

Home-range sizes of social groups of Mongolian gerbils *Meriones unguiculatus*

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ABSTRACT

Spacing behavior is important to the population regulation and social organization of rodents. However, little is known regarding the factors influencing space use by rodent social groups. We tested the hypotheses that food resources in the typical steppe would be so abundant that food availability would not be a limiting factor of home-range sizes of social groups of Mongolian gerbils (*Meriones unguiculatus*). We also assessed the effects of social organization on the home-range size of social groups of gerbils, using capture–recapture methods. Home ranges of social groups of Mongolian gerbils did not differ in size between the breeding and non-breeding periods; however, home ranges overlapped more during the breeding period than during the non-breeding period. Overlap of home ranges might allow male gerbils to access female mates of neighboring colonies during the breeding period. Home-range sizes of social groups were positively related to number of males during the breeding period, but positively related to group size and number of females during the non-breeding period. Therefore, social organization influenced home-range sizes of social groups. Our hypothesis that food availability is not a limiting factor of space use by social groups of Mongolian gerbils from spring through autumn was supported.

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1. Introduction

A suite of extrinsic factors (e.g., the availability of food and space, predation and habitat structure) and intrinsic factors (such as animal abundance and reproductive condition) influences animal space use and home-range size (Hayes et al., 2007 and references therein). Understanding the effects of ecological factors on space use of animals is critical to elucidating ecological mechanisms underlying the social organization of animals (Emlen and Oring, 1977; Hayes et al., 2007). Increased food availability is hypothesized to reduce home-range sizes needed to meet the food requirement of rodents and consequently reduce the space needed (Travis and Slobodchikoff, 1993). For instance, supplemental food reduces the home-range size of Arctic ground squirrels (*Spermophilus parryi*; Hubbs and Boonstra, 1998). However, the home-range size of *Octodon degus* is not related to food biomass (Hayes et al., 2007). Supplemental food does not affect social group sizes of Mongolian gerbils (*Meriones unguiculatus* Milne-Edwards, 1867)

during the breeding period (Liu et al., 2009a). Thus, we hypothesize that home-range size of social groups of Mongolian gerbils is not limited by food in a typical steppe where green plants are abundant and renewable during the growing season. However, few studies have tested the hypothesis.

Rodent spacing behavior may change seasonally as the reproductive condition of rodents and resource availability vary from season to season (Madison and McShea, 1987; Ostfeld, 1990). Rodents may expand home ranges during the breeding period to meet increased demands for energy and resources, but reduce home ranges during the non-breeding period (Hoset et al., 2008; Urayama, 1995). Home-range sizes of female pampas mice *Akodon azarae* are larger during the breeding period than during the non-breeding period (Bilenca and Kravetz, 1998). Social organization can also affect rodent space use (Branch, 1993; Burton and Krebs, 2003; Rayor, 1988) and demography (Blumstein and Armitage, 1998; McGuire et al., 2002). The size of the home range of a social group (combining the locations of all individuals living in a group) may vary with the size of the social group. For Mongolian gerbils, the home-range size of a social group is positively related to social group size and body mass of the largest male (Ågren et al. 1989a,b). The social organization of rodents can vary seasonally due to differences in reproductive activity between

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seasons. Although recent studies have improved our understanding of seasonal variation in the home-range size of solitary rodents (Bond and Wolff, 1999; Hoset et al., 2008; Ostfeld, 1990; Schradin and Pillay, 2006), few studies have investigated the factors influencing seasonal changes in the home-range size of rodent social groups.

The Mongolian gerbil (*M. unguiculatus*) is widely distributed in the dry and desert grasslands of the southeast Bakal area in Russia, Mongolia and northern China (Luo et al., 2000; Mallon, 1985). Mongolian gerbils live in social groups or burrow systems year-round. Group sizes vary from 2 to 18 animals (Ågren et al., 1989a; Liu et al., 2004, 2009b). Mongolian gerbils reproduce mainly during spring and summer. In late autumn, reproduction ceases and all members of a group hoard food for winter (Ågren et al., 1989b; Liu et al., 2001). *M. unguiculatus* is also a model species for studies of rodent social behavior conducted in a laboratory (Clark and Galef, 2000; Prates and Guerra, 2005) and under semi-natural conditions (Ågren, 1976; Roper and Polioudakis, 1977); however, under semi-natural conditions, studies of social behavior and spacing behavior are affected by limited space and restricted movement (Ågren, 1976; Roper and Polioudakis, 1977). Recent work has helped to elucidate the ecology and the population ecology of wild Mongolian gerbils (Ågren et al., 1989a,b; Liu et al., 2009b; Wang and Zhong, 2006; Xia et al., 1982). Ågren et al. (1989a) studied the spacing behavior of Mongolian gerbils during the breeding period and found that home-range size of social groups was related to group size. However, little is known regarding seasonal changes in the spacing behavior of Mongolian gerbils. The main objectives of this study were to: (1) test our hypothesis that the home-range size of Mongolian gerbils is limited by social organization (group size, the number of males, the number of females and body mass), but not by food availability in the typical steppe; and (2) investigate seasonal variation in the home-range size of gerbil social groups. We predicted that home-range size of social groups of gerbils is not related to the height and cover of food plants within their home ranges, but is correlated with the complexity of social groups, such as group sizes, numbers of males and numbers of females of a social group.

2. Methods

2.1. Study area

Our study was conducted at Xima Gou (village; 42°07'N, 115°22'E; the elevation of 1450 m), about 30 km north of Baochang, Taipusi Qi (county), Inner Mongolia, China. The area was situated in a typical region where steppes were intermixed with croplands. The climate was semiarid and continental with relatively hot summers and cold winters. Average monthly temperatures ranged from -19 to 21.1 °C. Mean annual total precipitation was about 350 mm, ranging from 258 to 550 mm; more than 70% of the total precipitation fell in June, July and August. Snow cover lasted for about 90 days, from mid- or late October to early April, with the average monthly depth of 50 mm (Liu et al., 2007). June, July and August were the warmest months, with average monthly temperatures from 16.0 to 18.0 °C, and average monthly temperatures ranged from -14.0 to -4.0 °C during the coldest period from November to the following March in 2006. The total precipitation was 415 mm in 2006. The soil of the area was sandy and loamy Chestnut soil (Scheibler et al., 2006).

Our study site was situated on a 9-ha grassland (300 × 300 m) surrounded by wheat (*Triticum* spp.) and cabbage (*Brassica* spp.) croplands. The vegetation was dominated by the grass *Leymus chinense* and the herb *Corispermum mongolicum* with a mixture of grasses such as *Cleistogenes squarrosa* and *Setaria viridis*, herbs

Artemisia sieversiana, *Artemisia scoparia* and *Heteropappus altaicus* and small shrubs *Caragana microphylla* and *Caragana korshinskii*. No livestock grazed on the study site during our study.

2.2. Trapping procedures

We established a 2-ha (200 × 100 m) trapping plot in the center of our 9-ha study site in early April of 2006. The trapping plot exhibited a higher density of gerbil burrows compared to the rest of our study site, encompassing 15 (65%) gerbil colonies at the beginning of our study. To enhance the probability of captures, we used a concentric circle trapping method (Liu et al., 2007). Trap stations were arranged in 3–4 concentric circles, with equal spacing, at each burrow system, which was adjusted based on the area occupied by a burrow system. The radius was about 1–2, 2–3, 4–5 and 6–8 m for the inner, second, third, and outer circle, respectively. The four trap circles had 4–6, 8–10, 12–14, and 15–16 trap stations, respectively, with an average distance of 1–2 m between trap stations. One wire-mesh live trap (28 × 13 × 10 cm) was placed at each station with the trap door opening facing a burrow entrance or gerbil runway to maximize the probability of capture (Liu et al., 2007). In the concentric trapping, traps were clustered only at burrow systems, with no traps placed between the two outer trap circles; therefore, we used a trap grid to supplement gerbil location data on space use between burrow systems. Between two concentric circle trapping periods, a 29 × 14 trap grid with a total of 406 trap stations, at 7-m spacing, was set within our trapping plot. Therefore, we combined data from our grid trapping and the concentric circle trapping to estimate home-range sizes of gerbil social groups. Each trapping period lasted for 3 consecutive days and we checked traps at the same times throughout the study.

Mongolian gerbils were live trapped from 28 April to 21 October in 2006 at a 2-week interval (Liu et al., 2009b). The gerbils remain active mainly under the snow during winter and move on the surface of the snow only on calm, sunny days (Wei Liu, personal observation). Therefore, we did not trap during winter to avoid trap mortality due to low temperatures. Traps were set at 0500 h–0600 h, and checked every 1–2 h until about 1100 h. Traps were closed from 1100 h to 1500 h to avoid trap mortality from heat stress; trapping was resumed at 1600 h and continued until 1900 h. In April, September and October, traps were set at 0630 h and 0730 h and monitored until 1730 h. Since Mongolian gerbils are diurnal, we did not trap during the night (Ågren et al., 1989a; Liu et al., 2007).

All captured gerbils were toe-clipped at the first capture for permanent identification (ID). We clipped only one toe per foot, removing one-half of a toe at the joint with a pair of sharp thin-bladed scissors; no more than three toes were removed from a gerbil. Captured gerbils were sexed and weighed to the nearest 0.1 g. Reproductive condition, trap location, and ID number were recorded for each capture. Males were considered in reproductive condition if they had scrotal testes and visible ventral scent glands with either clear contour or large, visible pores surrounded by secreted substance. Female gerbils were considered in reproductive condition if they had a bulging abdomen, enlarged nipples surrounded by white mammary tissue, or opened pubic symphysis (Liu et al., 2007; Payman and Swanson, 1980). Captured animals were immediately released at the same trap station of their capture. Our trapping and handling of Mongolian gerbils followed the guidelines of the Animal Care and Use Committee of the American Society of Mammalogists (Gannon and Sikes, 2007) and was approved by the Institutional Animal Use and Care Committee of the Institute of Zoology, the Chinese Academy of Sciences.

2.3. Vegetation analysis

The vegetation around each burrow system was sampled once in a month to assess the influence of plant availability on home-range sizes. Three 1 × 1 m quadrats were placed on each of the middle (the second or third circle) and outer trap circles (six quadrats in total) at each burrow system. Plants within a quadrat were classified into four groups, *Salsola* spp., *Artemisia* spp., monocots and other dicots. We measured heights of 10 randomly chosen individuals for each plant group within a quadrat and ocularly estimated the coverage of each plant group within a quadrat to the nearest 1%. The average coverage and average height of each plant group and the total vegetation at each gerbil burrow system were calculated over six quadrats. No plant was clipped during the survey. We used average plant height and average coverage as the indices of the availability of food plants within a gerbil home range. Vegetation in a gerbil home range was usually low and sparse and unlikely to provide overhead protective cover.

2.4. Size and composition of social groups

A social group was composed of individuals that were caught using the same burrow system at least twice a week for two successive trapping weeks (Getz et al. 1993). Social group sizes were estimated for each sampling week using the minimum number of animals known to be alive method (MNA; Krebs, 1999). Gerbils were considered juveniles if body mass was ≤30 g (Liu et al., 2007).

2.5. Home range analysis

We only included data on social groups of two more gerbils in our statistical analysis. Home-range size of a social group was estimated by the 95% minimum convex polygon (MCP) method (Mohr, 1947) with the software Biotas (Ecological Software Solutions, 2000). The coordinates of each trap station on a trap circle were determined to the nearest 0.1 m using the 29 × 14 trap grid as the reference. We calculated the size of a composite home range by combining the capture locations of all individuals of a social group over three consecutive trapping weeks (two circle trapping weeks and one grid trapping week in between) or a month (Branch, 1993). Number of locations used to estimate group home-range size averaged 30.8 (±2.7 SE) in summer and 40.2 (±12.3 SE) in autumn. Mean overlap of composite home ranges between two social groups was calculated using an index that varies between 0 and 100, with 100 indicating complete overlap (Minta, 1992),

$$\text{Mean overlap} = \frac{\text{HROverlap} \times 100}{\sqrt{\text{HR}(A) \times \text{HR}(B)}} \quad (1)$$

where HROverlap is overlap of two home ranges A and B, HR(A) is the size of home range A, and HR(B) is the size of home range B. Based on the reproductive condition and food hoarding behavior of gerbils, data were divided into two periods: the breeding period (from April to August) and the non-breeding period (from September to October).

We used stepwise multiple linear regression to determine relationships among home-range size, vegetation and social organization of gerbils. To avoid multicollinearity among explanatory variables, we carried out Spearman's correlation analyses to detect highly correlated explanatory variables. We used only one variable from a group of correlated variables in our full linear regression, which included all uncorrelated explanatory variables. The coverage of the total vegetation was highly positively correlated with the coverage of *Salsola* spp., *Artemisia* spp., other dicots and

monocot, respectively, with the Spearman correlation coefficient ranging from 0.44 to 0.89 ($p < 0.05$). The height of the total vegetation also was highly positively correlated with the height of the four plant groups, respectively ($p < 0.05$). We used the coverage and height of the total vegetation in our full regression models as total vegetation coverage and height represented the availability of all plant groups, including *Salsola* spp. and *Artemisia* spp., due to the positive correlation. Additionally, social group size was positively correlated with the number of the males and the number of females of a social group, respectively, with the Spearman correlation coefficient ranging from 0.54 to 0.92 ($p < 0.05$). Male gerbils were more mobile than female gerbils; thus, we predict the more the males, the greater the home range. Therefore, we included number of males in the full model.

We used linear mixed models with group identification (ID) number as a random-effect factor to account for temporal autocorrelation in the response variable, i.e., home-range size (Faraway, 2006). We determined the optimal structure of random-effect components following a top-down approach suggested by Diggle et al. (2002). We ran a full mixed model that included all uncorrelated fixed-effect variables and the random factor, using restricted maximum likelihood (REML) methods. We compared the full mixed model with its linear regression counterpart, which included the same set of fixed-effect variables but the random-effect variable, using log-likelihood ratio test at the significance level of 0.05 (Zuur et al., 2007). If the mixed model was insignificant ($p > 0.05$), we carried out stepwise multiple linear regressions using a two-step variable selection approach. First, we removed all insignificant variables ($p > 0.05$) from the full model in a stepwise manner until all remainders were significant ($p < 0.05$). Second, if a variable was removed from the final model of the first step, we added each of the variables, which was correlated with the removed variable and were not initially included in the full model, to the final model of the first step (only one at a time). We then tested for the significance of the variable at the significance level of 0.05. In doing so, we avoided any model mis-specification of fixed-effect variables of vegetation and social organization due to our initial variable selection for the full model. We ran mixed linear models and linear regressions using the R software (R Development Core Team, 2006) and function lme() within the package nlme (Pinheiro et al., 2009). We used analysis of covariance (ANCOVA) to test for the difference in average home-range sizes of social groups between the two periods with group size as a covariate, using the SPSS software (SPSS, 2004). We tested the normality assumption for home-range sizes of social groups using the Kolmogorov–Smirnov test. Home-range sizes of social groups were not distributed normally during the breeding period ($p = 0.04$, $n = 46$). Therefore, we log transformed home-range sizes to normalize data on home-range sizes. Means were reported as mean ± SE (standard error).

3. Results

3.1. Seasonal variation in home-range sizes of social groups

A total of 205 gerbils were captured in the 2-ha site from 28 April to 21 October 2006. We treated all gerbils that were captured at the same burrow system four or more times during a month as a social group. There were 15 active burrow systems within our trapping plot at the beginning of the breeding period. Gerbils suffered high mortality during the breeding period; 10 burrow systems became unoccupied by gerbils due to mortality, emigration and (or) local extinction during the breeding period. Therefore, there were five active burrow systems left during the non-breeding period. We captured 42 social groups with two or more gerbils

during the 4-month breeding period, with some burrow systems locally extinct during the breeding period. Additionally, one burrow system in June and three in July were occupied by a solitary gerbil. There were nine social groups with two or more gerbils during the non-breeding period. Average monthly home-range sizes of social groups were $309.10 \pm 50.97 \text{ m}^2$ ($n = 42$) during the breeding period and $262.5 \pm 103.6 \text{ m}^2$ ($n = 9$) during the non-breeding period. According to ANCOVA with group size as a covariate, home-range size of social groups did not differ between breeding and non-breeding periods ($F_{1,48} = 0.41$, $p = 0.84$).

During the breeding period, home ranges of nine social groups overlapped only with that of one social group, three social groups overlapped with two social groups, and one social group overlapped with three social groups. Overlap averaged $5.67 \pm 1.85\%$ and ranged from 0.04% to 17.17%. Mongolian gerbils often visited neighboring burrow systems during the breeding period. However, home ranges of the nine social groups during the non-breeding period were spatially separated from each other.

3.2. Mixed models and linear regressions

Our full mixed model was insignificant, compared to its linear regression counterpart ($\chi^2 = 0.018$, $df = 1$, $p = 0.9$). Residuals of the full linear regression were homogenous over time, suggesting that ordinary linear regression was sufficient. Therefore, we used step-wise multiple linear regression to determine the influence of vegetation and social structure on home-range size. Our final model included the number of males of a social group as the only significant variable at the step-1 model selection for the breeding period; no other variable was selected at the significance level of 0.05 at the step-2 model selection for the breeding period. The final model for the non-breeding period included only an intercept at the step-1 model selection. At the step-2 model selection, the number of females and social group size were selected by two different models, respectively, as the only explanatory variable. However, no model of more than one explanatory variable was significant ($p > 0.05$), probably due to small sample size ($n = 9$).

3.3. Home ranges and vegetation

Our final linear model did not include any vegetation variable for either the breeding or the non-breeding period. Although *Salsola* spp. and *Artemisia* spp. were two species of preferred food plants of Mongolian gerbils and common within the home ranges of gerbil social groups, home-range size of social groups was not correlated with either the coverage or the height of *Salsola* spp. (coverage: $\chi^2 = 0.001$, $df = 1$, $p = 0.93$; height: $\chi^2 = 0.0$, $df = 1$, $p = 1.0$) and *Artemisia* spp. (coverage: $\chi^2 = 0.03$, $df = 1$, $p = 0.67$; height: $\chi^2 = 0.13$, $df = 1$, $p = 0.39$) during the breeding period. Likewise, home-range size of social groups was not correlated with either the coverage or the height of *Salsola* spp. (coverage: $\chi^2 = 0.4$, $df = 1$, $p = 0.09$; height: $\chi^2 = 0.03$, $df = 1$, $p = 0.9$) and *Artemisia* spp. (coverage: $\chi^2 = 0.12$, $df = 1$, $p = 0.42$; height: $\chi^2 = 0.05$, $df = 1$, $p = 0.61$) during the non-breeding period.

3.4. Home-range size, social group size, and body mass of gerbils

3.4.1. Group size

Most marked individuals were present on our site for less than two months; thus, we reported monthly social group sizes of Mongolian gerbils. Group sizes averaged 6.9 ± 0.64 gerbils ($n = 42$ social groups), varying from 2 to 17 individuals, during the breeding period and averaged 6.3 ± 1.4 gerbils ($n = 9$ social groups), ranging from 2 to 14 individuals, during the non-breeding period. Group size was not related to either the coverage ($t = -1.08$, $p = 0.09$) or

height ($t = 0.98$, $p = 0.34$) of the total vegetation during the breeding season. Home-range size of social groups was correlated with group size during the non-breeding period ($R^2 = 0.52$, $t = 2.71$, $p = 0.03$; Fig. 1).

3.4.2. Numbers of males and females

There was a significantly positive correlation between home-range size of social groups and number of males during the breeding period (Fig. 2a, $R^2 = 0.14$, $t = 2.40$, $p = 0.02$), whereas during the non-breeding period, home-range size was positively correlated with the number of resident females (Fig. 2b, $R^2 = 0.56$, $t = 2.96$, $p = 0.02$).

3.4.3. Body mass

Home-range size of a social group was not correlated either with body mass of the largest males of a social group (breeding period: $t = 0.38$, $p = 0.71$; non-breeding period: $t = -1.33$, $p = 0.41$) or with body mass of the largest female (breeding period: $t = -0.55$, $p = 0.58$; non-breeding period: $t = 0.29$, $p = 0.82$).

4. Discussion

The availability, distribution and quality of food, shelter, mates and other resources vary seasonally in a seasonal environment (Forman, 1995). Animals may use physiological and behavioral means to cope with seasonal environmental changes. However, home-range size of social groups of gerbils did not differ between the breeding and non-breeding periods and was not correlated with food plant abundance. Food availability and defense against intruders have been recognized as the primary benefits and costs of maintaining a territory (Fryxell and Lundberg, 1998; Ostfeld, 1985; Schoener, 1983). To be cost-effective, a territory must be large enough to ensure an adequate food supply for the survival and reproduction of resident organisms, but small enough to allow for effective defense against intruders. The home ranges of arctic ground squirrels (*S. parryii*) were 7–8 times smaller on a food-supplemented grid compared to an unsupplemented grid (Hubbs and Boonstra, 1998). Mongolian gerbils mainly feed on the foliage of *Artemisia sieversiana*, *Salsola* spp., *Setaria viridis* and *Leymus chinense* (Ågren et al., 1989a), which were abundant at our study site, during the breeding period and eat plant seeds during autumn (Wang and Zhong, 1998). Home-range size of social groups was not correlated with either height or cover of plants, but was correlated with social group size during non-breeding periods, number of males during the breeding period and number of females during the non-breeding period. Liu et al. (2009a) did not find food to be

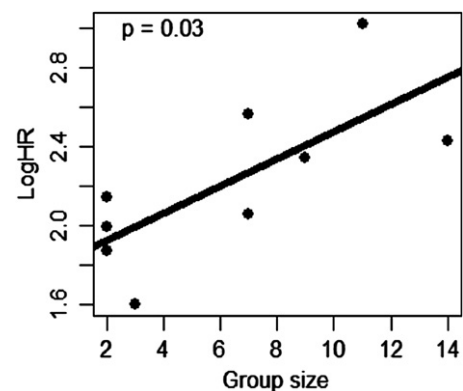


Fig. 1. Relationships between the home-range size of social groups and social group size of wild Mongolian gerbils (*Meriones unguiculatus*) during non-breeding period in Inner Mongolia, China.

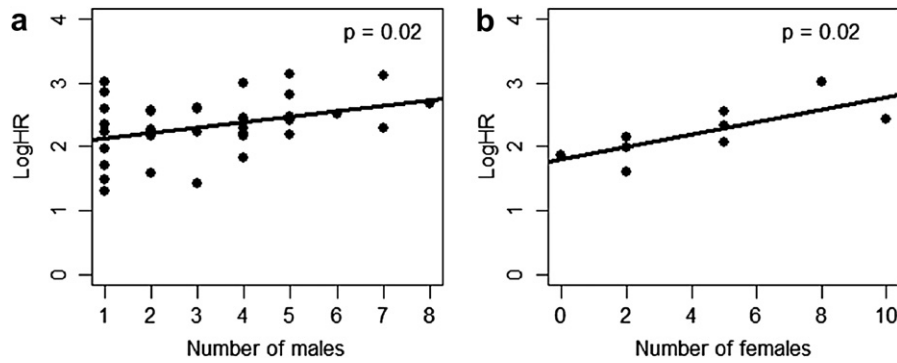


Fig. 2. Relationships (a) between the home-range size of social groups of Mongolian gerbils (*M. unguiculatus*) and number of males of a social group during the breeding period and (b) between the home-range size of social groups and number of females of a social group during the non-breeding period in Inner Mongolia, China.

a limiting factor of the social organization of Mongolian gerbils during the breeding period. Additionally, abundance of food plants was not a predictor of home-range sizes of *O. degus* (Hayes et al., 2007). Therefore, food availability is unlikely to limit home-range sizes of social groups of Mongolian gerbils.

Size and composition of social groups are important factors influencing home-range sizes of rodent social groups. Home-range sizes of social groups of gerbils were positively related to numbers of group members (Ågren et al., 1989a; Fig. 1, this study). A larger social group requires more food resources to support group members (Batzli and Henttonen, 1993). In addition, home-range size of a social group of Mongolian gerbil increased with the increased number of males in the social group during the breeding period (Fig. 2a). Male gerbils are the primary defenders of a territory and aggressively chase male intruders (Ågren et al., 1989a). More male gerbils in a social group allow for the cooperative defense of a larger territory during breeding periods. However, home-range sizes of social groups increase with increased numbers of females during the non-breeding period (Fig. 2b). Home ranges are likely to increase with more females because additional resources are necessary to support more females and their offspring. Female reproductive success is highly dependent on body condition and converting resources to offspring. For these females to survive and reproduce the following year, they likely need to be in good condition in the autumn and procure large food caches for the coming winter.

Home ranges of social groups of Mongolian gerbils overlap more during the breeding period than during the non-breeding period. We observed that male Mongolian gerbils visited neighboring burrow systems during the breeding period. Ågren et al. (1989a) found that female gerbils entered neighboring burrow systems to mate with extra-pair males. However, Mongolian gerbils may become more resource territorial and reduce overlap of home ranges during autumn when storing food. Alternatively, Mongolian gerbil densities declined from spring to autumn during our study (Liu et al., 2009b). Home ranges did not overlap at low densities. Our study demonstrated that home-range size of a social group of Mongolian gerbils is related to social organization. However, the cause–effect relationship between the social organization and spatial use of Mongolian gerbils is unknown. We are not certain whether social organization determines spacing behavior or spacing behavior underlies the social organization of Mongolian gerbils. The current study had only one year of data on the home range of gerbil social groups, providing the preliminary results of seasonal variation in home-range size of Mongolian gerbils. Long-term studies are needed to better understand seasonal variation in the spacing behavior of Mongolian gerbils in the future.

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