

Winter food availability limits winter survival of Mongolian gerbils (*Meriones unguiculatus*)

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Abstract Food availability is important to the dynamics of animal social organizations or populations. However, the role of winter food availability in animal population dynamics is still controversial. We carried out an experimental study to test Lack's hypothesis that reduced food in winter limits survival and spring numbers of breeding individuals of social groups, using the Mongolian gerbil (*Meriones unguiculatus*) as model species. We established 24 gerbil social groups in 24, 10×10 m, pens in September 2008. We provided wheat seeds as supplemental food in 12 enclosures from September 2008 to March 2009; the other 12 enclosures, not provided with supplemental food, served as controls. We live-trapped gerbils at a 2-week interval from September to April. Supplemental food during winter increased biweekly survival by 10% relative to that in control groups. Only four control social groups survived to the end of our study whereas all 12 food-supplemented social groups survived through our study period. Supple-

mental food also increased cumulative numbers of recruits and group sizes of gerbils. We conclude that winter food availability limits winter survival and spring social groups or population sizes of Mongolian gerbils.

Keywords Demography · Food limitation · MARK · Rodents · Social groups · Supplemental food

Introduction

Food availability can influence the physiology, behavior, life history, and abundance of terrestrial vertebrates (Boutin 1990). Initial hypotheses on influences of food limitation were put forth for altricial birds, whereby clutch size and reproductive success would be adjusted to quantity of food available to parents (Lack 1947, 1954). Experiments that provide supplemental food to rodents also have been used to test Lack's food limitation hypothesis. Experiments were based on the premise that food supplementation would increase rodent population sizes if food was limited (Boutin 1990). Studies have shown that supplemental food can advance the breeding season (Andrzejewski 1975; Taitt and Krebs 1981), reduce age of the first reproduction (Hansen and Batzli 1979; Taitt 1981), increase proportions of reproducing females (Flowerdew 1972; Andrzejewski 1975), improve reproductive success, and affect home range sizes in rodents (Koskela et al. 1998; Jonsson et al. 2002). Thus, supplemental food can substantially influence individual life histories in rodents as well as the demography of populations.

Supplemental food can increase early summer densities of rodents by attracting immigrants to food-supplemented areas (Hansen and Batzli 1979). Food addition increases population densities of cotton rats (*Sigmodon hispidus*)

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through the enhancement of recruitment and reproduction, but does not improve survival (Doonan and Slade 1995). Likewise, supplemental food during winter increases population densities of Azara's grass mice (*Akodon azarae*) with increased numbers of immigrants and increased proportions of breeding females (Cittadino et al. 1994). Nevertheless, supplemental food does not improve survival and recruitment of mice and voles under growing season conditions (i.e., summer; Flowerdew 1972; Hansen and Batzli 1979; Liu et al. 2009). In about 60% of the studies of rodents reviewed by Boutin (1990), survival remained unchanged by supplemental food. Despite some inconsistencies, supplemental food can increase rodent population densities through increases in immigration and reproduction. Here, we investigate influences of food availability on overwinter survival and spring densities of Mongolian gerbils (*Meriones unguiculatus* Milne-Edwards, 1867).

Studies have provided supplemental food during summer or the breeding season; however, few studies detected increases in the summer survival of rodents (Boutin 1990; Doonan and Slade 1995; Liu et al. 2009). Often, rodents used in experiments are either herbivores (voles) or omnivores (rats, mice, and gerbils). When natural foods plants are renewable (i.e., breeding season plant growth and seed dispersal), supplemental food may not improve survival and reproduction of rodents (Boutin 1990; Liu et al. 2009). Conversely, Lack (1954) hypothesized that winter food availability would limit winter survival of birds and densities of breeding birds the following spring. Thus, increased food availability during winter would result in higher breeding bird densities the following spring. Despite numerous studies of the effects of supplemental food on the reproductive performance and recruitment of rodents, there are few studies of demographic effects of food supplementation during winter in northern temperate rodents (Ylonen and Eccard 2004).

Additionally, many previous studies also suffer from small sample sizes (or replicates of experimental units). Most of the studies did not control competitors and predators and allowed rodents to freely move in and out of study sites; thus, rodents on the food-unsupplemented sites might have access to food resources outside the study sites. In our study, we used 12, each, social groups of Mongolian gerbils as experimental units for control and treatment. Each social group was placed in an enclosure protected from both mammalian and avian predators.

The Mongolian gerbil is a social rodent widely distributed in the Mongolian Plateau (Liu et al. 2007). Gerbils live in social groups and are active over winter. Gerbils cache food, mainly annual herbs and seeds, during autumn for winter. Gerbils are easily live-trapped with a capture probability of about 90% (Liu et al. 2009). Their docility and unique social behavior make the gerbil a suitable model species for

behavioral and population studies (Thiessen and Yahr 1977; Liu et al. 2007). Our main objective was to test Lack's hypothesis that winter food limits overwinter survival and further limits numbers of breeding individuals in social groups in spring. We predicted that supplemental food would enhance overwinter survival and increase numbers of breeding gerbils the following spring; therefore, winter supplemental food would attenuate the winter decline of group sizes and population densities of Mongolian gerbils.

Materials and methods

Study area

Our study was conducted during autumn and winter from mid-September of 2008 to early April of 2009 at the Taipusi Qi Field Research Station (E 115°17'–N 41°58', 1,500-m elevation), about 8 km north of Baochang in Inner Mongolia, China. The area is in a region where grasslands are intermixed with croplands. The climate was semi-arid, with a relatively hot summer (June to August) and a cold, dry winter (November to February). Average annual precipitation was about 350 mm. Average monthly temperatures ranged from –19.1°C to 21.1°C. Snow fell from October to April the following year. Annual average number of snow days was 90 days, and monthly average snow depth was 50 mm. The frozen soil layer was about 150–200 cm deep during winter. During our study period, monthly average temperatures ranged from –16.7°C in January 2009 to 12.0°C in September 2008 and averaged –3.4°C. Snow fell in 83 days, and monthly average snow depth was 34.2 mm. Vegetation was composed primarily of grasses and herbs such as *Potentilla* spp., *Heteropapus altaicus*, and *Serratula centauroides*. The dominant plant was *Leymus chinense*. Plant growth began in early May and ended in early September. Therefore, plants on our site were dormant with the aboveground parts senesced during our study period.

Experimental design

We conducted our supplemental food experiments in two 20×60-m enclosures, each of which consisted of 12 sub-enclosures (10×10 m each). The outer enclosure and sub-enclosures were constructed of cement walls approximately 100 cm above and 100 cm below the ground to prevent either the escape of the gerbils or the entry of other burrowing rodents. Holes in the wall at the ground level that connected two neighboring chambers were plugged during our experiment to prevent the gerbils from moving between the chambers (Liu et al. 2009). The top of the enclosure was covered with nylon netting to prevent avian predation (e.g., *Bubo bubo*).

A gerbil family group occupying a chamber comprised an experimental unit. Two weeks prior to our treatment, we live-trapped and removed all gerbils from our enclosures. We then captured wild Mongolian gerbils from 32 gerbil burrow systems in a fallow field in Hou-Wa-Yao Gacha (village) near our study site. We randomly selected three male and three female gerbils weighing 40–65 g from a wild gerbil social group and released the six selected gerbils into a chamber as founders to establish experimental populations in early September. No more than two siblings from a social group were selected for each chamber. Six gerbils per chamber are close to the average number of seven gerbils per burrow system in the field. All founders were toe-clipped for individual identification. Two weeks after release, social groups were formed by 117 surviving gerbils (58 males and 59 females) in all 24 chambers with an average of 4.9 ± 0.3 gerbils per group. We randomly chose one half (12) 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).

In the end of August 2008, we randomly placed two 1×1 -m quadrants in each chamber and cut all plants within a sampling quadrant at the ground level. Plants were weighed to the nearest 0.1 g to determine fresh biomass (grams per square meter). We compared average standing plant biomass in the end of August between the two treatments using *t* tests. Average standing fresh plant biomass did not differ between control and treatment chambers at the beginning of our study (fed chambers, 458.9 ± 21.9 g/m², unfed chambers, 445.6 ± 22.6 g/m²; $t=0.42$, $df=46$, $P=0.67$). The fresh plant biomass was 6.2–139.5 g/m² in the wild habitat of gerbils (Ågren et al. 1989). The average home range size of social groups of Mongolian gerbils is 262.5 ± 103.6 m² during autumn (Wang et al. 2010). However, a core area of a gerbil burrow system, which encompasses more than 80% of the total burrow entrance of the burrow system, is 4.1 m² on average (Hsia and Wang 1956). Therefore, an experimental chamber met the minimum requirement of space for a gerbil social group, relative to those in the natural habitat of gerbils.

Supplemental food was provided in the middle of each month from September 2008 to mid-March 2009. A bundle of wheat stems with heads was placed at the center of each food supplemental chamber. Each bundle of wheat plants weighed 8 kg and contained 3.7 ± 0.2 kg ($n=10$) of wheat seeds on average. Provision of wheat grains triggered group-hoarding behavior of gerbils. Gerbils removed and carried all seeds to the underground food storage chambers of their burrow systems within 2–3 days after placement. The average daily food consumption of Mongolian gerbils is about 5.5 g of wheat grains per adult (Hsia & Wang, 1956); hence, we provided 26 kg of wheat seeds in each

food-supplemented chamber and were sufficient for about 30 gerbils over a 5-month period. Meanwhile, we placed a bundle of wheat stems without heads at the center of each food-unsupplemented chamber. Wheat stems were removed from the food-supplemented and -unsupplemented chambers after all seeds were removed by the gerbils.

Monitoring gerbil populations and family groups

We used live-trapping to determine the size and composition of gerbil social groups from mid-September 2008 through the early April 2009. One or two wire-mesh live traps ($28 \times 13 \times 10$ cm) were placed at each burrow entrance of a gerbil colony (Liu et al. 2007). We trapped gerbils for five consecutive days in the first trapping session in mid-September to capture and mark as many gerbils as possible and then trapped gerbils for three consecutive days at a 2-week interval. Traps were baited with peanuts, set at 0800–0900 hours, checked every 1–2 h in March, April, September, and October and every 0.5 h from November to February the following year, and closed at about 1600 hours. Gerbils rarely ate peanut baits when captured; thus, peanut baits were not considered a substantial supplemental food. Gerbils are diurnal and were active during our trapping hours (Liu et al. 2007).

All unmarked gerbils were individually toe-clipped for permanent identification at their release. 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 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 (Liu et al. 2007). Females were considered in reproductive condition if they had a bulging abdomen, enlarged nipples surrounded by white mammary tissue, or opened pelvic symphyses. Recruits were defined as newly marked animals that were captured after the initial population was marked in the first trapping session in mid-September. Gerbils under 30 g were considered juveniles. We used the minimum number known-alive method (Krebs 1999) to estimate group sizes for each trapping session. We also used data on reproductive condition and identification from our trapping to confirm the residence of individual gerbils in a colony.

Data analysis

Each chamber was an independent replicate in our study. We used repeated-measures analysis of variance (ANOVA) to test for differences in group sizes and proportions of females in a colony over time (trapping sessions) and between food-supplemented and -unsupplemented groups. We used arcsine transformations to normalize proportions

of females. We used the analysis of covariance (ANCOVA) with group size at the beginning of the experiment as a covariate to test for differences in cumulative recruitment (males and females combined) per family group from September through April between food-supplemented and -unsupplemented groups. Proportions of gerbil social groups surviving till the end of our experiment and sex-specific, cumulative proportions of recruits that reached sexual maturity were compared between the two treatment groups using Fisher's exact tests.

We used the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) within the program MARK (White and Burnham 1999) to estimate biweekly, apparent survival probabilities of Mongolian gerbils. We first tested for differences in the probability of apparent survival and probabilities of capture between the sexes, including sex as a group variable. We built 16 different candidate models, which included all possible combinations of time, sex, and sex \times time interaction. We used Akaike information criterion (AIC) or quasi-AIC (when the over-dispersion was present) to select the most parsimonious models from the 16 candidate models (Burnham and Anderson 2002). The best approximating model had the lowest AIC value. The Δ AIC value of a model was computed as the AIC difference between the model and the most parsimonious model, and a model of Δ AIC < 4 was counted as a competing model (Burnham and Anderson 2002). We did not detect significant effects of sex on the survival and capture probabilities; thus, the sex effect was not included in any further CJS models. To test for effects of supplemental food on apparent survival, we used a group variable (F) for the food-supplemented and -unsupplemented treatments and included main effects of time (t) and food (F), and time–food interactions ($t \times F$) in our models for the probabilities of apparent survival and capture, respectively. The CJS models were implemented using the design matrix in MARK (White and Burnham 1999; Burnham and Anderson 2002). We used the median c -hat to assess the goodness-of-fit and used the variance inflation factor (median c -hat) estimated from MARK to correct for the over-dispersion in the data prior to model selection (White and Burnham 1999). If food (F) was included in the best model or competing models, we concluded that supplemental food significantly influenced gerbil survival.

Results

All 12 food-supplemented social groups survived through our experiment whereas only four food-unsupplemented groups survived till the end of our experiments (Fisher's exact test, $P=0.001$). Sizes of social groups changed over

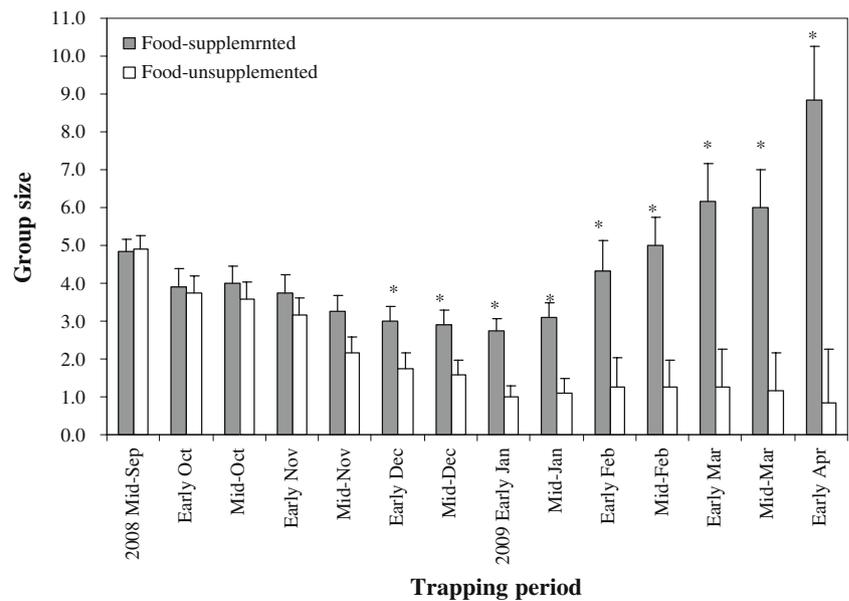
time ($F_{13, 286}=5.55$, $P<0.001$) and differed between the two treatments ($F_{1, 22}=15.92$, $P=0.001$, Fig 1, Appendix 1). At the beginning of the experiments, social group sizes did not differ between the treatments ($t=0.17$, $df=22$, $P=0.864$, Fig. 1), but differed by the end of the experiment (t test, $t=3.96$, $df=22$, $P=0.001$); average group sizes of food-supplemented and food-unsupplemented groups were 8.8 ± 2.0 and 0.8 ± 0.5 , respectively. Proportion of females did not change over time ($F_{13, 182}=0.83$, $P=0.63$) or between the two treatments ($F_{1,14}=0.005$, $P=0.94$, Fig. 2, Appendix 2). The cumulative number of recruits over our experiment period was 99 individuals in the food-supplemented treatment and only 12 individuals in the food-unsupplemented treatment. Recruitment per family group differed between food-supplemented and food-unsupplemented groups (fed treatment, 8.3 ± 1.6 gerbils per colony; unfed treatment, 1.0 ± 0.6 gerbils per colony; ANCOVA, $F_{1, 21}=20.61$, $P<0.001$). By the end of the experiment, eight male recruits reached sexual maturity in the food-supplemented chambers, whereas none of male recruits were sexually mature in the food-unsupplemented chambers (Fisher's exact test, $P=0.593$). No female recruits had the signs of sexual maturity in either food-supplemented or food-unsupplemented chambers.

The median c -hat of our saturated models with the time effects on both survival and capture probability is 1.36, indicating over-dispersion in our capture–recapture data; thus, we used quasi-AIC to select the most parsimonious model and competing models. Only top six competing models had Δ quasi-AIC < 7 (Table 1), and the remaining ten models had Δ quasi-AIC > 7 (not presented here). Our most parsimonious model of the lowest quasi-AIC value included the effect of supplemental food on survival of the gerbil (Table 1). Survival (model average values) of gerbils in food-supplemented chambers was greater than in food-unsupplemented chambers throughout the experiment (Fig. 3). In addition, our best approximating CJS model (of the lowest QAICc value) suggested that the probability of capture varied over time, averaged 0.800 ± 0.035 (SE), ranging from 0.569 to 0.972

Discussion

Our results support Lack's hypothesis regarding the effects of winter food availability on winter survival and spring densities of animals. Social group sizes were greater in food-supplemented chambers than in food-unsupplemented chambers in the spring 2009. Thus, a greater number of gerbils survived winter and were available to reproduce in food-supplemented chambers than in food-unsupplemented chambers (Fig. 1). Enhancements of group sizes by supplemental food were partially from improved winter survival; on

Fig. 1 Social group sizes of Mongolian gerbils, *Meriones unguiculatus*, in food-supplemented and -unsupplemented chambers from mid-September of 2008 to early April of 2009 in Taibusi Qi, Inner Mongolia, China. Vertical lines represent one standard error



average, supplemental food enhanced winter survival by 0.1 relative to survival probabilities in food-unsupplemented chambers (Fig. 3). Furthermore, supplemental food increased reproductive activities and recruitment during winter. Average group sizes increased in food-supplemented chambers from mid-winter to early spring, but group sizes declined in food-unsupplemented chambers (Fig. 1). Our enclosures prevented gerbil immigration into experimental chambers; thus, increases in group sizes in mid-winter indicate that gerbils reproduced during winter with supplemental food. Cumulative recruits of food-supplemented chambers were four times greater than those in food-unsupplemented chambers. Mongolian gerbils extend the breeding season into winter with supplemental food, indicating that food was a limiting factor to population growth.

Seasonality increases from low to high latitudes and influences life history traits (Boyce 1979; Tkadlec 2000). Green plants are sparse or absent during winter in northern latitudes. However, no agreement on effects of winter food supplementation on winter survival of mammals has been reached among previous studies (Boutin 1990). In only seven of the 16 studies reviewed by Boutin (1990), survival of mammals was improved by food supplementation during winter. Supplemental food was not found to improve winter survival of bank voles (*Clethrionomys glareolus*; Ylonen and Eccard 2004). Among many other reasons, Boutin (1990) listed several problems of previous winter supplemental food studies, including lack of sufficient replications. Immigrants and predators attracted by supplemental food may confound the effects of supplement food on winter survival of

Fig. 2 Proportions of female Mongolian gerbils, *Meriones unguiculatus*, in social groups in food-supplemented and -unsupplemented chambers from mid-September of 2008 to early April of 2009 in Taibusi Qi, Inner Mongolia, China. Vertical lines represent one standard error

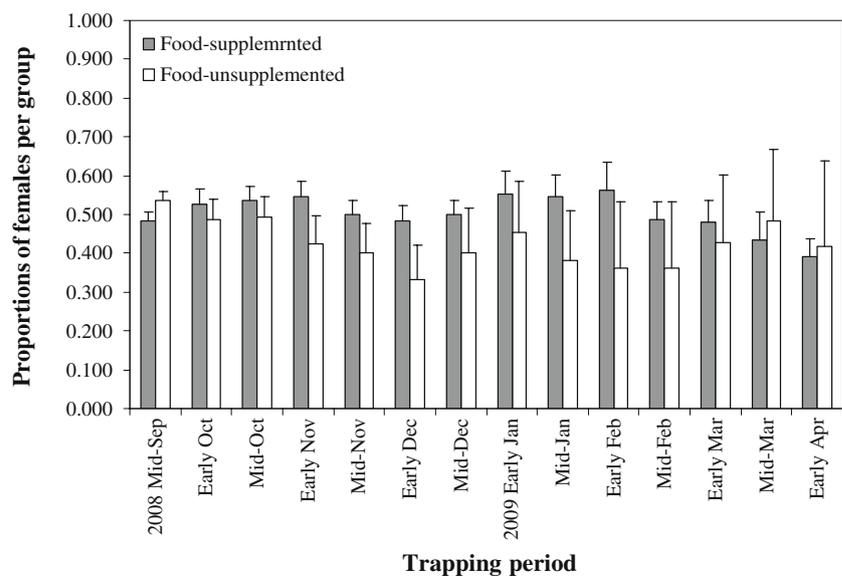


Table 1 Model selection of the Cormack–Jolly–Seber models for biweekly apparent survival probabilities of Mongolian gerbils, *Meriones unguiculatus*, in food-supplemented and -unsupplemented

Model	QAICc	Delta QAICc	QAICc weights	Model likelihood	Number of parameters	Q deviance
$\{\Phi(F) p(t)\}$	946.270	0.000	0.478	1.000	15	333.278
$\{\Phi(F) p(F \times t)\}$	948.409	2.140	0.164	0.343	27	310.142
$\{\Phi(t) p(F \times t)\}$	948.832	2.560	0.133	0.278	35	293.298
$\{\Phi(F \times t) p(t)\}$	949.129	2.860	0.114	0.239	34	295.773
$\{\Phi(F \times t) p(F \times t)\}$	949.660	3.390	0.088	0.184	43	276.513
$\{\Phi(t) p(t)\}$	952.439	6.170	0.022	0.046	25	318.437

Symbol ϕ (Φ) denotes the estimate of apparent survival, p the estimate of trapping probability, t time effects, and F food effects, and $t \times F$ time–food interaction, respectively. *Dot* (.) denotes constant survival. Deviance is two times negative log-likelihood value of a model. Quasi-AIC (QAICc) is Akaike's information criterion corrected for small sample size and over-dispersion ($\hat{c}=1.36$)

mammals. Unlike previous studies, we used 12 replicates for each treatment and protected gerbils in the experimental chambers from avian and mammalian predators. No burrowing animals could move in or out of our experimental chambers. Therefore, our results indicate that winter food availability limits overwinter survival of Mongolian gerbils.

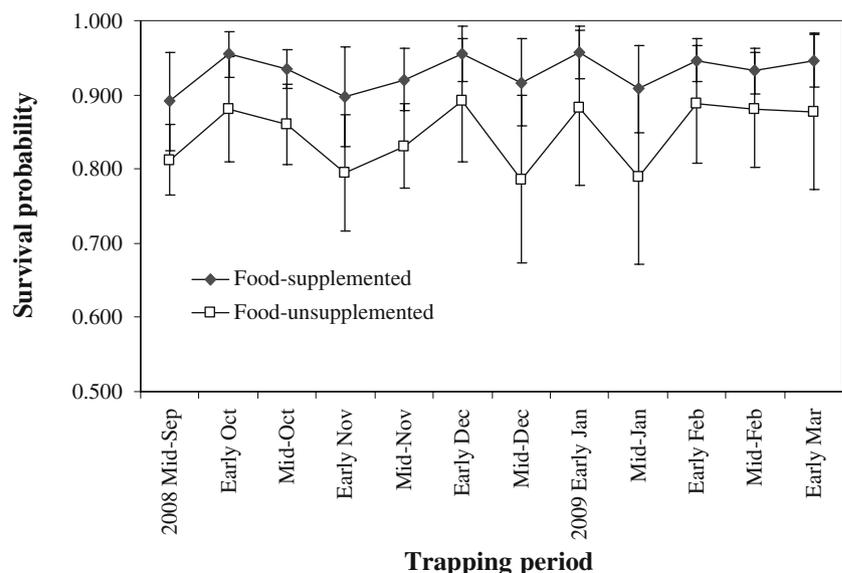
The Mongolian gerbil is a social rodent, living in groups year-round. Group-living rodents require more food to support social groups compared to solitary rodents (Lacey and Wiczorek 2003). Mongolian gerbils store seeds and annual herbs in the underground chambers for winter and are active during winter. At the end of our study, only two control chambers (food-unsupplemented) had more than two gerbils, making social groups, and the other two active controls chambers had only one gerbil each; in contrary, 11 of the 12 food-supplemented chambers had more than two gerbils. Our results suggest that limited food availability in our control chambers could not sufficiently support gerbil social groups. Similarly, reduction in food availability

chambers from mid-September of 2008 to early April of 2009 in Taibusi Qi, Inner Mongolia, China

appeared to increase winter mortality of the Daurian pika (*Ochotona dauurica*) in Inner Mongolia, which live in groups year-round as well (Zhong et al. 2008). Populations of group-living, non-hibernating small mammals may be food-limited during winter in northern temperate regions because of increased demands for food.

The onset and length of the breeding season are important to rodent population growth patterns (Ylonen and Eccard 2004). Annual dynamics of short-tailed shrew (*Blarina brevicauda*) populations are ascribed to predictable shortage of winter food and short breeding seasons (Merritt et al. 2001; Getz et al. 2004). Winter supplemental food may advance age at first reproduction of individuals and extend the breeding season (Boutin 1990). Breeding of gerbils during mid-winter in food-supplemented chambers increased group sizes in contrast to declines in group sizes in food-unsupplemented chambers (Fig. 1). Moreover, supplemental food increased numbers of gerbils available for breeding populations in the spring and may subsequently increase population growth rates during

Fig. 3 Model-averaged biweekly apparent survival probabilities of Mongolian gerbils, *Meriones unguiculatus*, in food-supplemented and -unsupplemented chambers from mid-September of 2008 to early April of 2009 in Taibusi Qi, Inner Mongolia, China. Vertical lines represent one standard error



spring. The density-independent mortality or survival-based model for the winter dynamics and density-dependent fertility-based model for the summer dynamics have been proposed to explain non-cyclic population dynamics of rodents (Hansen et al. 1999; Yoccoz et al. 2001). Future studies of the demographic mechanisms for seasonal differences in population regulation are needed for better understanding population dynamics of northern rodents.

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Appendix 1

Repeated-measures analysis of variance (ANOVA) of effects of time (t), food (F), and time–food interaction ($t \times F$) on overwinter social group sizes of Mongolian gerbils, *Meriones unguiculatus*,

from mid-September of 2008 to early April of 2009 in Taibusiqi, Inner Mongolia, China

Source		Type III sum of squares	<i>df</i>	Mean square	<i>F</i>	Sig. (<i>P</i>)
Tests of within-subjects effects (time)						
t	Sphericity assumed	280.301	13	21.562	5.554	0.000
	Greenhouse–Geisser	280.301	2.697	103.915	5.554	0.003
	Huynh–Feldt	280.301	3.250	86.240	5.554	0.001
	Lower-bound	280.301	1.000	280.301	5.554	0.028
$t \times F$	Sphericity assumed	414.301	13	31.869	8.209	0.000
	Greenhouse–Geisser	414.301	2.697	153.592	8.209	0.000
	Huynh–Feldt	414.301	3.250	127.468	8.209	0.000
	Lower-bound	414.301	1.000	414.301	8.209	0.009
Error(t)	Sphericity assumed	1110.327	286	3.882		
	Greenhouse–Geisser	1110.327	59.343	18.710		
	Huynh–Feldt	1110.327	71.505	15.528		
	Lower-bound	1110.327	22.000	50.469		
Tests of between-subjects effects (food treatment)						
Intercept	3516.574	1	3516.574	119.312	0.000	
F	469.074	1	469.074	15.915	0.001	
Error	648.423	22	29.474			

Appendix 2

Repeated-measures analysis of variance (ANOVA) of effects of time (t), food (F), and time–food interactions ($t \times F$) on arcsine-transformed proportions of overwinter females of Mongolian gerbils, *Meriones*

unguiculatus, from mid-September of 2008 to early of April 2009 in Taibusi Qi, Inner Mongolia, China

Source		Type III sum of squares	<i>df</i>	Mean square	<i>F</i>	Sig. (<i>P</i>)
Tests of within-subjects effects (time)						
t	Sphericity assumed	0.576	13	0.044	0.828	0.630
	Greenhouse–Geisser	0.576	2.721	0.212	0.828	0.476
	Huynh–Feldt	0.576	3.683	0.156	0.828	0.505
	Lower-bound	0.576	1.000	0.576	0.828	0.378
$t \times F$	Sphericity assumed	0.685	13	0.053	0.985	0.468
	Greenhouse–Geisser	0.685	2.721	0.252	0.985	0.404
	Huynh–Feldt	0.685	3.683	0.186	0.985	0.419
	Lower-bound	0.685	1.000	0.685	0.985	0.338
Error (t)	Sphericity assumed	9.740	182	0.054		
	Greenhouse–Geisser	9.740	38.099	0.256		
	Huynh–Feldt	9.740	51.565	0.189		
	Lower-bound	9.740	14.000	0.696		
Tests of between-subjects effects (food treatment)						
Intercept		52.221	1	52.221	61.051	0.000
F		0.004	1	0.004	0.005	0.945
Error		11.975	14	0.855		

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