Effects of supplemental food on the social organization of Mongolian gerbils during the breeding season

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Abstract

Social groups occur in many rodents and vary in size and complexity under varying environments. Food availability is often limited in northern temperate regions and alters the life history and behavior of rodents. Increased food availability is hypothesized to increase the size and complexity of rodent social groups by enhancing individual survival and philopatry. We tested this hypothesis in Mongolian gerbils *Meriones unguiculatus* under semi-natural conditions in Inner Mongolia, China. The Mongolian gerbil is a cooperative breeder living in groups year-round. Gerbil colonies in 10 m × 10 m chambers were the experimental units, with four replicate chambers each for food supplementation and food unsupplemented controls in 2004 and six replicate chambers for each treatment in 2005. At 2-day intervals wheat grain supplemented the normal food in experimental chambers throughout the breeding season (May through August). We estimated founder mortality, cumulative recruitment, proportion of philopatric juveniles, ages at sexual maturity and social group size in each colony from May through August. Rates of change in group size were inversely related to social group size. The social organization of Mongolian gerbils did not differ in any of the measured parameters between food-supplemented and -unsupplemented chambers. Therefore, additional food does not influence the social organization of Mongolian gerbils during the breeding season.

Introduction

Group living occurs in at least 70 rodent species (Lacey & Sherman, 2007). Group living benefits rodents in their defense against predators, in food acquisition and defense and in adaptation to cold or to shortage of suitable habitats (Ebensperger, 2001; Krause & Ruxton, 2002). In some social rodents, offspring remain at their natal nests after weaning and may provide alloparental care (Madison, 1984; Solomon & French, 1997; Lacey & Sherman, 2007). Group living may have costs as group living may increase the risk of predation and disease (Krause & Ruxton, 2002) or may increase intra-group competition for food (Madison, 1984; Lacey & Wieczorek, 2003).

The Mongolian gerbil *Meriones unguiculatus* (Milne-Edwards, 1867) is widely distributed in semi-arid and arid grasslands and farmlands in the south-east of the Bakal area in Russia, Mongolia and northern China (Gromov *et al.*, 1963; Mallon, 1985; Luo *et al.*, 2000). Mongolian gerbils are cooperative breeders, living in groups year-round (Gromov, 1981; Ågren, Zhou & Zhong, 1989*a*). A group consists of a male and female breeding pair (often founders) and their siblings and offspring, ranging from two to 17 individuals (Ågren *et al.*, 1989*a*; Ågren, Zhou & Zhong, 1989*b*). Each social group excavates and occupies a complex burrow

system (Wang & Zhong, 1998; Scheibler *et al.*, 2006). The core area of a burrow system is about 4.1 m², covering about 80% of the burrow entrances (Hsia & Wang, 1956). Dispersal of Mongolian gerbil is male biased and the average body mass of dispersers is 45.1 g (W. Liu, pers. obs.). The average life span of male and female gerbils in a semi-natural condition is 4.6 months (standard deviation [SD] = 3.93) and 5.3 months (SD = 4.95), respectively, and the maximum life span is 21 months for male gerbils and 30 months for female gerbils (W. Liu, pers. obs.). Mongolian gerbils are as a model species for studies of rodent social behavior, particularly under laboratory conditions (French, 1994; Clark & Galef, 2001; Scheibler, Weinandy & Gattermann, 2004; Randall, 2007). However, little is known about the ecology and social behavior of this species under natural or semi-natural conditions (Ågren *et al.*, 1989*a,b*; Liu, Wan & Zhong, 2007).

Food has crucial effects on the body mass, reproductive performance and population structure of Mongolian gerbils (Zhou, Zhong & Sun, 1985). Most members of a gerbil social group take part in food hoarding during autumn and store food in communal caches (Ågren *et al.*, 1989*b*). Experimental provisions of wheat grains induce food-hoarding and territorial behavior of Mongolian gerbils (Ågren *et al.*, 1989*b*), but influences on social organization

of Mongolian gerbils have not been investigated. We conducted a 2-year experimental study to determine the effects of supplemental food on the social organization of Mongolian gerbils under semi-natural conditions in Inner Mongolia, China. The main predictions of our study were that food supplementation would increase philopatry of individuals in social groups, improve gerbil survival and recruitment into social groups and subsequently increase social group size.

Study area and methods

Study area

Our study was conducted during the breeding season from early May to late August in 2004 and 2005 at the Taipusiqi Field Research Station (115°17′E, 41°58′N, 1500 m elevation), *c.* 8 km north of Baochang in Inner Mongolia, China. The area is in a region where grasslands are intermixed with croplands. The climate is semi-arid and continental with a relatively hot summer (June through August) and a cold, dry winter (November through February). The average annual precipitation is about 350 mm. Average monthly temperatures range from −19.1 to 21.1 °C. Vegetation is composed primarily of grasses and herbs; the dominant plant is *Leymus chinense*, which begins to grow in early May. A detailed description of the study area and climate is given in Liu *et al.* (2007).

Experimental design

We conducted our supplemental-food experiments in a 20 m × 60 m enclosure, which consisted of 12 sub-enclosures (10 m × 10 m each). The outer enclosure and sub-enclosures were constructed of cement walls *c.* 100 cm above and 100 cm below ground to prevent either the escape of the gerbils or the entry of other burrowing rodents (e.g. *Spermophilus dauricus* or *Myospalax aspalax*). A hole in the wall at the ground level connected two neighboring chambers and allowed gerbils to move between the two. The top of the enclosure was covered with a nylon netting to prevent avian predation (e.g. *Bubo bubo*).

A gerbil family group occupying a chamber comprised an experimental unit. An experimental chamber (100 m²) was about 25 times as large as the core area (4.1 m²) of a gerbil burrow system (Hsia & Wang, 1956). Two weeks before our treatment (i.e. provisioning wheat grains), we trapped and removed all over-wintered gerbils from the enclosure and then released 20 or 26 wild, adult gerbils (50–60 g) of each sex (founders) into the enclosure to establish experimental populations in mid May of each year. We captured over-wintered founder gerbils from 10 burrow systems (or social groups) of a wild population near Baochang, Inner Mongolia, in 2004 and from 13 burrow systems of the same wild gerbil population in 2005. Two males and two non-pregnant females were selected from each wild gerbil social group and released into a chamber. Four gerbils per chamber are less than the average number (seven) of gerbils per burrow system in the field and increase the chance for a chamber to

have at least a pair of male and female for a social group. The released founders were allowed to move among all chambers through the holes in the cement walls. All founders were toe-clipped for individual identification. Two weeks after release, eight communal groups were spontaneously formed by 28 (13 males, 15 females) surviving gerbils in 2004 (Fig. 1a); 12 groups were formed by 41 (16 males, 25 females) surviving gerbils in 2005 (Fig. 1b). We randomly chose one half of the family groups as our treatment groups (hereafter food-supplemented groups) and the other half as our control groups without supplemental food (hereafter food-unsupplemented groups), using a random number generator.

Supplemental food was placed at five stations around the center of a burrow system in the morning when gerbils were highly active (Fig. 1). A plastic can (6 cm in diameter and 9 cm in length) with about 200 g of wheat grains placed at each food station. Each can had only a small opening (to prevent birds from taking grains), but allowed the gerbils access. Food cans were refilled every 2 days during the 76 days of the study each year. The average daily food consumption of Mongolian gerbils is about 5.5 g of wheat grains per adult (Hsia & Wang, 1956); hence, five cans of supplemental food were sufficient for 20 gerbils for 2 days. Five empty plastic food cans were also placed in the burrow centers of food-unsupplemented groups (Fig. 1).

Provision of wheat grains triggered group-hoarding behavior. All group members, with the exception of juveniles under 20 g, carried grains into communal food caches within 20–30 min after the supplemental food was provided (Ågren *et al.*, 1989b; Liu, Wan & Zhong, 2005). We plugged the holes between adjacent chambers (Fig. 1) when wheat grains were provided and re-opened the holes after all wheat grains were removed from food stations. In so doing, we ensured that supplemental food was used exclusively by gerbil groups that occupied the food-supplemented burrows and that the gerbils were allowed to move between the chambers when food was not provided. Moreover, our behavioral observations suggested that the territoriality of Mongolian gerbils deterred the gerbils in food-unsupplemented groups from taking cached food from the food-supplemented burrow systems.

Monitoring gerbil populations and family groups

We used live trapping and behavioral observations to determine the size and composition of gerbil social groups. Mongolian gerbils were monitored from the end of May through the end of August in 2004 and 2005. One or two wire-mesh live traps (28 cm × 13 cm × 10 cm) were placed at each burrow entrance of a gerbil colony (Liu *et al.*, 2007). We began the first trapping session 3 days after the first food provision and trapped gerbils for 3 consecutive days at a 2-week interval. Traps were baited with peanuts, set at 05:00–06:00 h, checked every 1–2 h until about 11:00 h and closed from 11:00 to 15:00 h to avoid trap mortality from heat; trapping resumed at 16:00 h and continued till 19:00 h.
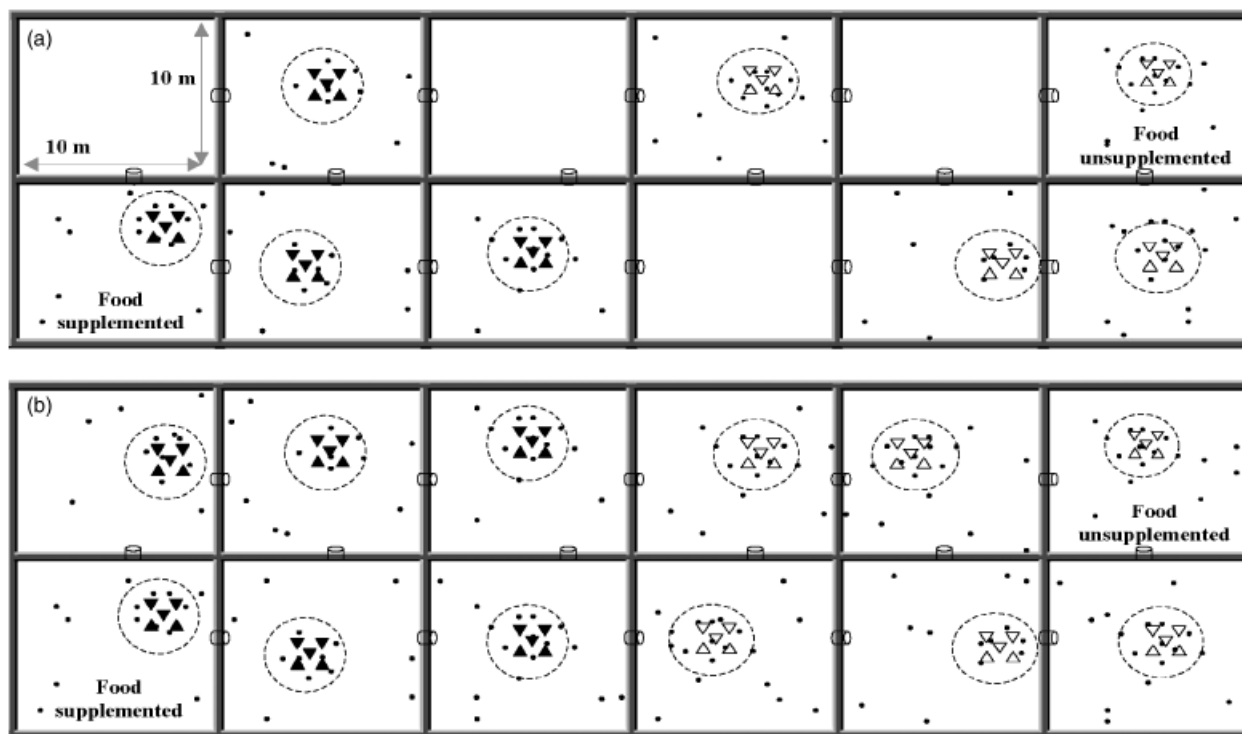
Figure 1 Layout of the 20 m × 60 m experimental enclosure with 12 small chambers (10 m × 10 m) and locations of the food-supplemented and -unsupplemented family groups of Mongolian gerbils *Meriones unguiculatus* in May of (a) 2004 and (b) 2005 in Taibusi Qi, Inner Mongolia, China.

Gerbils rarely eat peanut baits when captured; thus, peanuts are not significant supplemental food. Gerbils were active during our trapping hours (Ågren, Zhou & Zhong, 1990).

All unmarked gerbils were individually toe-clipped at the first capture. One or more small patches of fur on the forehead, back and hips were dyed with black hair dye at each trapping session. Individuals had different combinations of dyed patches for identification at a distance. Captured gerbils were sexed and weighed to the nearest 1 g. Reproductive condition, trap location and identification were recorded for each capture. Males were considered to be in a reproductive condition if they had scrotal testes and visible ventral scent glands with either clear contour or large, visible pores surrounded by secreted substance (Liu *et al.*, 2007). Females were considered to be in a reproductive condition if they had a bulging abdomen, enlarged nipples surrounded by white mammary tissue or open pelvic symphyses. Recruits were defined as newly marked animals that were captured after the initial population was marked in the first tapping session in May. Gerbils under 30 g were considered juveniles. We used the minimum number known-alive method (MNA; Krebs, 1999) to estimate group sizes for each trapping session.

We induced and observed group-hoarding behavior to determine the members of each social group (Ågren *et al.*, 1989b; Liu *et al.*, 2005) after the second trapping session in May. We supplied 10–20 g of wheat grains in three or four Petri dishes placed randomly around the central part of a burrow system to induce gerbil family members to hoard

grains immediately. We considered gerbils that hoarded wheat grains into the same burrow system to be members of a social group (Ågren *et al.*, 1989b; Liu *et al.*, 2005). We induced gerbil food hoarding only once; thus, wheat added to both treatment and control enclosures was ignored as supplemental food. Additionally, we used data on reproductive condition and identification from our trapping to confirm the residence of individual gerbils in a colony, particularly for juveniles who did not participate in communal food hoarding. In June 2004 and 2005, we chose 10 control chambers and 10 treatment chambers to measure plant biomass. We randomly placed a 1 m × 1 m quadrant in each selected chamber using a random number generator and a 10 m × 10 m grid of 1 m spacing and cut all plants within a sampling quadrant at ground level. Plants were weighed to the nearest 0.1 g to determine fresh biomass (g m^{-2}).

Data analysis

Each chamber or sub-enclosure was an independent replicate in our study. We used repeated-measures analysis of variance (repeated-measures ANOVA) to test for differences in group size and the proportion of females in a colony over time (trapping sessions) and between food-supplemented and -unsupplemented groups. We used analysis of covariance (ANCOVA) with group size at the beginning of the experiment as a covariate to test for differences in sex-specific, cumulative recruitment (males and females

combined) per family group from May through August between food-supplemented and -unsupplemented groups. We used arcsine transformation to normalize the data on the proportion of females (Quinn & Keough, 2002). Sex-specific, apparent mortality of founding gerbils, that is, the proportion of founders of each sex that died during the entire study period, was compared between food-supplemented and -unsupplemented groups, using Fisher's exact test. We defined individuals as philopatric if they survived and remained at their natal sites from the time of their initial captures through the end of the experiment and used the proportion of juveniles remaining philopatric to measure philopatry of a gerbil family group (McGuire *et al.*, 1993). We compared the proportion of philopatric juveniles between fed and unfed gerbils, using Fisher's exact test. In addition, we compared the age at sexual maturity, that is, initial body mass of females with a perforated vagina and males with scrotal testes caught for the first time, between the two groups, using *t*-tests.

We used years as a factor in repeated-measures ANOVA and ANCOVA to test for any year effects on group size and cumulative recruitment, respectively. We also tested for differences in founder mortality, proportions of philopatric juveniles and age at sexual maturity between 2 years (2004 and 2005) for each treatment, using Fisher's exact test and *t*-test, respectively. If no year effects were detected, we pooled our data over the 2 years within each treatment to increase our sample sizes for further analyses. Results are reported as means ± 1 standard error, and the significance level of the statistical tests was 0.05.

We calculated weekly growth rates of group size as $(\ln N_{t+1} - \ln N_t)/WK$, where N_t is the size of a gerbil social group in week t; N_{t+1} is the social group size in week $t+1$; WK is the number of weeks between two successive trapping periods; and the symbol ln denotes the natural logarithm. We used mixed generalized linear models (Faraway, 2006)

to test for density dependence in the growth of social group size with year and social group as random factors. We regressed the growth rate of gerbil social groups from week t to week $t+1$ on naturally logged group size in week t and used order-1 autocorrelative covariance to account for temporal autocorrelations in the growth rate of social group size (Faraway, 2006).

Results

In our preliminary analysis, we did not find differences in group size between 2 years either in food-supplemented chambers ($F_{1,8} = 0.03$, $P = 0.87$, Table 1) or in food-unsupplemented chambers ($F_{1,6} = 0.19$, $P = 0.68$, Table 1) in repeated-measures ANOVA. The proportions of females did not differ between 2004 and 2005 in either treatment group (food-supplemented chambers: $F_{1,8} = 0.88$, $P = 0.38$; food-unsupplemented chambers: $F_{1,6} = 0.63$, $P = 0.46$, Table 2). Founder mortality did not differ between 2 years in either food supplementation (male: $\chi^2 = 0.44$, d.f. = 1, $P = 1.0$; female: $\chi^2 = 0.51$, d.f. = 1, $P = 0.63$, Table 3) or food unsupplementation (male: $\chi^2 = 2.29$, d.f. = 1, $P = 0.47$; female: $\chi^2 = 0.003$, d.f. = 1, $P = 1.0$, Table 3). Cumulative recruitment per group did not differ between 2 years in either treatment group (food-supplemented chambers: 9.0 ± 3.8 in 2004, 7.8 ± 1.7 in 2005, $F_{1,7} = 0.24$, $P = 0.64$; food-unsupplemented chambers: 5.0 ± 2.3 in 2004, 6.5 ± 1.5 in 2005, $F_{1,7} = 0.52$, $P = 0.50$) in ANCOVA. Moreover, neither the percentage of sexually mature recruits ($\chi^2 = 4.09$ d.f. = 1, $P = 0.08$, Table 4) nor the age at sexual maturity ($t = 1.75$, d.f. = 4, $P = 0.16$, Table 4) differed between the years 2004 and 2005 in food supplementation, whereas the percentage of sexually mature recruits did differ between 2 years in food unsupplementation ($\chi^2 = 6.16$, d.f. = 1, $P = 0.04$, Table 4). We caught one female and two male sexually mature juveniles in food-unsupplemented chambers

Table 1 Social group size of Mongolian gerbils *Meriones unguiculatus* in food-supplemented and -unsupplemented chambers during the breeding season of 2004 and 2005 in Taibusi Qi, Inner Mongolia, China

Trapping week	Year	Food-supplemented		Food-unsupplemented	
		The number of sampled family groups	Total number of residents per group (mean $\pm$ SE)	The number of sampled family groups	Total number of residents per group (mean $\pm$ SE)
0th week	2004	4	3.3 ± 0.5	4	3.8 ± 0.6
	2005	6	3.5 ± 0.2	6	3.3 ± 0.3
	Pooled	10	3.4 ± 0.2	10	3.5 ± 0.3
4th week	2004	4	7.0 ± 2.3	4	6.8 ± 2.8
	2005	6	5.7 ± 1.7	6	7.7 ± 1.6
	Pooled	10	6.2 ± 1.3	10	7.3 ± 1.4
6th week	2004	4	10.0 ± 4.7	3	6.0 ± 4.0
	2005	6	8.0 ± 1.6	5	8.2 ± 1.3
	Pooled	10	8.8 ± 2.0	8	7.4 ± 1.6
8th week	2004	4	5.5 ± 2.2	3	5.0 ± 3.0
	2005	6	8.8 ± 1.1	5	6.4 ± 1.5
	Pooled	10	7.5 ± 1.2	8	5.9 ± 1.4
10th week	2004	4	5.3 ± 2.3	3	4.3 ± 2.3
	2005	6	6.7 ± 1.3	5	5.8 ± 1.1
	Pooled	10	6.1 ± 1.1	8	5.3 ± 1.0

Table 2 Proportions of female Mongolian gerbils *Meriones unguiculatus* in social groups in food-supplemented and -unsupplemented chambers during the breeding season of 2004 and 2005 in Taibusi Qi, Inner Mongolia, China

Trapping week	Year	Food-supplemented		Food-unsupplemented	
		The number of sampled family groups	Proportions of females per group (mean ± SE)	The number of sampled family groups	Proportions of females per group (mean ± SE)
0th week	2004	4	0.583 ± 0.102	4	0.475 ± 0.105
	2005	6	0.625 ± 0.042	6	0.597 ± 0.045
	Pooled	10	0.608 ± 0.044	10	0.548 ± 0.051
4th week	2004	4	0.578 ± 0.170	4	0.570 ± 0.153
	2005	6	0.636 ± 0.099	6	0.541 ± 0.096
	Pooled	10	0.613 ± 0.085	10	0.552 ± 0.079
6th week	2004	4	0.358 ± 0.063	3	0.500 ± 0.000
	2005	6	0.599 ± 0.077	5	0.492 ± 0.059
	Pooled	10	0.503 ± 0.064	8	0.495 ± 0.059
8th week	2004	4	0.479 ± 0.071	3	0.485 ± 0.015
	2005	6	0.670 ± 0.096	5	0.578 ± 0.114
	Pooled	10	0.593 ± 0.069	8	0.543 ± 0.071
10th week	2004	4	0.521 ± 0.086	3	0.482 ± 0.019
	2005	6	0.558 ± 0.145	5	0.580 ± 0.114
	Pooled	10	0.595 ± 0.069	8	0.543 ± 0.071

in 2004 but no sexually mature recruits of either sex in food-unsupplemented chambers in 2005. The percentage of philopatric juveniles of either sex did not differ between 2 years in either the food-supplemented groups (male: $\chi^2 = 0.63$, d.f. = 1, $P = 0.54$; female: $\chi^2 = 4.63$, d.f. = 1, $P = 0.052$, Table 4) or the food-unsupplemented groups (male: $\chi^2 = 1.22$, d.f. = 1, $P = 0.45$; female: $\chi^2 = 2.60$, d.f. = 1, $P = 0.23$, Table 4). To improve the power of our statistical tests, we pooled data on all measured parameters over 2 years within each treatment, except for the percentage of sexually mature recruits. We analyzed the percentage of sexually mature recruit by year separately.

Gerbil group size increased over trapping sessions ($F_{4,64} = 7.38$, $P < 0.001$); group size did not differ between food-supplemented and -unsupplemented groups ($F_{1,16} = 0.02$, $P = 0.88$, Table 1). The proportions of females did not differ over time ($F_{4,64} = 0.77$, $P = 0.55$) or between treatments ($F_{1,16} = 0.60$, $P = 0.45$, Table 2). Nine (69.2%) of 13 male founders and six (28.6%) of 21 female founders died or disappeared from their initial colonies in food-supplemented chambers during our study period, whereas 14 (87.5%) of 16 male founders and 11 (57.9%) of 19 female founders in the control chambers died or disappeared from their initial colonies during the same period. Neither apparent mortality of male nor female founders differed between the treatments (male: $\chi^2 = 0.56$, d.f. = 1, $P = 0.36$; female: $\chi^2 = 2.41$, d.f. = 1, $P = 0.11$, Table 3). The average number of female breeding bouts was 1.8 ± 0.1 from mid May through the end of August. Thirty females bred more than once (two to four times) and 30 females only bred once during the study period; hence, observed recruits were the output of at least two breeding bouts.

The cumulative recruits were 83 (42 males, of which one was removed, and 41 females) in 10 food-supplemented chambers and 59 (33 males and 26 females) in 10 food-unsupplemented chambers (Table 4). The average cumulative number of recruits per colony was 8.3 ± 1.7 in food-supplemented chambers and 5.9 ± 1.3 in food-unsupplemented chambers, while the average initial group size was 3.4 ± 0.2 in food-supplemented chambers and 3.5 ± 0.3 in food-unsupplemented chambers. Recruitment per family group did not differ between food-supplemented and -unsupplemented groups (ANCOVA, $F_{1,17} = 1.47$, $P = 0.24$).

The percentage of sexually mature recruits was 13.8% (5/36) in food-supplemented chambers and 15.0% (3/20) in food-unsupplemented chambers in 2004, whereas the percentage of sexually mature recruits was 2.2% (1/46) in food-supplemented chambers and 0.0% (0/39) in food-unsupplemented chambers in 2005. Therefore, most recruits were not sexually mature in either food-supplemented or -unsupplemented chambers. Additionally, the percentage of sexually mature recruits did not differ between the food-supplemented and -unsupplemented chambers of either year ($\chi^2 = 0.01$, d.f. = 1, $P = 1.0$ for the year 2004; $\chi^2 = 0.86$, d.f. = 1, $P = 1.0$ for the year 2005). We pooled data on the age at sexual maturity over the years within each treatment because of small sample sizes (e.g. 1 in food supplemented and 0 in food unsupplemented chambers in 2005, respectively). The age at maturity did not differ ($t = 0.91$, d.f. = 7, $P = 0.39$) between food-supplemented groups (45.8 ± 2.1 g) and food-unsupplemented groups (41.9 ± 4.5 g).

Twenty-two (53.7%) of 41 male recruits in the food-supplemented groups and 18 (54.5%) of 33 male recruits in the food-unsupplemented groups remained at their natal groups and survived till the end of the study (Table 4). The percentage of philopatric female juveniles was 48.8% ($n = 41$) and 50.0% ($n = 26$) in the food-supplemented and -unsupplemented groups, respectively (Table 4). No differences in juvenile survival of either sex between the two groups (male: $\chi^2 = 0.10$, d.f. = 1, $P = 0.94$; female:

Table 3 The dynamics of social group founders of Mongolian gerbils *Meriones unguiculatus* in food-supplemented and -unsupplemented chambers during the breeding season of 2004 and 2005 in Taibusi Qi, Inner Mongolia, China

Year	Released 2 weeks before experiment		The beginning of the study						The end of the study					
	Male	Female	Supplemented			Unsupplemented			Supplemented			Unsupplemented		
			The number of sampled family groups	Male	Female	The number of sampled family groups	Male	Female	The number of sampled family groups	Male	Female	The number of sampled family groups	Male	Female
2004	20	20	4	5	8	4	8	7	4	1	5	4	2	3
2005	26	26	6	8	13	6	8	12	6	3	10	4	0	5
Pooled	46	46	10	13	21	10	16	19	10	4	15	8	2	8

$\chi^2 = 0.12$, d.f. = 1, $P = 0.92$) were apparent. We also analyzed our data by year and did not find any differences in any measured parameters between the two treatment groups ($P > 0.05$).

The growth rate of gerbil social groups was inversely correlated with group size (at the natural logarithmic scale) in control chambers (slope $\beta = -0.68$, $P < 0.01$, d.f. = 23) and in 2005 (slope $\beta = -0.65$, $P < 0.01$, d.f. = 29). Thus, the rate of change in the size of gerbil social groups decreased as the group size increased (i.e. density dependence). The average fresh plant biomass of control chambers was $53.4 \pm 7.1\,\mathrm{g\,m}^{-2}$ in 2004 and $51.7 \pm 7.0\,\mathrm{g\,m}^{-2}$ in 2005, whereas that of treatment chambers was $58.2 \pm 8.2\,\mathrm{g\,m}^{-2}$ in 2004 and $53.6 \pm 8.0\,\mathrm{g\,m}^{-2}$ in 2005. The average fresh plant biomass did not differ between control and treatment chambers either in 2004 ($t = 0.44$, d.f. = 6, $P = 0.67$) or in 2005 ($t = 0.19$, d.f. = 10, $P = 0.86$).

Discussion

During the breeding season, the social organization of Mongolian gerbils was similar between food-supplemented and -unsupplemented chambers. Group size did not differ between unfed and fed gerbils. Moreover, the similar demography of founders and new recruits between food-supplemented and -unsupplemented chambers suggested that food was not a major limiting factor influencing gerbil social organization in our enclosure during the breeding period. Likewise, the social group size of prairie voles *Microtus ochrogaster* in a natural population did not differ among the alfalfa, bluegrass and tall-grass prairies, which varied in food quantities and qualities (Getz, Gudermuth & Benson, 1992), or in food-supplemented and -unsupplemented enclosures (Cochran & Solomon, 2000).

Previous studies of supplemental food have reported mixed results. Supplemental food enhanced tolerance to conspecific individuals and consequently increased the social group size in prairie dogs *Cynomys ludovicianus* (Slobodchikoff, 1984). However, the social organization of prairie voles and meadow voles *Microtus pennsylvanicus* did not respond to supplemental food in experimental enclosures (Cochran & Solomon, 2000) or to changes in food availability and quality in natural habitats (Getz *et al.*, 2006). Supplemental food may alter the demography of rodents when food is limited. For example, the population of the yellow-necked mouse *Apodemus flavicollis*, the wood mouse *Apodemus sylvaticus*, the bank vole *Clethrionomys glareolus* and the prairie vole increased in abundance with supplemental food when food resources were scarce (Boutin, 1990; Solomon & Crist, 2008).

In our enclosures, fresh vegetation biomass averaged $55.9 \pm 5.1\,\mathrm{g\,m}^{-2}$ in 2004 and $52.7 \pm 5.1\,\mathrm{g\,m}^{-2}$ in 2005, about half of the average fresh plant biomass ($103\,\mathrm{g\,m}^{-2}$) in natural habitats (Ågren *et al.*, 1989*a*), but the average gerbil densities in our enclosures (458 gerbils ha^{-1} in 2004

Table 4 The cumulative number of recruits, the number of recruits that survived till the end of study and the cumulative number of sexually mature recruits of Mongolian gerbils *Meriones unguiculatus* in food-supplemented and -unsupplemented chambers during the breeding season of 2004 and 2005 in Taibusi Qi, Inner Mongolia, China

Treatments	Year	The number of sampled family groups	The cumulative number of recruits		The number of recruits that survived till the end of experiment		The cumulative number of sexually mature recruits		Age of mature (body weight, g)
			Male	Female	Male	Female	Male	Female	Male + female
Supplemented									
	2004	4	21	15	10	4	4	1	43.4 ± 2.0
	2005	6	21[R]	26	12	16	1	0	52.8
	Pooled	10	42[R]	41	22	20	5	1	45.8 ± 2.0
Unsupplemented									
	2004	4	10	10	4	3	2	1	41.9 ± 4.5
	2005	6	23	16	14	10	0	0	
	Pooled	10	33	26	18	13	2	1	41.9 ± 4.5

21[R] and 42[R] stand for one of 21 or 42 male recruits removed.

and 667 gerbils ha^{-1} in 2005) were five to seven times as high as the 93 animals ha^{-1} in natural habitats (Ågren et al., 1989a). Furthermore, the growth rate of gerbil social groups decreased with increasing group size in both food-unsupplemented and -supplemented chambers. Thus, the plants in the chambers probably did not provide the gerbils with sufficient food.

Population densities and numbers of suitable breeding sites or territories may also affect the social organization (Lott, 1984). In a saturated habitat, all suitable breeding sites or territories are occupied and dispersal may not be an option for sub-adult recruits (Wolff, 1994; Solomon & Getz, 1997; Cochran & Solomon, 2000; Ebensperger, 2001; Lucia et al. 2008). Aggressive behavior of territory owners toward conspecific intruders may form a 'social fence,' preventing juveniles and sub-adults from dispersal (Hestbeck, 1988). Mongolian gerbils are territorial during the breeding season (Ågren et al., 1989a,b). Gerbil population densities doubled in food-unsupplemented chambers in the first 6 weeks (Table 1). Fifty per cent of Mongolian gerbil juveniles in our experimental chambers remained at their natal sites and <20% of recruits reached sexual maturity by the end of our study. Juveniles that disappeared from their natal sites were not captured again in other colonies during our study; thus, they died either at their natal sites or during dispersal. Neither philopatry nor age at sexual maturity of young gerbils differed between fed and unfed gerbils (Table 4). This suggests that a social fence at high densities might deter juveniles from dispersal in each treatment. Moreover, the presence of parents or founders retarded sexual development of philopatric juveniles at their natal nests, as occurred in some laboratory studies (Payman & Swanson, 1980; Clark & Galef, 2001; Scheibler et al., 2004).

Group living may result from kinship (Hamilton, 1964a,b; Gompper, Gittleman & Wayne, 1998; Randall et al., 2005). In our studies, only two pairs of male and female adults were selected from a wild gerbil colony to initiate our experimental gerbil colonies; hence, the genetic relatedness of gerbil founders in our enclosures was likely lower than that of wild gerbil colonies. Comparable social organization of Mongolian gerbils between food-supplemented and -unsupplemented treatments might be due to the low genetic relatedness of the gerbils in the experimental chambers. Genetic relationships between group members need to be considered in future studies of the social organization of Mongolian gerbils.

Acknowledgments

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