

Population dynamics of the Mongolian gerbils: Seasonal patterns and interactions among density, reproduction and climate

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Abstract

The Mongolian gerbil (*Meriones unguiculatus*) is one of key rodents widely distributed in semi-arid, typical steppes, and desert grasslands in Inner Mongolia, China. We studied population dynamics of Mongolian gerbils under semi-natural conditions using monthly live trapping from 2001 to 2004 in south-central Inner Mongolia. Mongolian gerbils displayed seasonal fluctuations of density and population growth rate. Reproduction and recruitment of gerbils occurred primarily from March–August with a breeding lull in autumn. Population growth rates of Mongolian gerbils were not related to population density but were negatively related to temperature and precipitation. Enhanced reproductive performance and success of females increased population growth of gerbils in our enclosure. We also found that increased temperature and precipitation during the plant growing season negatively affected recruitment and rate of pregnancy. Mongolian gerbils prefer habitats with short, sparse vegetation and dry, loose and sandy soil. Increases in temperature and rainfall enhance vegetation growth; consequently, tall, dense and moist vegetation might reduce the suitability of habitats and retard population growth of Mongolian gerbils. Pronounced seasonal climatic fluctuations in northern latitudes may be the main cause of seasonal population dynamics of Mongolian gerbils.

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1. Introduction

The Mongolian gerbil, *Meriones unguiculatus* (Milne-Edwards, 1867) is one of the key rodents widely distributed in semi-arid, typical steppes, and desert grasslands of the south-east of the Bakal area in Russia, Mongolia, and Northern China (Gromov et al., 1963; Mallon, 1985; Luo et al., 2000). Gerbils mainly select seeds of annual dicots and some foliage as food (Zhong et al., 1985; Wang and Zhong, 1998). Mongolian gerbils live in social groups of 2–17 males and females (Ågren et al., 1989a) year-round and hoard food communally before winter. Mongolian gerbils prefer open habitat with short, sparse vegetation and dry, loose, and sandy soil; they are the dominant rodent species in the heavily degraded and desertified grasslands in Inner Mongolia (Zhong et al., 1985; Wang and Zhong, 1998). Mongolian gerbils can modify vegetation, micro-topography, soil structure, and nutrient cycling of grassland ecosystems through various activities, such as burrowing, digging, foraging, and food hoarding (Weiner et al., 1982; Steinberger and Whitford, 1983; Zhong et al., 1985; Schauer, 1987). These activities also enrich environmental heterogeneity to provide suitable habitats or resources for other organisms (Zhong et al., 1985; Dickman, 1999). Understanding fluctuations in abundance of Mongolian gerbils is important for evaluating its role in ecosystem processes and maintenance of biodiversity of grasslands.

Rodent populations in arid and semi-arid regions often show pronounced seasonal variation in numbers and structure. It is generally accepted that precipitation is the main limiting factor directly determining the primary productivity of plants, and population dynamics of rodents in the semi-arid and arid environments follows rainfall fluctuations (Brown and Heske, 1990; Fox et al., 1993; Masters, 1993; Predavec, 1994; Meserve et al., 1995; Southgate and Masters, 1996; Dickman et al., 1999; Madsen and Shine, 1999; Shenbrot and Krasnov, 2001; Jaksic and Lima, 2003; Letnic and Dickman, 2005). Bottom-up trophic processes are believed to be the underlying mechanisms for the positive relationships; accordingly, reproduction of rodents is stimulated by enhanced growth and seed production of annual and perennial plants after rain events (Brown and Heske, 1990). Nevertheless, rodent–rain relationships are complex and cannot be adequately represented by a simple bottom-up trophic model (Brown and Ernest, 2002). It is unknown how Mongolian gerbils respond to seasonal variations in rainfall in Inner Mongolia.

Little information was available about the dynamics of wild Mongolian population of grasslands (Ågren et al., 1989a, b). Although Xia et al. (1982) described the population dynamics of Mongolian gerbils in agricultural fields in Inner Mongolia, data was obtained with the removal method using snap traps or the burrow entrance number index method. Moreover, Xia et al. (1982) trapped gerbils only three times a year. More frequent live-trapping data are necessary for analyzing the seasonal dynamics of wild Mongolian gerbil populations. In the current paper, we present population data from a 4-year live-trapping study of Mongolian gerbils in Inner Mongolia. We aimed to: (1) determine whether the population of Mongolian gerbils was affected by density-dependent feedbacks; (2) determine how gerbil population responded to seasonal weather changes (i.e. temperature and precipitation); and (3) assess the roles of the reproductive performance of males and females in the seasonal population dynamics of gerbils. We also examined the difference in the effects of the aforementioned factors between the breeding and nonbreeding seasons.

2. Study area and methods

2.1. Study area

Our study was conducted at the Taipusiqi Field Research Station (E 115°17′–N 41°58′, 1500 m elevation), ca. 8 km north of Baochang in Inner Mongolia, China. The area was in a typical region where grasslands were intermixed with croplands. The Climate was semi-arid and continental with relatively hot summer (June–August) and cold, dries winter (November–February). Annual total precipitation was 257.9 mm in 2001, 345.8 mm in 2002, 550.0 mm in 2003, and 399.6 mm in 2004. Average monthly temperature ranged from –19.1 to 21.1 °C (Fig. 1).

A 0.5 ha (50 × 100 m) enclosure was constructed with corrugated fiberglass sheets on our study site. Fiberglass sheets were buried 40 cm deep below ground and 40 cm above-ground to prevent small mammals from entering or moving out of the enclosure; however, ground squirrels (*Spermophilus dauricus*) and zokor (*Myospalax aspalax*) were found occasionally inside the enclosure during our study. Steppe polecats (*Mustela evermanni*) occasionally

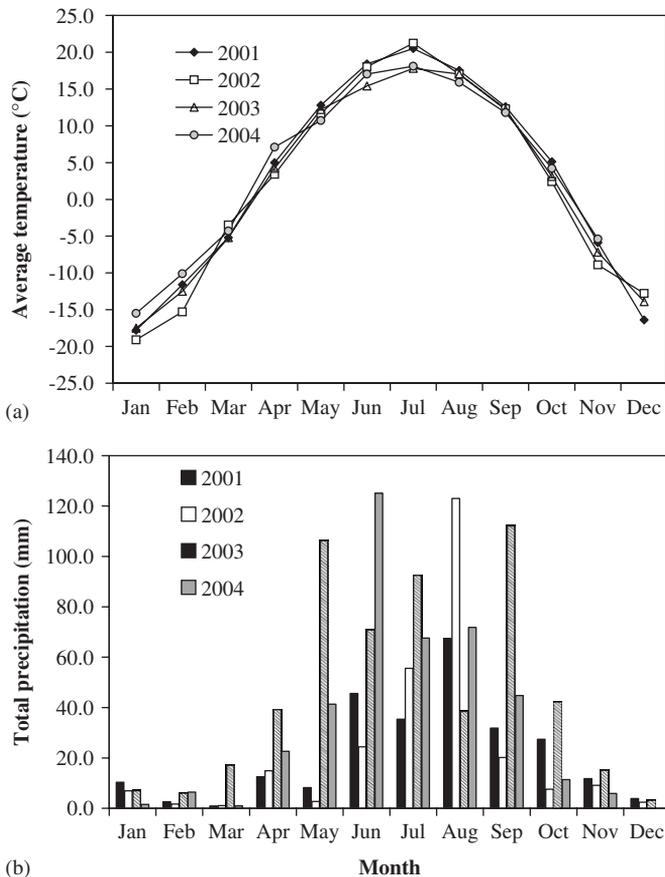


Fig. 1. Monthly average temperature (°C) (a) and total precipitation (mm) (b) recorded at Taipusiqi meteorological station, Inner Mongolia, China, during 2001–2004.

visited our study site and were captured using traps and removed when being found. Inside the enclosure, a 10×10 reference grid with 10 m between points was set up for behavioral observations. Each corner of a grid cell was marked with 2–3 small stones. The enclosure was surrounded by grasslands and croplands. Vegetation in the enclosure was composed primarily of grasses and herbs; the dominant plant was *Leymus chinense*.

2.2. Monitoring gerbil population

Mongolian gerbils in the enclosure were monitored monthly from March to October during 2000–2004 with the capture–mark–recapture (CMR) method (Krebs, 1999). Trapping started in October 2000 and ended in October 2004; we did not trap gerbils during winter (from November to February) to avoid trap mortality due to severe weather.

Trap stations were arranged in three concentric circles and at equal spacing (Wan and Zhong 2000). The three circles were centered on the geometric center of a gerbil colony (Fig. 2), with the radius of the circles adjusted according to the area a gerbil colony occupied. The radius was about 1–1.5, 2–3, and 4–6 m for the inner, middle, and outer circle, respectively. The inner circle, the middle circle, and the outer circle had 4–6 trap stations, 8–10 stations, and 12 trap stations, respectively. One or two wire-mesh live traps ($28 \times 13 \times 10$ cm) were placed at each station with the door open to an active gerbil entrance or runway if possible.

Each trapping session lasted for 3–5 consecutive days. Traps were baited with peanuts prior to trapping. Traps were set at 0500–0600 h from May to August, checked every 1–2 h until about 1100 h, and closed from the 1100 to 1500 h to avoid trap mortality from heat; trapping resumed at 1600 h and continued till 1900 h. In March, April, September, and October, trapping started between 0630 and 0730 h and continued till 1730 h. Gerbils were active during our trapping hours (Ågren et al., 1990; personal observation).

All captured gerbils were toe-clipped at the first capture for permanent identification. One or more small patches of fur on the forehead, back, and hips were dyed with black hair dye at each trapping session. Different individuals had different combinations of dyed patches as secondary identification for behavioral observations at a distance. Captured gerbils were sexed and weighed to the nearest 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 (Payman and Swanson, 1980; Liu et al., 2004). Female gerbils were considered in reproductive condition if they had bulged abdomen, enlarged nipples surrounded by white mammary tissue, or opened symphyses. There was no any other gerbil population around our study site during the 4-year study; therefore, recruits were defined as all newly marked animals captured after the initial population was marked in 2001 in this study. Gerbils were considered juveniles less than 1.5 month old if their body mass was less than or equal to 30 g.

2.3. Data analysis

Population size was estimated using the minimum number known alive method (MNA, Krebs, 1999). Monthly rate of population change from month t to month $t + 1$ ($r_{t \sim t+1}$) was calculated as follows:

$$r_{t \sim t+1} = (30/T) \log_e(N_{t+1}/N_t), \quad (1)$$

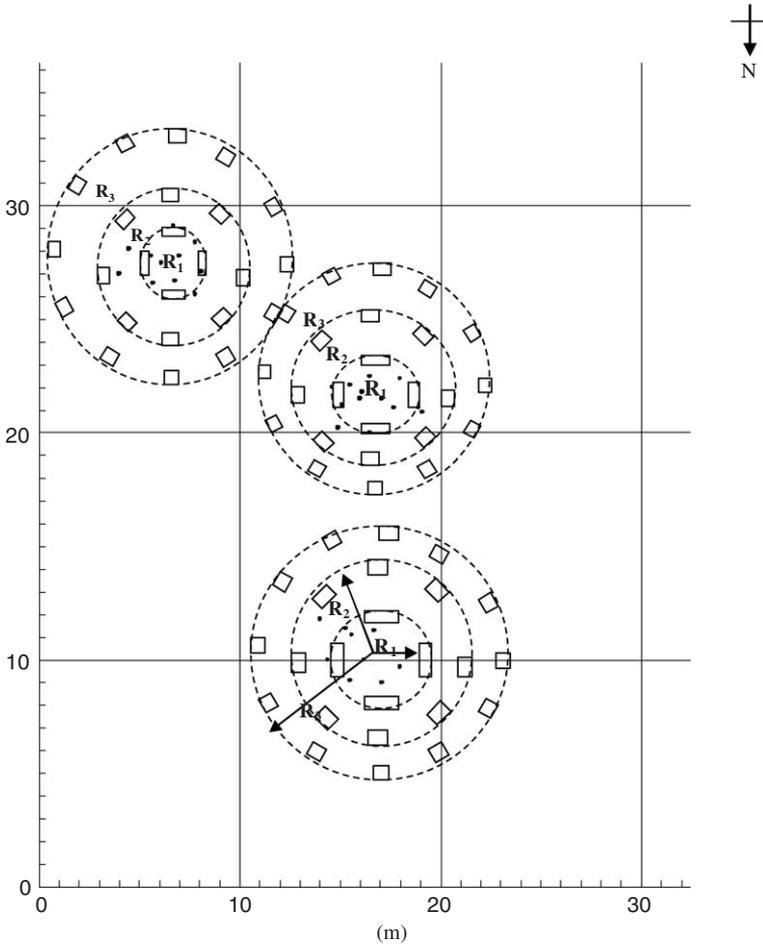


Fig. 2. Layout of the concentric circular trap stations (small squares). Black dots represent entrances of gerbil colony. Symbols R_1 , R_2 , and R_3 denote the radius of the inner, middle, and outer circles centered on the geometric center of a gerbil colony. R_1 , R_2 , and R_3 are about 1–1.5, 2–3, and 4–6 m, respectively.

where N_t is population size at time t ; N_{t+1} is population size at time $t + 1$; and T is the number of days between two successive trapping sessions. The interval between two successive trapping sessions was either less than or greater than 30 days in some trapping sessions.

We also calculated the monthly proportion of reproductively active males (PRM_t) or females (PRF_t), dividing the number of reproducing males or females by the total number of males or females captured in a trap session, respectively. The monthly ratio of recruits to reproductive females ($RRF_{t \sim t+1}$) between two consecutive trapping sessions was computed using the formula:

$$RRF_{t \sim t+1} = (30/T)(RC_{t+1}/RF_t), \tag{2}$$

where RC_{t+1} is the number of recruits captured at trapping session $t + 1$; and RF_t is the number of reproductive females captured at last trap session t . We also used $30/T$ to

adjust the monthly *RRF*. We calculated *RRF* for each month of April–October from 2001 to 2004.

We detected seasonal differences in population density and rate of population change using the one-way analysis of variance (ANOVA) with the trapping month as a factor. Data were pooled by month over 4 years in the ANOVA analysis. We regressed monthly population growth rates $r_{t \sim t+1}$ against population density N_t , monthly average temperature ($Temp_t$), and monthly total precipitation ($Preci_t$) to assess the effects of direct density dependence and climate on gerbil population dynamics, respectively. The relationship between monthly population growth rate and demographic variables was also evaluated by regressing $r_{t \sim t+1}$ on monthly PRM_t , monthly PRF_t , and monthly ratio of recruits to reproductive females ($RRF_{t \sim t+1}$), respectively.

In addition, in order to assess the effects of climate on reproductive performance of gerbils, we carried out the regressions of reproductive parameters PRF_t and $RRF_{t \sim t+1}$ over climate variables ($Temp_t$ and $Preci_t$). PRF_t and $RRF_{t \sim t+1}$ were transformed by $\sin^{-1} \sqrt{PRF_t}$ and $\log_e RRF_{t \sim t+1}$ (Quinn and Keough, 2002), respectively. The delayed effect of climate variables ($Temp_{t-1}$ and $Preci_{t-1}$) on male and female reproductive performance (PRM_t , PRF_t , and $RRF_{t \sim t+1}$) was also assessed using regressions. The ANOVA and regression analyses were performed with the SPSS software (SPSS, 1999).

3. Results

3.1. Seasonal population dynamics patterns

During October 2000–October 2004, 632 Mongolian gerbils were captured 3604 times. Thirty-one percent of the gerbils were caught just once. Population density of gerbils ranged from 23.0 to 122.6 gerbils/0.5 ha during the 4-year study. Gerbil populations fluctuated annually (Fig. 3), with highest population densities in July 2001 and June 2002–2004 and lowest densities in October each year. Furthermore, when 4 years of data were pooled by month, annual fluctuations of population density were significant (one-way ANOVA, $F_{7,29} = 4.64$, $p < 0.01$). The monthly rate of population change was greater than zero during spring and early summer, but below zero from mid-summer to autumn. Population growth rate also displayed significant seasonal fluctuations (one-way ANOVA, $F_{7,29} = 6.435$, $p < 0.01$; Fig. 4).

3.2. Seasonal changes in reproductive performance

Reproductive performance of males and females varied seasonally during the 4-year study (Fig. 5). Monthly proportions of reproductively active males (PRM) were higher and over 0.2 during March–August and then declined towards autumn. PRM was less than 0.15 in September–October (Fig. 5a). Female reproductive performance showed a similar seasonal pattern as did that of males (Fig. 5b). Reproductively active females were observed every month from March to August, but almost no reproductively active females were captured during September–October, except in September 2001 (Fig. 5b).

Peak recruitment was recorded in April 2001, March and June 2002, April 2003, and March and June 2004. Recruits per reproductive female (*RRF*) were found highest in March–April 2001 and 2002, April–May 2003, and May–June 2004 and were zero from September to October except in 2001 (Fig. 6). In addition, in the first trapping session of

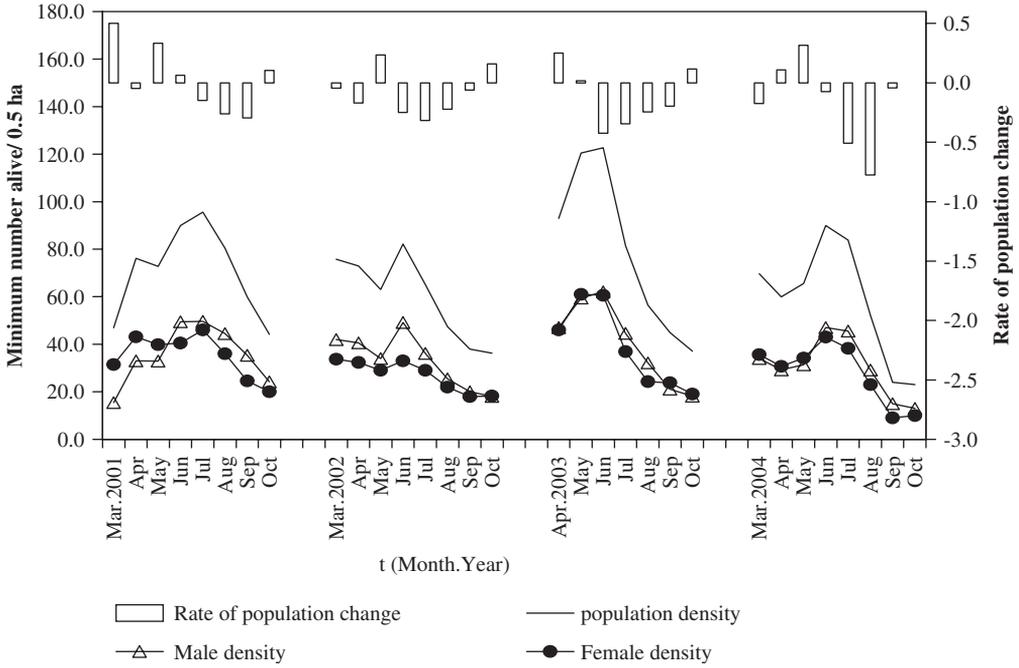


Fig. 3. Seasonal fluctuations of population density N_t (minimum number alive per 0.5 ha enclosure) and the rate of population change $r_{t \sim t+1}$ of Mongolian gerbils, *Meriones unguiculatus*, from 2001 through 2004 at Taipusiqi field research site, Inner Mongolia, China.

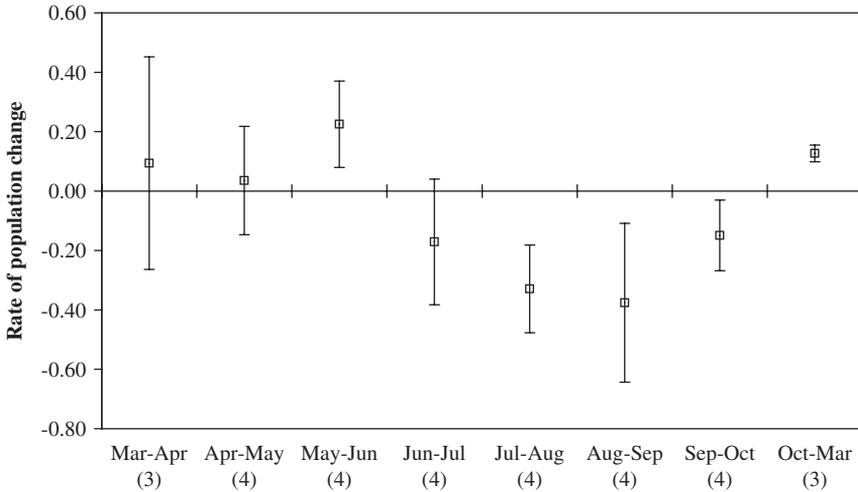


Fig. 4. Annual changes in the monthly rate of population change $r_{t \sim t+1}$ (mean \pm SD) of *Meriones unguiculatus*. Four years of data were pooled by month. Number of trapping sessions is in parentheses of the X-axis tick labels.

March or April every year, the percentage of unmarked gerbils with body mass above 30 g was 100% in 2001, 71.8% in 2002, 63.5% in 2003, and 90.6% in 2004. Mean body mass of these unmarked gerbils was 40.2 g (SE = 0.5) in 2001, 39.4 g (SE = 1.4)

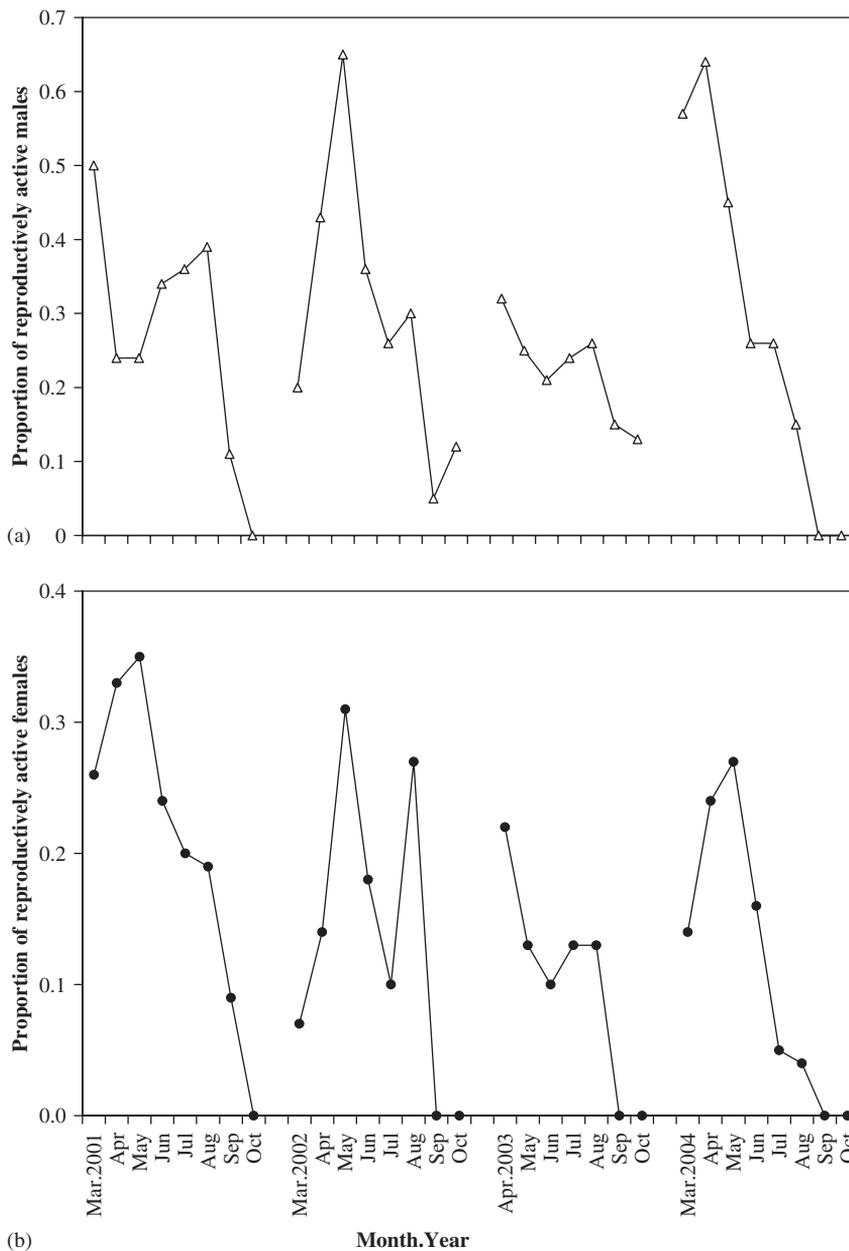


Fig. 5. The monthly proportion of reproductively active males (PRM) in the total number of captured males (a) and the monthly proportion of reproductively active females (PRF) in the total number of captured females (b) of *Meriones unguiculatus* from March 2001 through October 2004 at the Taibusiqi field research site, Inner Mongolia, China.

in 2002, 44.7 g (SE = 1.4) in 2003, and 41.3 g (SE = 2.2) in 2004. Age of these unmarked gerbils was above 1.5 months, indicating that reproductions took place in January or February.

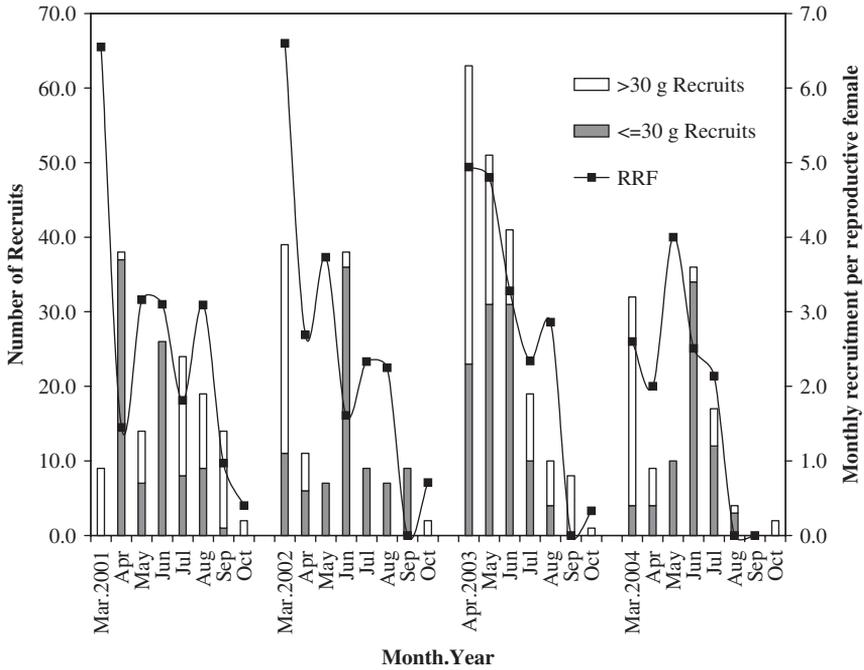


Fig. 6. The number of recruits entering the population and the ratio of recruits to reproductively active females ($RRF_{t \sim t+1}$) in *Meriones unguiculatus* from March 2001 to October 2004 at the Taibusiqi field research site, Inner Mongolia, China.

3.3. Effects of density, reproductive performance and climatic factors on the rate of population change

We detected density dependence in monthly population growth rates neither during spring–summer (March–August) ($R^2 = 0.011$, $F_{1,22} = 0.238$, $p = 0.631$; Fig. 7a) nor during spring, summer and autumn ($R^2 = 0.030$, $F_{1,29} = 0.861$, $p = 0.361$). However, the monthly rate of population change was positively related to the PRF and males (PRM) and RRF , respectively, during the spring–summer breeding season ($r_{t \sim t+1} = 2.538PRF_t - 0.566$, $R^2 = 0.554$, $F_{1,22} = 26.096$, $p = 0.000$; $r_{t \sim t+1} = 1.068PRM_t - 0.461$, $R^2 = 0.248$, $F_{1,22} = 6.914$, $p = 0.016$; $r_{t \sim t+1} = 0.127RRF_{t \sim t+1} - 0.479$, $R^2 = 0.427$, $F_{1,22} = 15.629$, $p = 0.001$; Fig. 7b–d). From spring to autumn, PRF and RRF had positive effects on monthly population growth rate ($r_{t \sim t+1} = 1.032PRF_t - 0.230$, $R^2 = 0.165$, $F_{1,29} = 5.551$, $p = 0.026$ (Fig. 7b); $r_{t \sim t+1} = 0.062RRF_{t \sim t+1} - 0.229$, $R^2 = 0.163$, $F_{1,29} = 5.456$, $p = 0.029$ (Fig. 7d)). The rate of population change, however, was not significantly related with PRM from spring to autumn ($R^2 = 0.07$, $F_{1,29} = 2.101$, $p = 0.158$ (Fig. 7c)). Thus, population growth rate increased with increasing female reproductive performance and success, especially during the spring–summer breeding season.

Monthly rate of population change was inversely related to monthly temperature both during spring–autumn ($r_{t \sim t+1} = 0.128 - 0.019Temp_t$, $R^2 = 0.273$, $F_{1,29} = 10.497$, $p = 0.003$) and during spring–summer ($r_{t \sim t+1} = 0.113 - 0.018Temp_t$, $R^2 = 0.232$, $F_{1,22} = 6.348$, $p = 0.02$ (Fig. 7e)). Precipitation negatively affected monthly rate of

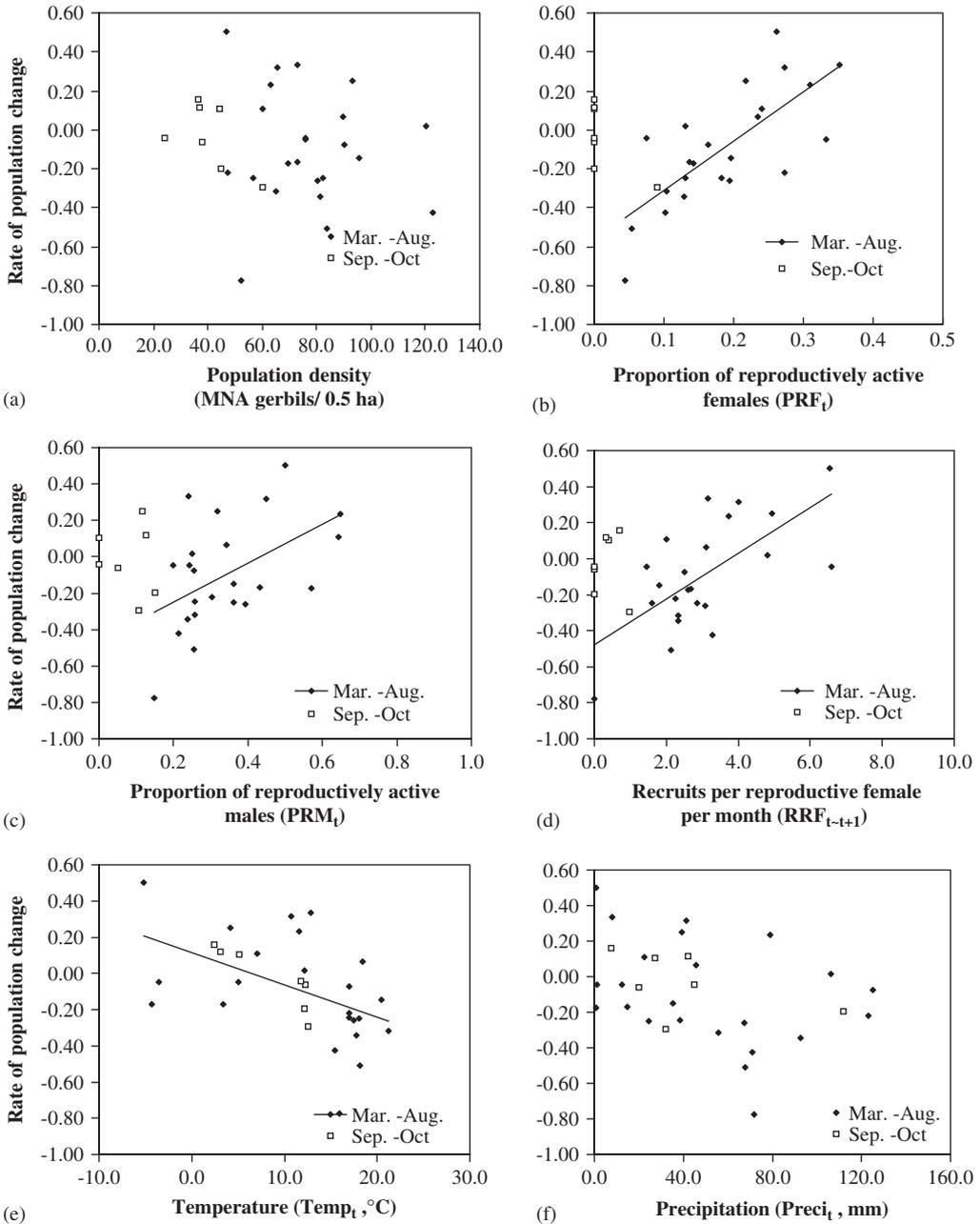


Fig. 7. The relationship between the monthly rate of population change $r_{t \sim t+1}$ and population density N_t (a), the proportion of reproducing females PRF_t (b), the proportion of reproductively active males PRM_t (c), monthly ratio of recruits to reproductively active females $RRF_{t \sim t+1}$ (d), monthly average ambient temperature ($Temp_t$) (e), and monthly total precipitation ($Preci_t$) (f) for the spring–summer breeding season (March–August) and breeding lull (September–October) periods.

population change for spring, summer, and autumn ($r_{t \sim t+1} = 0.051 - 0.003Preci_t$, $R^2 = 0.136$, $F_{1,29} = 4.397$, $p = 0.045$), but precipitation did not affect population growth for the spring–summer breeding period ($R^2 = 0.122$, $F_{1,22} = 2.915$, $p = 0.103$ (Fig. 7f).

Furthermore, in the stepwise multiple regression of monthly population growth rate against *Temp*, *Preci*, *PRF*, and *RRF* using data from spring to autumn, only two variables entered the model. The first was *Temp*, and the second was *PRF* ($r_{t \sim t+1} = 1.091PRF_t - 0.020Temp_t - 0.023$, $R^2 = 0.457$, $F_{1,29} = 11.369$, $p < 0.01$). However, in the stepwise multiple regressions using the spring and summer data, *PRF* and *RRF* entered the model ($r_{t \sim t+1} = 2.349PRF_t + 0.111RRF_{t \sim t+1} - 0.863$, $R^2 = 0.881$, $F_{1,22} = 73.800$, $p < 0.01$). Therefore, both female reproduction and temperature influenced gerbil population growth during spring, summer, and autumn, but only female reproduction affected gerbil population growth during the breeding season (March–August).

3.4. The effects of climate on reproductive performance of gerbils in spring and summer

Average temperature ($Temp_t$) affected *RRF* negatively during the spring–summer breeding season ($\log_e(RRF_{t \sim t+1}) = 1.365 - 0.025Temp_t$, $R^2 = 0.25$, $F_{1,21} = 6.675$, $p = 0.018$), but *PRF* was not related to $Temp_t$ ($R^2 = 0.020$, $F_{1,22} = 0.438$, $p > 0.05$). Neither *PRF* nor *RRF* was significantly related to precipitation ($Preci_t$) ($p > 0.05$). Monthly total precipitation, however, negatively affected *PRF* with one-month time lag ($\sin^{-1}\sqrt{PRF_t} = 0.500 - 1.714Preci_{t-1}$, $R^2 = 0.286$, $F_{1,22} = 8.411$, $p = 0.009$).

4. Discussion

During the 4-year study, Mongolian gerbils fluctuated in numbers seasonally. Concomitant with markedly annual fluctuations of density and rate of population change (Figs. 3 and 4), reproductive performance and success also showed distinct seasonal changes (Figs. 5 and 6). Reproduction and recruitment occurred primarily from March to August, with a breeding lull in autumn. This seasonal breeding pattern was also typical of Mongolian gerbils in agricultural croplands at this latitude (Xia et al., 1982). The autumn breeding lull may be an adaptation of Mongolian gerbils to local climate and vegetation phenology. From the end of August to mid-October, abundant plant seeds triggered communal food hoarding of gerbils that demanded a great amount of energy. Therefore, the trade-off between breeding and food hoarding in autumn might enhance winter survival and next spring's reproduction.

We did not detect density dependence in the gerbil populations (Fig. 7a). Mongolian gerbil populations were shown to display seasonal density-dependent growth from spring to autumn in the Erdos desert grasslands (Wang and Zhong, 2006). Wang and Zhong (2006) found per capita rainfall or per capita resource availability might be a limiting factor for survival and/or reproduction of gerbils during the breeding season in the Erdos desert grasslands. The difference in density dependence between the two studies might be due to differences in habitats and populations. Our gerbil population inhabited the typical grasslands and was an enclosed population without immigration; the population Wang and Zhong (2006) studied was a wild population with potential for immigration and dispersal. Difference between the minimum and maximum densities of gerbils was about five-fold on our site, but over 100-fold in the Erdos desert grasslands (Wang and Zhong,

2006). The site-specific effect of density dependence on rate of population change was also observed in Daurian pikas (*Ochotona daurica*) in Inner Mongolia (Wang and Zhong, 2006).

Relationships between vegetation and rainfall differed among plant life forms and depended on climate, e.g. temporal patterns of rain events (Southgate et al., 1996). Vegetation and habitat quality were more sensitive to rain events and underwent more dramatic changes in desert grasslands than in semi-arid typical grasslands during the plant-growing season. Gerbils might track the changes in vegetation and habitats and hence vary dramatically in numbers in desert grasslands. Rapid increases in density after rain events might result in density dependence.

Alternatively, weather effects may mask the influence of density-dependent feedbacks (Lima and Jaksic, 1999). We found a positive relationship between population growth rate and the percent of reproductive females (Fig. 7b); increased PRM and recruitment also enhanced population growth (Fig. 7c and d). Changes in population density and growth rate were the consequences of varying demographic parameters (Batzli, 1992; Dobson and Oli, 2001; Lima et al., 2003). Additionally, climate affected the demography of Mongolian gerbils. During the breeding season, high temperatures reduced recruitment of Mongolian gerbils; increased precipitation reduced female pregnancy with one-month time lag. Thus, density-independent factors, such as temperature and precipitation, played important roles in the dynamics of gerbil populations.

Precipitation had strong inverse effects on population growth rates of gerbils from spring to autumn (Fig. 7f). Monthly population growth rate was inversely related to monthly average temperature only during spring and summer (Fig. 7e). The negative effects of rainfall on population growth rate might be mediated through the PRF; likewise, the negative effects of temperature on population growth rate might be mediated through reduced recruitment. Hence, it was possible that the negative weather effects might keep gerbils from reaching the carrying capacity in typical steppes. Thus, pronounced seasonal weather fluctuations (Fig. 1) in northern latitudes might be the main cause of seasonal population dynamics of Mongolian gerbils.

Our results concerning the negative effects of weather on gerbil population dynamics were different from earlier studies (but see Brown and Ernest, 2002). Rainfalls enhanced desert rodent population growth and even caused the outbreaks of desert rodents of Australia, North America, and South America (Brown and Heske, 1990; Dickman et al., 1999; Madsen and Shine, 1999; Jaksic and Lima, 2003; Letnic and Dickman, 2005). Zhang et al. (2003) reported that the numerical response of Brandt's voles (*Microtus brandtii*) was determined mainly by availability of habitat with sparse, short grasses in our study area. Populations of Brandt's voles do not persist in habitat with high plant cover (>80%) and tall (>17–20 cm) grasses (Zhong et al., 1999). Mongolian gerbils prefer habitats of shorter, sparser vegetation than Brandt's voles (Zhong et al., 1985). Mongolian gerbils were territorial during the breeding season, and size of a social group was positively related to the area of food resources (Ågren et al., 1989a,b). Increased temperature and precipitation during spring and summer enhanced plant coverage, height, and productivity (Jiang, 1990; Wang et al., 1999, 2001); thus, tall, dense vegetation dominated gerbil habitats, reduced the suitability of habitats, and might retard population growth of Mongolian gerbils. Such indirect effects of weather may also impose significant impacts on population dynamics of Mongolian gerbils.

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