

Communal food caches and social groups of Brandt's voles in the typical steppes of Inner Mongolia, China

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Abstract

We studied colony composition and communal food caching of Brandt's voles (*Lasiopodomys brandtii*) in Hexiten Banner, Inner Mongolia, China. Brandt's voles lived in colonies throughout the year. The average number of voles in a colony was 16.7 voles in 1986 ($n = 18$) and 21.6 voles in 1987 ($n = 14$). Average sex ratios of vole colonies were about 1:1 in October. Voles born in spring and summer (3–6 months old) accounted for 74% of a vole colony in 1986 and 69% in 1987. Voles born in autumn (1.5–3 months old) constituted 23.2% of a vole colony in 1986 and 25.7% in 1987. Brandt's voles stored food collectively in communal food caches in late autumn. *Artemisia frigida* was the dominant plant in the food caches of Brandt's voles, comprising 44.7% of the stored food in 1986 and 71.4% in 1987. The average dry weight of food stored by a vole colony was 4.4 kg in 1986 and 6.4 kg in 1987. Higher population densities might stimulate Brandt's voles to store more food; however, given a certain plant standing biomass, increased colony size did not appear to improve the food acquisition efficiency of a vole colony. More studies are needed to reveal the effects of limited food caches on winter survival and spring reproduction of Brandt's voles in Inner Mongolia.

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1. Introduction

The Brandt's vole (*Lasiopodomys* [= *Microtus*] *brandtii*) is widely distributed in the grasslands and steppes of Inner Mongolia, China and Mongolia. Brandt's voles have

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attracted increasing attention because of their important roles in grassland ecosystems, extreme sociality, and potential conflicts with humans (Zhong et al., 1999; Zahler et al., 2004). Winter is very severe in the range of Brandt's voles; the minimum temperature can reach -40°C . Brandt's voles do not hibernate during winter and live in colonies throughout the year. A colony consists of 10–38 voles of mixed sex and age ratios and occupies a territory about 25 m in diameter. Communal groups of prairie voles (*Microtus ochrogaster*) in North America are present throughout the year, but are more common during later autumn to spring (McGuire et al., 2002). Social group size of prairie voles ranges from 3 to 9 (McGuire et al., 2002). Meadow voles (*Microtus pennsylvanicus*) in North America also nest communally in winter and early spring but not during the breeding season (Madison, 1984). Communal nesting and food caching are critical components of adaptation to cold in social rodents (Wolff and Lidicker, 1981; Madison, 1984; Smith and Reichman, 1984; Wolff, 1984; but see Getz et al., 1993). Knowledge of food hoarding, age structure, and sex ratios of vole colonies at the onset of winter will significantly improve our understanding of the winter ecology of Brandt's voles of the Mongolian Plateau.

Little information on the age structure, sex ratio, and size of Brandt's vole colony at the beginning of winter is available. Formozov (1966) provided an anecdotal description of food caching and communal nesting of Brandt's voles in Mongolia. Zhang and Zhong (1981) conducted a brief study of the composition and size of vole colonies in the Hulunbeir grasslands based on only a few colonies, but they reported several reproducing females lived in a colony during the breeding season. Microtine rodents have been hypothesized to live in communal groups or colonies to avoid predators, defend territories, improve the efficiency of food acquisition, and adapt to habitat scarcity (Madison, 1984). Microtines living in groups also incur fitness costs, such as conspicuousness to predators, increased resource competition, and greater likelihood of disease transmission (Madison, 1984). Brandt's vole population size decreases dramatically over the winter; however, the exact cause of this decline is not known. Few studies have addressed the relationship between colony size and food caching of Brandt's voles. Relationships between colony size and the quantity of stored food are unknown.

Our current study focuses on the relationships between composition and size of social groups and food caching of overwintering Brandt's voles in central Inner Mongolia, China. Our main objectives were to: (1) determine the size, age structure, and sex ratio of vole colonies in late autumn; (2) determine the average weight of food stored by a vole colony and dominant plant species of cached food in the onset of winter; and (3) examine the relationships between the quantity of stored food, colony size, and age structure of vole colonies. Our data on food caches were gathered when the first snow fell, a probable end of vole food caching for the year.

2. Methods

Our study site was located in the typical steppe at Aqiwula ($\text{N}43^{\circ}24'$, $\text{E}116^{\circ}46'$), Hexiten Banner, Inner Mongolia, China. The study site was situated in a flat, open grassland. Soil was the well-drained chestnut soil. The climate was semi-arid and continental (Jiang, 1985). Average annual precipitation was about 350 mm, and most rainfall fell in June, July, and August. Snow cover lasted from November to March or April of the following year. Average annual temperature was about -0.1°C . Temperature ranged from -40°C to

30 °C. Vegetation was dominated by *Stipa krylovii*, *Leymus chinensis*, and *Artemisia frigida* and was degraded due to overgrazing by livestock.

Brandt's voles dug new caches or food storage chambers and maintained old chambers from late August to early September. Nests were located on the geometric centre of a burrow system; and 2–4 elongated food chambers radiated from the nests and were connected to the central nests by a tunnel (Schauer, 1987). Nest material in nests was made of dry grasses, whereas cached food in food chambers was composed of relatively fresh plants in October. Fresh soil from digging covered the central part of a burrow system and formed a clear boundary of the burrow system; the boundary encompassed over 95% of the burrow entrances and all food chambers of a burrow system (Schauer, 1987; Zhou et al., unpublished). Therefore, by late autumn, different colonies or burrow systems of Brandt's voles could be identified by these distinct boundaries.

Brandt's voles gathered and stored food plants for winter from early September through mid-October and usually stopped gathering food plants when the first snow fell in October or November. We conducted our field investigations during October 3–11 of 1986 and October 11–16 of 1987 immediately after the first snow fell; hence, our data represent the weight and species composition of stored food plants at the end of the food gathering season. Before excavating the burrow systems, we collapsed all burrow entrances of a burrow system in the afternoon, counted all reopened burrow entrances of each colony the following morning, and placed a snap trap at every active entrance to remove all voles. We checked traps, removed captured voles, and re-activated traps every half hour for 12 h. Then we collapsed all burrow entrances of a burrow system. In the following morning, we inspected the collapsed burrow entrances for any re-opened entrances (probably by remaining voles in the colony). If no burrow entrances were re-opened, we concluded that all voles in the colony were removed; otherwise, we continued trapping until all voles were removed from a colony. We then excavated the burrow systems to determine the total weight and species composition of stored food for each colony. We excavated 18 burrow systems in 1986 and 14 burrow systems in 1987 by removing the top of nesting chambers and the top of storage chambers. Nests and caches could be located using a pointed iron rod as a probe. All food plants in the storage of a burrow system were weighed to the nearest 1 g immediately after excavation to determine fresh weight. Food plants were put into a cloth bag by colony and were transported to a laboratory for sorting and drying. Food plants were sorted into three groups, *L. chinensis*, *A. frigida* and other plant species. Sorted plants were put into cloth bags by group, were air dried for 20 days, and were weighed to the nearest 1 g by group to determine the dry weights of *L. chinensis*, *A. frigida*, and total cached food, respectively. Total weights of nest material were recorded also for each colony.

Captured voles were counted, sexed, and aged for each colony. Aging was based on the morphological aging criteria for Brandt's voles (Animal Ecology Group I, 1978), including the inter-orbital width, the greatest cranial length, and body length. Brandt's voles were divided into four age groups, juvenile (1–1.5 months old), sub-adult (1.5–3 months old), adult I (3–6 months old), and adult II (>6 months old, some had over-wintered and had been born in the previous year). Carcasses of females were dissected and examined for indications of reproduction, such as fetuses in utero or placental scars. Colony size, sex ratio, and age composition were recorded for each colony. We computed the burrow entrance index as the number of captured animals divided by the number of entrances for

each colony, i.e., the number of animals per entrance. The average entrance index was computed for 1986 ($n = 18$) and 1987 ($n = 14$), respectively.

We also determined vole population densities using the burrow entrance method (Liro 1974; Wang et al. 2003). Twelve to nineteen 0.25-ha circular plots spaced 50 m apart were arranged in a line transect across the study area. We sampled 12 plots in October of 1986 and 19 plots in August of 1987. We collapsed all burrow entrances within the 0.25 ha plots in the later afternoon and counted all reopened burrow entrances as active burrow entrances in a sampling plot the following morning. Vole population density was estimated with the formula, $D = 4 * I * N$, where D is density (animals ha^{-1}), I the burrow entrance index, and N the number of active entrances in a 0.25-ha plot.

We used the t -test to detect differences in vole population densities and colony size between 1986 and 1987, respectively. We carried out linear regressions of dry weights of *A. frigidus* against total dry weights of stored food and applied the permutation test (Edgington, 1987) for the significance of the regression slopes with 4000 permutations of the total dry weights of cached food. We computed the proportion of sub-adults (born in July–August) in a colony and regressed the proportion of sub-adults against the number of adult voles (adult I + adult II), respectively, for 1986 and 1987. We took the natural logarithm of the proportions of sub-adults (Sokal and Rohlf, 1995). The normality of data was tested and confirmed with the Kolmogorov–Smirnov test ($P > 0.1$; Sokal and Rohlf, 1995).

3. Results

Mean vole density was almost 4 times higher in 1987 ($X = 2287.4$ voles ha^{-1} , $\text{SE} = 136.4$) than in 1986 ($X = 590.2$ voles ha^{-1} , $\text{SE} = 53.7$; $t = 3.3$, d.f. = 29, $P < 0.01$). Mean burrow entrance density was significantly greater also in 1987 ($X = 3465.7$ holes ha^{-1} , $\text{SE} = 206.7$) than in 1986 ($X = 2459.0$ holes ha^{-1} , $\text{SE} = 224.0$; $t = 3.3$, d.f. = 29, $P = 0.003$). The means of colony size, numbers of burrow entrances in a vole colony, fresh and dry weights of stored plants, dry weights of nest material, and proportions of *A. frigidus* and *L. chinensis* in the total weight of stored plants are presented

Table 1

Means of numbers of Brandt's voles, numbers of burrow entrances, burrow entrance index, fresh weight (kg) and dry weight (g) of stored food, dry weight (kg) of nest material, and proportions of *A. frigidus* and *L. chinensis* in the total weight of stored food of 18 Brandt's vole colonies excavated in October of 1986 and 14 colonies in October of 1987 in central Inner Mongolia

Year	Colony size	Number of entrances	Burrow entrance index	Fresh weight of stored food (kg)	Dry weight of stored food (kg)	Weight of nest material (g)	% of <i>A. frigidus</i>	% of <i>L. chinensis</i>
1986	16.72 (0.95)	72.89 (3.81)	0.24 (0.02)	6.68 (0.68)	4.44 (0.45)	931 (110.32)	44.71 (3.61)	0.86 (0.17)
1987	21.57 (2.13)	36 (4.57)	0.66 (0.07)	10.73 (1.06)	6.35 (0.57)	950 (123.09)	71.36 (4.27)	0.44 (0.09)

Numbers in parentheses are one standard error. The number of burrow entrances is the count of burrow entrance in a burrow system. Burrow entrance index is the ratio of the number of voles captured in a burrow system over the number of burrow entrance in a burrow system.

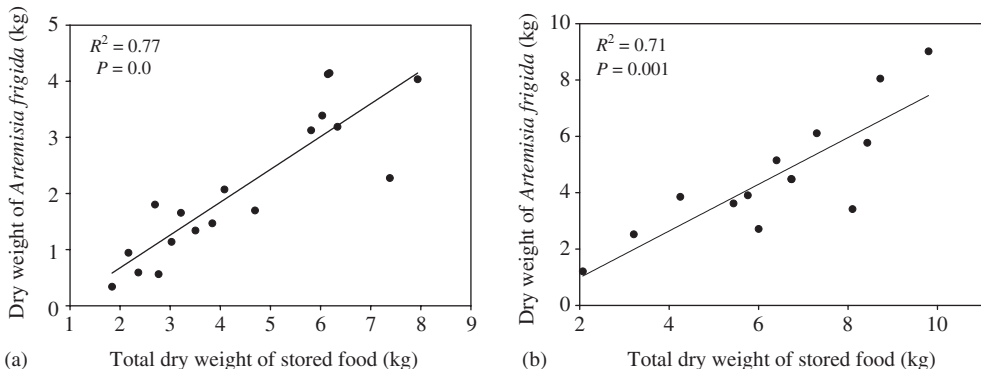


Fig. 1. Relationships between dry weights of *A. frigida* and total weights of stored food in the Brandt's vole colonies in central Inner Mongolia in 1986 (a) and 1987 (b).

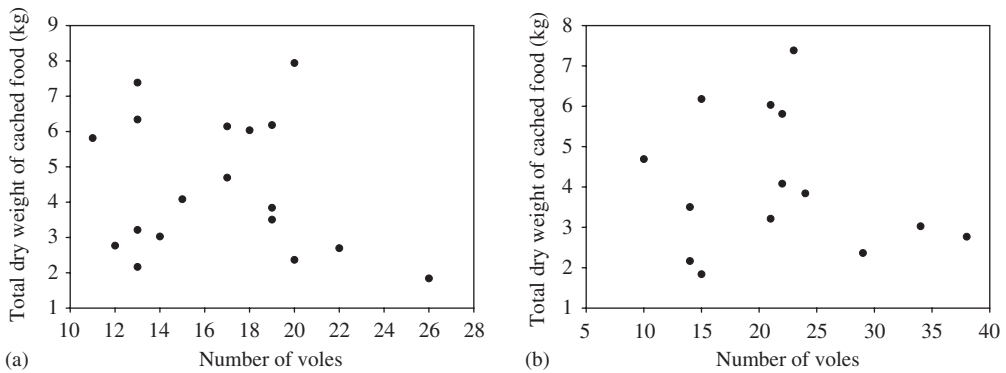


Fig. 2. Relationships between total dry weights of food stored by a colony and colony size of Brandt's voles of central Inner Mongolia in 1986 (a) and 1987 (b).

in Table 1. The average total dry weight of cached plants was greater in 1987 than in 1986 ($t = 2.62$, d.f. = 30, $P = 0.01$). Average colony size was significantly greater in 1987 than in 1986 ($t = 2.25$, d.f. = 30, $P = 0.03$). The dry weight of nest material did not differ between 1986 and 1987 ($t = 0.10$, d.f. = 30, $P = 0.92$).

Dry weights of *A. frigida* were positively related to total dry weights of stored plants in both 1986 and 1987 (Fig. 1a and b, the permutation-test $P < 0.05$). However, we did not detect a significant linear relationship between colony size and total dry weight of cached plants for either year (Fig. 2a and b, $P > 0.05$). Total dry weights of cached plants were related neither to proportions of sub-adult voles nor to proportions of adult voles. Therefore, age structure did not appear to affect the quantity of food cached by a colony.

Average numbers of voles, by age and sex, in a colony are presented in Table 2. We did not find any juvenile voles (< 1.5 months) in either year. The mean sex ratio (proportion of females) of vole colonies was 0.47 in 1986 and 0.5 in 1987. The proportion of sub-adult voles was inversely related to the number of adults in vole colonies for both 1986 and 1987 (Fig. 3a and b, $P < 0.05$). We did not find any females with fetuses in utero or corpora lutea present in either year. However, 15.1% (14/93) of the adult-I females and 100% (8/8) of the adult-II females had placental scars in 1986 and 20.7% (19/92) of the adult-I females, and

Table 2

Mean numbers of Brandt's voles by sex and age over 18 colonies in 1986 and 14 colonies in 1987 in central Inner Mongolia

Year	Sub-adult voles		Adult-I voles		Adult-II voles		Total	
	Male	Female	Male	Female	Male	Female	Male	Female
1986	1.6 (0.4)	2.4 (0.55)	7.1 (0.5)	5.2 (0.7)	0.1 (0.06)	0.4 (0.15)	8.7 (0.59)	8.1 (0.83)
1987	1.9 (0.56)	3.1 (0.77)	8.7 (0.3)	6.6 (1.2)	0.3 (0.13)	0.9 (0.21)	11.0 (1.4)	10.1 (1.13)

Numbers in parentheses are one standard error.

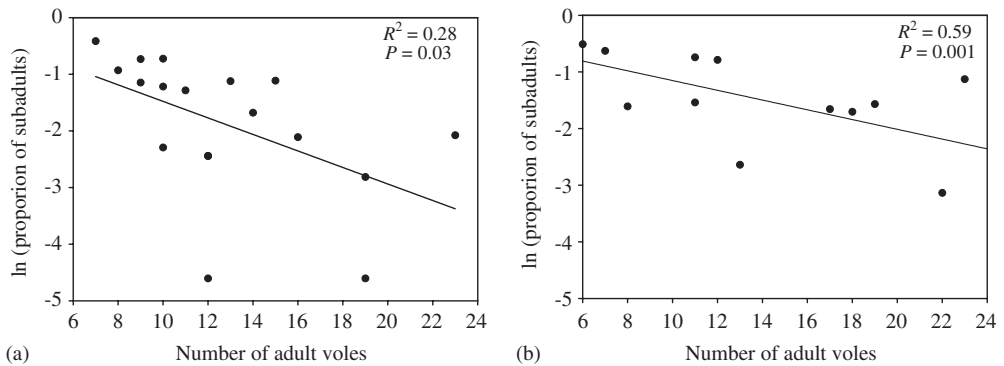


Fig. 3. Relationships between proportions of sub-adult voles and numbers of adult voles of Brandt's vole colonies in central Inner Mongolia in 1986 (a) and 1987 (b).

58.3% (7/12) of the adult-II females had placental scars in 1987. These results suggest that female reproduction had ceased by mid October in 1986 and 1987.

4. Discussion

Brandt's voles cached more food in the high-density year of 1987 compared to that in the low-density year of 1986. Mappes (1998) found that higher con-specific densities stimulated food hoarding of the bank vole (*Clethrionomys glareolus*) in autumn. Animals competing for limited resources may be stimulated to hoard more food (Vander Wall, 1990). Wan et al. (1997) and Shi et al. (1997) observed territory defense behaviour between two Brandt's vole colonies. Mongolian gerbils (*Meriones unguiculatus*), another communal-nesting, food-sharing rodent in Inner Mongolia, competed for caching food along the border of two colonies (Agren et al., 1989). At higher population densities, competition among vole colonies might stimulate a vole colony to store more food for winter. We did not measure plant standing biomass at our site; hence, we could not test if differences in plant standing biomass resulted in differences in vole densities and average dry weights of food cached by a vole colony. It is possible that higher plant standing biomass or availability of cached plants caused higher vole population densities and stimulated vole colonies to store more food.

The quantity of *A. frigida* in the food cache of Brandt's voles increased linearly with increasing total weight of stored food in 1986 and 1987 (Fig. 1a and b). Brandt's voles preferred caching *A. frigida*. *A. frigida* accounted for 94.73% of the total cached food in Taibusi Banner, Inner Mongolia, and the preference index (proportion in the stored food/proportion in total biomass of vegetation) was 6.57 (Shi et al., 1997). In Taiga voles, the percentage of each cached food item was correlated with its frequency of occurrence in the vegetation (Wolff and Lidicker, 1981). In addition, *A. frigida* made up 6.5% of the diet of free-ranging Brandt's voles in summer but 32.4% in autumn; *A. frigida* was, therefore, the most important food of Brandt's voles in autumn on our study site (Wang et al., 2001). *A. frigida* is rich in proteins. The content of crude proteins is about 19–21% of dry weight in autumn; the content of digestible protein is 154 g kg⁻¹ (Shi and Hai, 1996). Shi and Hai (1996) found that Brandt's voles on the *A. frigida*-only diet survived for 285.2 h at -20 °C, more than twice as long as that on the diet of other cached food plants. Zhong et al. (1985a) concluded that *A. frigida* was an important factor influencing habitat selection by Brandt's voles. Brandt's voles select degraded grasslands with abundant *A. frigida*, which is common in the overgrazed grasslands of central Inner Mongolia (Zhong et al., 1985b). However, *A. frigida* is inferior at competition for light with tall grasses and is less abundant in tall and non-degraded grasslands. The restoration of degraded grasslands in central Inner Mongolia resulted in a decline of *A. frigida*, depressed the populations of Brandt's voles, and prevented vole outbreaks (Zhong et al., 1991, 1999).

The quantity of food cached by a vole colony was not related to colony size in either 1986 or 1987 (Fig. 2, $P > 0.05$). It is likely that the standing biomass of *A. frigida* or other plants limited the quantity of food cached by a vole colony. There might not be enough *A. frigida* in the vicinity of a large colony. Wan et al. (1997) found that vegetation standing biomass affected the size of territory used by a Brandt's vole colony for food caching in October; territory size was inversely related to the standing biomass of vegetation. Moreover, the size of storage chambers or con-specific interference might also limit food caching in a large colony. Our results did not support the hypothesis that increased social group size enhances the food acquisition efficiency of overwintering Brandt's voles in a given year or plant biomass.

Several microtine species cache food for winter in northern latitudes (Formozov, 1966; Gates and Gates, 1980; Mappes, 1998; Benedict and Benedict, 2001). Taiga voles (*Microtus xanthognanthus*) also had collective, communal food caches (Wolff and Lidicker, 1981). Communal food sharing is an adaptive strategy of social rodents for food scarcity during the winter (Wolff, 1984; Vander Wall, 1990). Construction and maintenance of storage chambers as well as food gathering are energy-consuming, labor-intensive tasks. Communal food caching probably contributes to social bonding of Brandt's voles (Vander Wall, 1990; Lacey and Wiczorek, 2003). On the other hand, communal food caching would incur fitness costs because only a few voles of a colony survived severe winters (Wan, pers. comm.). It is still unknown how the quantity of stored food in a colony affects the survival of over-wintering voles and the reproduction of the voles in spring. Prairie voles have an optimal size social group; the fitness of individual voles in male–female pairs and social groups of more than 3 voles is lower than that of communal groups of 3 individuals (McGuire et al., 2002). Future studies with manipulation of colony size and quantity of stored food are needed to reveal ecological importance of cached food for winter survival and spring reproduction of Brandt's voles.

Proportions of sub-adult voles, born in July, decreased with increasing number of adult voles in October of both years (Fig. 3a and b). By November, female reproduction had ceased. Brandt's voles regrouped before food caching, and some sub-adult voles emigrated (Wan, pers. comm.). However, the emigration of sub-adult voles before food caching is poorly understood in Brandt's voles.

Communal nesting of New World microtine rodents displays seasonal patterns. Communal or group nesting mainly took place during the winter and early spring (Madison, 1984; Wolff and Lidicker, 1981), but pine voles (*Microtus pinetorum*) communally nested throughout the year (Madison, 1984). Although some prairie voles communally nested throughout the year, communal groups were rare in spring and summer (Getz et al., 1993). Seasonality of communal nesting invokes the hypothesis that communal nesting is an evolutionary adaptation to cold. However, Getz et al. (1993) did not find correlations between social group size and daily temperature during winter. Instead Getz et al. (1993) attributed prevalent communal groups in winter to reduced predation pressure, resulting in increased survival. Communal food caching is less common in prairie voles compared to Brandt's voles. Only two of 30 excavated burrows of prairie voles contained food caches (Mankin and Getz, 1994). Prairie voles also have smaller social groups than Brandt's voles. It is uncertain how the difference in food caching behaviour contributes to the difference in social behaviour between the two, year-round communal nesting voles.

Burrow digging of small mammals imposes extensive, long-lasting perturbations to soil and biogeochemical cycling of ecosystems (Weiner et al., 1982; Schauer, 1987; Whitford and Kay, 1999). Burrows with food chambers are somewhat more complex (Reichman and Smith, 1991). In prairie voles, communal-burrow systems occupied a greater area, and volumes of nest chamber of communal groups were greater than that of male–female pairs (Mankin and Getz, 1994). Brandt's voles constructed complex burrows in the Mongolian Plateau (Schauer, 1987). Construction and maintenance of burrows redistribute and mix soil across soil layers of different depths. However, it is unknown how colony size of Brandt's vole affects the perturbation to soil and ecosystem functions through burrowing behaviour. Future studies of the relationships between vole colony size, rate of surface soil deposition from burrowing, volume of burrows, and nitrogen cycling will improve understanding the roles of Brandt's voles in Inner Mongolian grassland ecosystems.

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