succulent vegetation (Schradin and Pillay, 2004).

Great gerbils probably make the “best of a bad situation” in the fluctuating conditions of desert environments. Under favorable conditions for survival and reproduction, kin groups can be maintained, but under conditions of limited food and high mortality that disrupt social behavior and group formation more females live solitarily. Male gerbils adjust to the distribution of females and reside with female groups at high densities and travel between solitary females when densities are low and solitary females are dispersed (Emlen and Oring, 1977). Although the ability of gerbils to tolerate the presence of conspecifics in conditions of limited space may be a preadaptation for the evolution of cooperative breeding, it is also necessary for great gerbils to be flexible and adapt to unpredictable environmental conditions and population fluctuations.

We conclude that great gerbils are facultatively social. The lack of temporal stability in kin associations may have precluded the evolution of complex, kin-selected patterns of cooperative breeding with helpers as seen in social mammals such as the fossorial mole-rats (Chesser, 1991; Faulkes and Bennett, 2001). Nevertheless, compared with the majority of semifossorial desert rodents, great gerbils have achieved a high level of sociality (Randall 1994, in press). Fascinating questions remain to be answered about the ecophysiological adaptations and social cues that mediate social behavior in these rodents (Rogovin et al., 2004b).

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## REFERENCES

- Ågren G, Zhou Q, Zhong W, 1989a. Ecology and social behaviour of Mongolian gerbils, *Meriones unguiculatus*, at Xilinhote, Inner Mongolia, China. *Anim Behav* 37:11–27.
- Ågren G, Zhou Q, Zhong W, 1989b. Territoriality, cooperation and resource priority: hoarding in the Mongolian gerbil, *Meriones unguiculatus*. *Anim Behav* 37:28–32.
- Alexander RD, 1974. The evolution of social behavior. *Annu Rev Ecol Syst* 5:325–383.
- Allaine´ D, 2000. Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. *Behav Process* 51:21–34.
- Armitage KB, 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36–49.
- Austad SN, 1984. A classification of alternative reproductive behaviors and methods of field testing ESS models. *Am Zool* 24:309–319.
- Bekoff M, 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *Am Nat* 111:715–732.
- Bertram BCR, 1978. Living in groups: predators and prey. In: *Behavioural ecology: an evolutionary approach*, 1st ed (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific Publications; 64–96.
- Blumstein DT, Armitage KB, 1997. Does sociality drive the evolution of communicative complexity? A comparative test with grounddwelling sciurid alarm calls. *Am Nat* 150:181–200.
- Blumstein DT, Daniel JC, 2004. Yellow-bellied marmots discriminate among the alarm calls of individuals and are more responsive to calls from juveniles. *Anim Behav* 68:1257–1265.
- Chesser RK, 1991. Influence of gene flow and breeding tactics on gene diversity within populations. *Genetics* 129:573–583.
- Devillard S, Allaine´ D, Gaillard J, Pontier D, 2004. Does social complexity lead to sex-biased dispersal in polygynous mammals? A test on ground-dwelling sciurids. *Behav Ecol* 15:83–87.
- Dobson FS, 1982. Competition for mates and predominant juvenile dispersal in mammals. *Anim Behav* 30:1183–1192.
- Dubiansky MA, Dubianskaya LD, 1977. Character of population number dynamic of great gerbil at the territory of Kazakhstan in 1956–1974. In: *Ecology and medical significance of gerbils of the fauna of USSR* (Kutcheruk VV, ed) (in Russian). Moscow: Nauka Press; 136–137.
- Ebensperger LA, 2001. A review on the evolutionary causes of rodent group living. *Acta Theriol* 46:115–144.
- Ebensperger LA, Bozinovic F, 2000. Communal burrowing in the hystricognath rodent, *Octodon degus*: a benefit of sociality. *Behav Ecol Sociobiol* 47:365–369.
- Ebensperger LA, Cofre´ H, 2001. On the evolution of group-living in the New World cursorial hystricognath rodents. *Behav Ecol* 12:227–236.
- Elgar MA, 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev* 64:13–33.
- Emlen ST, 1982. The evolution of helping. I. An ecological constraints model. *Am Nat* 119:29–39.

- Emlen ST, 1994. Benefits, constraints and the evolution of family. *Trends Ecol Evol* 9:282–285.
- Emlen ST, 1995. An evolutionary theory of the family. *Proc Natl Acad Sci USA* 92:8092–8099.
- Emlen ST, 1997. Predicting family dynamics in social vertebrates. In: *Behavioral ecology: an evolutionary approach* (Krebs JR, Davies NB, eds). Oxford: Blackwell Science; 228–253.
- Emlen ST, Oring LW, 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- Faulkes CG, Bennett NC, 2001. Family values: group dynamics and social control of reproduction in African mole-rats. *Trends Ecol Evol* 16:184–190.
- Faulkes CG, Bennett NC, Bruford MW, O'Brien HP, Aguilar GH, Jarvis JUM, 1997. Ecological constraints drive social evolution in the African mole-rats. *Proc R Soc Lond B* 264:1619–1627.
- Flaxman SM, 2000. The evolutionary stability of mixed strategies. *Trends Ecol Evol* 15:482–484.
- Ganem G, Nevo E, 1996. Ecological constraints associated with aggression and evolution toward pacifism in *Spalax ehrenbergi*. *Behav Ecol Sociobiol* 38:245–252.
- Genoways HH, Brown JH, 1993. *Biology of the heteromyidae*. Special publication 10 of the American Society of Mammalogists. Lawrence, Kansas: Allen Press.
- Georges M, Lequarre AS, Castelli M, Hanset R, Vassart G, 1988. DNA fingerprinting in domestic animals using four different minisatellite probes. *Cytogenet Cell Genet* 47:127–131.
- Getz LL, Gutermuth DF, Benson SM, 1992. Pattern of nest occupancy of the prairie vole, *Microtus ochrogaster*, in different habitats. *Am Midl Nat* 123:365–371.
- Gittleman JL, 1985. The functions of communal care in mammals. In: *Evolution: essays in honour of John Maynard Smith* (Greenwood PJ, Harvey PH, Slatkin M, eds). Cambridge: Cambridge University Press; 187–205.
- Goltzman ME, Naumov NP, Nikolsky AA, Ovsianikov NG, Paskhina NM, Smirin VM, 1977. Social behaviour of a great gerbil (*Rhombomys opimus* Licht). In: *Mammalian behavior* (Sokolov VE, ed) (in Russian). Moscow: Nauka Press; 5–69.
- Greenwood PJ, 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162.
- Gromov VS, 2000. Ethological mechanisms of population homeostasis in gerbils (Mammalia, Rodentia) (in Russian). Moscow: A. N. Severtzov Institute of Ecology and Evolution Publication; 392 p.
- Haccou P, Iwassa Y, 1995. Optimal mixed strategies in stochastic environments. *Theor Popul Biol* 47:212–243.
- Hamilton WD, 1964. The genetical evolution of social behavior I. *J Theor Biol* 7:1–16.
- Hatchwell BJ, Komdeur J, 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim Behav* 59:1079–1086.
- Hayes LD, 2000. To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Anim Behav* 59:677–688.
- Idris M, Prakash I, 1985. Social and scent marking behaviour in Indian gerbil, *Tatera indica*. *Biol Behav* 10:31–39.
- Jarvis JUM, O'Riain MJ, Bennett NC, Sherman PW, 1994. Mammalian eusociality: a family affair. *Trends Ecol Evol* 9:47–51.
- Jeffreys AJ, Wilson V, Thein S, 1985. Hypervariable minisatellite regions in human DNA. *Nature* 314:67–73.
- Johnson DDP, Kays R, Blackwell PG, Macdonald DW, 2002. Does the resource dispersion hypothesis explain group living? *Trends Ecol Evol* 17:563–569.



- Karpov AA, Korneev GA, 1979. Peculiarities of great gerbils' (Rodentia, Cricetidae) behavior in conditions of fluctuating density during the plague epizootic process. *Zool Zh* 58:890–895.
- Klump GM, Shalter MD, 1984. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting structure of alarm signals. II. The functional significance and evolution of alarm signals. *Z Tierpsychol* 66:189–226.
- Koenig WD, Pitelka FA, 1981. Ecological factors and kin selection in the evolution of cooperative breeding birds. In: *Natural selection and social behavior* (Alexander RD, Tinkle DW, eds). New York: Chiron Press; 261–280.
- Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT, 1992. The evolution of delayed dispersal in cooperative breeders. *Q Rev Biol* 67:111–150.
- Kokko H, Johnstone RA, Clutton-Brock TH, 2001. The evolution of cooperative breeding through group augmentation. *Proc R Soc Lond B* 268:187–196.
- Kokko H, Lundberg P, 2001. Dispersal, migration, and offspring retention in saturated habitats. *Am Nat* 157:188–202.
- Komdeur J, Huffstadt A, Prast W, Castle G, Mileto R, Wattel J, 1995. Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour. *Anim Behav* 49:695–708.
- Krause J, Ruxton GD, 2002. *Living in groups*. Oxford: Oxford University Press.
- Kutcheruk VV, Kulik IL, Dubrovsky YaA, 1972. *Rhombomys opimus* Licht as a life form of the desert. In: *Fauna and ecology of rodents*, vol. 11 (Kutcheruk VV, ed) (in Russian). Moscow: Moscow University Press; 5–70.
- La Galliard J, Ferrière R, Dieckmann U, 2005. Adaptive evolution of social traits: origin, trajectories, and correlations of altruism and mobility. *Am Nat* 165:206–224.
- Lacey EA, Wieczorek JR, 2004. Kinship in colonial tuco-tucos: evidence from group composition and population structure. *Behav Ecol* 15:988–996.
- Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Lott DF, 1991. *Intraspecific variation in the social systems of wild vertebrates*. Cambridge: Cambridge University Press.
- Lynch M, 1988. Estimation of relatedness by DNA fingerprinting. *Mol Biol Evol* 5:584–599.
- Lynch M, 1990. The similarity index and DNA fingerprinting. *Mol Biol Evol* 7:479–484.
- Manser MB, Bell BB, Fletcher LB, 2001. The information that receivers extract from alarm calls in suricates. *Proc R Soc Lond B* 268:2485–2491.
- Mappes T, Ylönen H, Vitala J, 1995. Higher reproductive success among kin groups of bank voles (*Clethrionomys glareolus*). *Ecology* 76:1276–1282.
- Marfori MA, Parker PG, Gregg TG, Vandenberg JG, Solomon NG, 1997. Using DNA fingerprinting to estimate relatedness within social groups of pine voles. *J Mammal* 78:715–724.
- Matocq MD, Lacey EA, 2004. Philopatry, kin clusters, and genetic relatedness in a population of woodrats (*Neotoma macrotis*). *Behav Ecol* 15:647–653.
- McGuire B, Getz LL, Oli MK, 2002. Fitness consequences of sociality in prairie voles, *Microtus ochrogaster*: influence of group size and composition. *Anim Behav* 64:645–654.
- Michener GR, 1983. Kin identification, matriarchies and the evolution of sociality in ground-dwelling sciurids. In: *Advances in the study of mammalian behavior* (Eisenberg JF, Kleiman DG, eds). Special publication 7 of the American Society of Mammalogists. Lawrence, Kansas: Allen Press; 528–572.
- Mokrousov NYa, 1978. The great gerbil—*Rhombomys opimus* Lichtenstein, 1823. In: *Mammals of Kazakhstan*, vol. 3 (Sludsky AA, ed) (in Russian). Alma-Ata: Nauka Press; 64–115.

- Moore J, Ali R, 1984. Are dispersal and inbreeding avoidance related? *Anim Behav* 32:94–112.
- Moshkin MP, Gerlinskaya LA, Zavialov EL, Kolosova IE, Rogovin K, Randall JA, 2003. Stress and nutrition in the wild. *Recent Adv Anim Nutr Aust* 14:11–22.
- Naumov NP, 1965. Territorial peculiarities and mechanism of population dynamics of terrestrial vertebrates (in Russian). *Zh Obshch Biol* 26(6):625–633.
- Naumov NP, 1967. Population structure and dynamics in numbers of terrestrial vertebrates (in Russian). *Zool Zh* 46(10):1470–1486.
- Naumov NP, Lobachev VS, 1975. Ecology of desert rodents of the USSR (jerboas and gerbils). In: *Rodents in desert environments* (Parkash I, Ghosh CK, eds). The Hague: Junk; 465–598.
- Naumov NP, Lobachev VS, Dmitriev PP, Smirin VM, 1972. Natural foci of plague of the north Aral desert (in Russian). Moscow: Moscow University Press.
- Parker PG, Jones TC, Haydock J, Dickinson J, Worden BD, 1999. Multilocus mini-satellite DNA fingerprinting and cooperative breeding. *Behav Ecol Sociobiol* 47:108–111.
- Parker PG, Snow AA, Schug MD, Booton GC, Fuerst PA, 1998. What molecules can tell us about populations: choosing and using a molecular marker. *Ecology* 79:361–382.
- Pavlinov IYa, Dubrovsky YuA, Rossolimo OL, Potapova EG, 1990. *Gerbils of the world* (in Russian). Moscow: Nauka Press.
- Peare T, Parker PG, 1996. Local genetic structure within two rookeries of *Chelonia mydas* (the green turtle). *Heredity* 77:619–628.
- Perrin N, Lehmann L, 2001. Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin-discrimination mechanisms. *Am Nat* 158:471–483.
- Perrin N, Mazalov V, 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am Nat* 155:116–127.
- Pusey A, Wolf M, 1996. Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201–206.
- Quenette PY, 1990. Functions of vigilance behavior in mammals: a review. *Acta Oecol* 11:801–818.
- Rabenold PP, Rabenold KN, Piper WH, Decker MD, Haydock J, 1991. Using DNA fingerprinting to assess kinship and genetic structure in avian populations. In: *The unity of evolutionary biology: Proceedings IV International Congress Systematic Evolutionary Biology* (Dudley EC, ed). Portland, Oregon: Dioscorides Press; 615–620.
- Randall JA, 1993. Behavioural adaptations of desert rodents (Heteromyidae). *Anim Behav* 45:263–287.
- Randall JA, 1994. Convergence and divergence in communication and social organisation of desert rodents. *Aust J Zool* 42:405–433.
- Randall JA, in press. Environmental constraints and the evolution of sociality in semi-fossorial desert rodents. In: *Rodent societies* (Wolff JO, Sherman PW, eds). Chicago, Illinois: Chicago University Press.
- Randall JA, Rogovin K, 2002. Variation in and meaning of alarm calls in a social desert rodent *Rhombomys opimus*. *Ethology* 108: 513–527.
- Randall JA, Rogovin K, Shier DM, 2000. Antipredator behavior of a social desert rodent: footdrumming and alarm calling in the great gerbil, *Rhombomys opimus*. *Behav Ecol Sociobiol* 48:110–118.
- Reeve H, Emlen S, Keller L, 1998. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behav Ecol* 9:267–278.
- Rogovin K, Moshkin MP, Randall JA, Kolosova IE, Chikin Y, 2003a. Availability of resources, social demography and physiological stress in population of great gerbil (*Rhombomys opimus*) in conditions of peak and decline of density (in Russian). *Zool Zh*

- 82:497–507.
- Rogovin K, Randall JA, Kolosova I, Moshkin M, 2003b. Social correlates of stress in adult males of the great gerbil, *Rhombomys opimus*, in years of high and low population densities. *Horm Behav* 43:132–139.
- Rogovin K, Randall JA, Kolosova I, Moshkin M, 2004a. Predation on a social desert rodent, *Rhombomys opimus*: effect of group size, composition and location. *J Mammal* 85:723–730.
- Rogovin K, Randall JA, Kolosova IE, Moshkin MP, 2004b. Social environment and morpho-physiological status of young males in the fall groups of great gerbil (*Rhombomys opimus* Licht): effects of adults' presence (in Russian). *Zh Obshch Biol* 65(4):426–432.
- Schradin C, Pillay N, 2004. The striped mouse (*Rhabdomys pumilio*) from the succulent karoo of South Africa: a territorial group living forager with communal breeding and helpers at the nest. *J Comp Psychol* 118:37–47.
- Schradin C, Pillay N, 2005. Intraspecific variation in the spatial and social organization of the African striped mouse. *J Mammal* 86:99–107.
- Seyfarth RM, Cheney DL, Marler P, 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Anim Behav* 28:1070–1094.
- Slobodchikoff CN, 1984. Resources and the evolution of social behavior. In: *A new ecology: novel approaches to interactive systems* (Price PW, Slobodchikoff CN, Gaud WS, eds). New York: John Wiley; 227–251.
- Shenbrot GI, Krasnov BR, Rogovin K, 1999. *Spatial ecology of desert rodent communities*. Berlin: Springer.
- Solomon NG, 2003. A reexamination of factors influencing philopatry in rodents. *J Mammal* 84:1182–1197.
- Tchabovsky AV, Popov SV, Krasnov BR, 2001. Intra-and interspecific variation in vigilance and foraging of two gerbillid rodents, *Rhombomys opimus* and *Psammomys obesus*: the effect of social environment. *Anim Behav* 62:965–972.
- Travis SE, Slobodchikoff CN, Keim P, 1995. Ecological and demographic effects on intraspecific variation in the social system of prairie dogs. *Ecology* 76:1794–1803.
- Waser PM, 1988. Resources, philopatry, and social interactions among mammals. In: *The ecology of social behavior* (Slobodchikoff CN, ed). San Diego, California: Academic Press; 109–130.
- Wetton JH, Carter RE, Parkin DT, Walters D, 1987. Demographic study of house sparrow populations by DNA fingerprinting. *Nature* 327:147–149.
- Wolff JO, 1992. Parents suppress reproduction and stimulate dispersal in opposite-sex juvenile white-footed mice. *Nature (Lond)* 359:409–410.
- Wolff JO, 1994. Reproductive success of solitary and communally nesting white-footed mice and deer mice. *Behav Ecol* 5:206–209.
- Wrangham RW, Rubenstein DI, 1986. Social evolution in birds and mammals. In: *Ecological aspects of social evolution* (Rubenstein DI, Wrangham RW, eds). Princeton, New Jersey: Prince University Press; 452–470.
- Xia V, Liao Ch, Whong W, Sun Ch, Tian Y, 1982. On the population dynamics and regulation of *Meriones unguiculatus* in the agricultural region north of the Yin mountains, Inner Mongolia. *Acta Theriol Sin* 2:51–72.
- Zar JH, 1999. *Biostatistical analysis*. Englewood Cliffs, New Jersey: Prentice-Hall.
- Zuberbu"hler K, 2000. Referential labelling in Diana monkeys. *Anim Behav* 59:917–927.