Shifts in activity patterns of *Microtus gregalis*: a role of competition or temperature?

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Although temporal partitioning has long been viewed as a valid mechanism in reducing competition, direct field evidence is rare, and the temporal niche is often considered less important than other factors in promoting coexistence. Furthermore, the relative importance of biotic and abiotic factors in shaping diel activity patterns of animals is poorly understood. We conducted controlled experiments in a little-studied area (Hulunbuir meadow steppe, China) to explore the effects of presence of a larger species, *Spermophilus dauricus*, and ambient temperature in shaping diel activity patterns of *Microtus gregalis*. Our results suggest that although interference competition existed between *S. dauricus* and *M. gregalis*, the presence of *S. dauricus* did not significantly affect the diel activity patterns of *M. gregalis* ($P > 0.05$). Timing of activity of *M. gregalis*, however, was always significantly correlated with ambient temperature ($P < 0.001$). As winter approached, ambient temperature appeared to be a major factor in shaping activity patterns of *M. gregalis*. To our knowledge, this is the 1st experimental study conducted in an East Asian steppe to integrate the roles of both biotic and abiotic factors in shaping rodent activity patterns.

Key words: activity pattern, ambient temperature, interspecific competition, rodent, temporal niche

Due to the rotation of the earth, living organisms face a periodically changing world. A relatively rigid and self-sustaining biological clock is thus adaptive in a highly predictable environment; however, flexibility for responding to ecological events that occur less regularly and are more difficult to anticipate also is necessary. On a behavioral level, this flexibility is indicated by masking effects, that is, rapid and reversible shifts in activity patterns that do not involve a pacemaker (Mrosovsky 1999). Shifts in diel activity patterns may reflect interspecific competition and partitioning along temporal niche axes may reduce competition and foster coexistence (Ziv et al. 1993; Ziv and Smallwood 2000; Gutman and Dayan 2005). Although temporal partitioning has been considered relatively unimportant (Schoener 1974), a growing body of empirical evidence for this phenomenon has accumulated in the last few decades (Kronfeld-Schor and Dayan 2003).

Many field studies on temporal partitioning focus on interaction between taxonomically close species, for example, common vole (*Microtus arvalis*) and east European vole (*M. rossiaemeridionalis*) (Tikhonov et al. 2009), common spiny mouse (*Acomys cahirinus*) and golden spiny mouse (*A. russatus*) (Shkolnik 1971; Gutman and Dayan 2005), and *Gerbillus allenbyi* and *G. pyramidum* (Ziv et al. 1993). This emphasis reflects the belief that species with similar morphologies and ecological niches are prone to competition. However, it is suggested that different activity patterns mean different evolutionary adaptations and taxonomically close species tend to possess similar activity patterns (Daan 1981). Under this scenario, evolutionary constraints may limit the potential for temporal partitioning; this may partly explain the relative scarcity of temporal segregation observed in the field (Daan 1981; Kronfeld-Schor et al. 2001; Roll et al. 2006). By contrast, both theoretical and empirical evidence support the hypothesis that interference competition stimulates temporal partitioning (Glass and Slade 1980; Carothers and Jaksic 1984; Ziv et al. 1993), which to some extent relaxes the requirement for similarity between species. Thus, temporal partitioning may occur between distantly related species or even within various functional groups.

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In addition to interspecific competition, a number of other biotic and abiotic factors may lead to shifts in an individual's activity patterns. Such factors include predation risk (Flecker 1992; Orr 1992; Fenn and Macdonald 1995), intraspecific competition (Alanara et al. 2001), food availability (Lockard 1978; Orpwood et al. 2006), reproductive status (Schrader et al. 2009), nutritional status (Metcalfe and Steele 2001), habitat (Wasserberg et al. 2006), and physical factors (Griffiths 1984; Fraser et al. 1993). Most studies of diel activity patterns tend to focus on only one of these aspects (Wasserberg et al. 2006) and fail to consider the relative importance of other factors. Meanwhile, direct evidence supporting temporal partitioning as a result of interspecific competition is rare (Kronfeld-Schor and Dayan 2003). Mechanistic and experimental approaches are needed to identify the drivers responsible for shifts in diel activity patterns.

Here, we report our 2-year study on 2 sympatric rodent species with a distant taxonomic relationship and differences in body size. This study was conducted on the Hulunbuir meadow steppe, which hosts a rodent community that is typical of East Asia, although it has received little attention from researchers thus far. It features 2 sympatric, distantly related rodent species: the relatively large Daurian ground squirrel (*Spermophilus dauricus*, 250 g) and the smaller narrow-headed vole (*Microtus gregalis*, 30 g). Previous studies indicate that interference competition exists between these 2 species and *M. gregalis* seems to be individually inferior to *S. dauricus* (see "Materials and Methods" for details). In the present study, we report that *M. gregalis* changes its activity patterns when *S. dauricus* hibernates (see "Results" for details), which might also result from interspecific interactions. However, other factors also may contribute to this shift in diel activity patterns. For small rodents faced with the challenge of thermal regulation, ambient temperature is a frequently cited constraint on activity patterns (Bozinovic et al. 2000; Paise and Vieira 2006; Vieira et al. 2010). This may be extremely important on the Hulunbuir meadow steppe because of the large variation in near-ground temperatures throughout the day.

In this study, we investigated the roles of interspecific interference and ambient temperature in shaping activity patterns of *M. gregalis*. We conducted field experiments, spanning different seasons, in which *M. gregalis* was kept in enclosures with and without *S. dauricus*. We were particularly interested in 2 questions: would *M. gregalis* adopt temporal avoidance to reduce interference of *S. dauricus*?, and would ambient temperature be significantly correlated with the activity level of *M. gregalis*?

MATERIALS AND METHODS

Study system.—Our study area was located on the Hulunbuir meadow steppe in northeastern China (49°19′N, 120°05′E, 600 m above sea level). The climate is markedly seasonal, with an average annual temperature of −3–1°C and average annual precipitation of 250–520 mm.

Spermophilus dauricus and *M. gregalis* are the 2 most common species found in this area, although Daurian pikas (*Ochotona dauurica*) and striped dwarf hamsters (*Cricetulus barabensis*) also are found at the site. According to previous trapping records (Ma 1965; Luo 1975), *S. dauricus* and *M. gregalis* have been coexisting here for at least 35 years. Both species are completely ground-dwelling herbivores, although *S. dauricus* also eats some insects during summer (Luo 1975). *S. dauricus* hibernates in winter, whereas *M. gregalis* does not. *S. dauricus* reproduces once a year (normally in spring—Luo and Zhong 1990), whereas *M. gregalis* generally reproduces twice a year (normally in late spring and summer—Ma 1965). In autumn, both species are most active and abundant in number. In a previous enclosure experiment carried out in 2011 (with similar experimental population densities as used in the enclosure experiments below), *M. gregalis* significantly altered its spatial distribution after *S. dauricus* was introduced to the area (L.-Y. Shuai, pers. obs.). Moreover, when *S. dauricus* was present, *M. gregalis* was significantly less active (C.-L. Ren, pers. obs.). When both species were kept in a small arena (2 × 2 m), *S. dauricus* often attacked and even killed *M. gregalis* although *S. dauricus* never fed on voles (L.-Y. Shuai and C.-L. Ren, pers. obs.). These findings suggest that interference competition exists between these 2 species and *M. gregalis* is at a competitive disadvantage compared to *S. dauricus*, although the precise nature of these interactions remains unclear.

Pilot study.—First, a pilot study was performed to characterize natural activity patterns of *S. dauricus* and *M. gregalis* in our study area. It was conducted in a large, cattle-proof enclosure (~34 ha). The vegetation was diverse and dominated by *Leymus chinensis*, *Artemisia tanacetifolia*, *Stipa baicalensis*, *Carex duriuscula*, and *Iris ventricosa*. The vegetation cover was about 65% and the height of the tallest vegetation was about 25 cm. Livetrapping was launched in mid-July 2009 and lasted until late September 2009. Twenty trapping rounds were conducted, and each included 3 full days of trapping. We randomly selected 12 plots in the cattle-proof enclosure and placed a square grid with 36 trapping stations (spaced at 10 m apart) in each plot. To assure independence among plots, all plots were spaced at least 150 m apart. During each round, we conducted livetrapping in 4 randomly selected plots, but no plot was used in 2 successive rounds. A locally made wire cage (12 × 15 × 30 cm) was placed at each trap station, and fried peanuts were used as bait. A piece of cotton was placed in each cage to keep the animals warm during the night.

Each cage was equipped with a digital timer, similar to that used by Paise and Vieira (2006). The timer was triggered when the cage closed, indicating the time of capture to the nearest minute. We checked cages, rebaiting them as necessary, at dawn (0700–0800 h), noon (1100–1300 h), and dusk (1700–1900 h). The location and time of each capture was noted. Each trapped animal was weighed, sexed, marked with dye (if captured for the 1st time), and then released immediately.

Experiments.—Our experiments were carried out in 4 vole-proof enclosures (50 × 50 m) near the pilot study site. They

were similar to the cattle-proof enclosure used in the pilot study with respect to topography and vegetation and were constructed of 10-mm wire mesh, buried 70 cm into the ground and standing 100 cm high. The top 30 cm of both sides of the fence were covered with aluminum flashing to prevent rodents from escaping. Prior to the experiments, all resident animals were trapped and removed. Natural enemies, such as raptors, could enter the enclosures freely. However, based on the data collected in the pilot study, these predators did not represent a significant source of mortality for the enclosed rodents.

We adopted a classical additive experimental design (Gurevitch et al. 1992) in which the behavior of the target species (*M. gregalis*) with and without the presence of the potential competitor (*S. dauricus*) was compared. This is equivalent to the Type 1 design defined by Connell (Connell 1983). In each enclosure, a square grid with 49 trapping stations (spaced at 8 m apart) was designated and a cage equipped with a digital timer was placed at each station. Animals used in this study were captured from the cattle-proof enclosure used in the pilot study. We placed 20 nonbreeding adult *M. gregalis* (8 males and 12 females) in each enclosure. In each of the 2 treatment enclosures, we also added 4 adult *S. dauricus* (2 males and 2 females) 1 day later. The remaining 2 enclosures served as controls. The experimental densities of both species were based on their natural distribution, as determined in previous studies. All individuals were permanently marked and introduced into the enclosures at least 2 weeks before the experiments started, allowing them to acclimate to the enclosures, bait, and cages. Because our aim was to characterize the effect of *S. dauricus* on the behavior of *M. gregalis*, we used smaller cages (7 × 8 × 20 cm) in our experiments to minimize trapping of *S. dauricus*. Our whole study followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and ethics approval was given by Animal Ethics Committees at Institute of Zoology, Chinese Academy of Sciences.

Experiments were carried out in the autumn and early winter of 2012 (late August to early October). The experiments were initiated about 1 month later in the year than the pilot study, conducted in 2009, due to a relatively long summer in 2012. Four rounds of trapping (each lasting 4 days) were conducted, separated by intervals of at least 10 days. During these breaks, cages were kept in place but left unbaited and closed. To avoid the potential effects of lunar phases on animal behavior, all rounds were carried out on days associated with a half-full moon at night. Trapping procedures were similar to those described for the pilot study.

Air temperature was measured 15 cm above the ground every 10 min during trapping rounds using 4 Hobo data loggers (Onset Corporation, Bourne, Massachusetts; measurement range: −10–50°C, to the nearest 0.1°C). A data logger was placed at the center of each enclosure, and temperature data were extracted immediately after each round ended.

Data analysis.—In the pilot study, we collected trapping data for both *M. gregalis* and *S. dauricus*. Trapping data were first divided into 2 parts: Period 1 (14 July–28 August, during

which the presence of *S. dauricus* was recorded with average temperature 13.62°C ± *SE* 1.54°C), and Period 2 (29 August–29 September, during which no individuals of *S. dauricus* were captured with average temperature 7.58°C ± 2.21°C). For each species in each period, we pooled the captures in 1-h periods (summed over all measurement days) and used the number of captures in each hour (hereafter referred to as capture frequency) to represent the activity level for that hour. To detect the effect of the presence of *S. dauricus* on the activity patterns of *M. gregalis*, we conducted Kolmogorov–Smirnov 2-sample tests to compare the temporal distribution of capture frequencies of *M. gregalis* in Periods 1 and 2. We also conducted Kolmogorov–Smirnov 2-sample tests to assess differences in activity patterns between the 2 species in Period 1.

In our experiments, we also collected capture data for both *M. gregalis* and *S. dauricus*, but because of the small number of trappings of *S. dauricus*, only data for *M. gregalis* were analyzed. As in the pilot study, we used capture frequencies to represent the activity level in a given period. For each experimental round, we first assessed the potential effects of sex and enclosure (stratified by treatment) on diel activity patterns by comparing capture frequencies in different time periods using Kolmogorov–Smirnov 2-sample tests. No significant differences were found, so we pooled the data for subsequent analysis.

We adopted the index of diurnality (I_D) introduced by Halle (1995) to assess the relative distribution of activity between day and night for each round. I_D is positive if animals are mainly diurnal (maximum +1, if totally diurnal) and negative if nocturnal activity prevails (minimum −1, if totally nocturnal). To determine whether the presence of *S. dauricus* affected the activity patterns of *M. gregalis*, we compared distribution patterns of capture frequencies between treatments in each round using Kolmogorov–Smirnov 2-sample tests. We then conducted a Kruskal–Wallis 1-way analysis of variance to assess seasonal effects on activity patterns (experimental round represented the group factor) and used Kolmogorov–Smirnov 2-sample tests to perform pairwise between-round comparisons. We assessed the relationship between activity level and ambient temperature using linear regression, using capture frequencies in each hour as the dependent variable and the average of 24 measures of air temperature (6 measures per logger) during that period as the independent variable. All statistical work was conducted using SPSS Statistics 19 (SPSS Inc., Chicago, Illinois) and Microsoft Excel 2007 (Microsoft Corp., Redmond, Washington).

RESULTS

Pilot study.—During the pilot study we captured 91 *S. dauricus* (47 males and 44 females; 122 trapping records), 475 *M. gregalis* (211 males and 264 females; 1,282 trapping records), 24 *O. dauurica* (14 males and 10 females; 24 trapping records), and 4 *C. barabensis* (3 males and 1 female; 4 trapping records). Trappings of *O. dauurica* and *C. barabensis* were
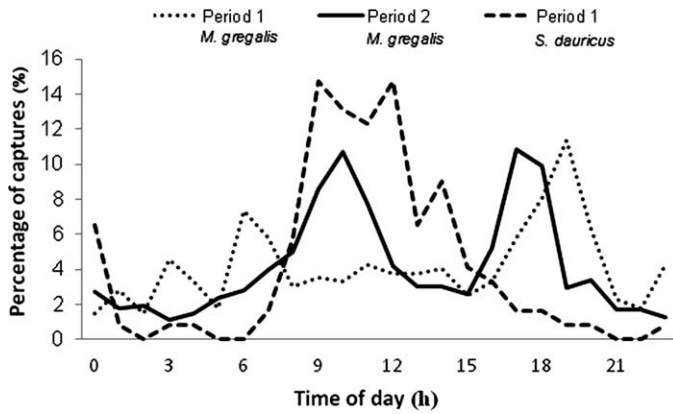
FIG. 1.—Diel activity patterns of *Microtus gregalis* and *Spermophilus dauricus* during the pilot study. Data for *M. gregalis* were subdivided into 2 parts (Period 1—from 14 July to 28 August, and Period 2—from 29 August to 29 September, in 2009). For convenience of comparison, here we used percentage of captures rather than capture frequencies to represent activity level. Number of captures: 396 *M. gregalis* in Period 1, 122 *S. dauricus* in Period 1, and 886 *M. gregalis* in Period 2.

relatively rare at this site, and their effects on *M. gregalis* and *S. dauricus* may have been negligible. The capture rate for *M. gregalis* in Period 2 (143 males and 197 females; 886 trapping records) was much higher than in Period 1 (68 males and 67 females; 396 trapping records).

Microtus gregalis and *S. dauricus* displayed significantly different diel activity patterns in Period 1 ($P < 0.001$; see Fig. 1). *S. dauricus* had an approximately unimodal pattern with a peak at midday, whereas *M. gregalis* displayed a polyphasic pattern. Although it may appear from Fig. 1 that *M. gregalis* was less active during the activity peak of *S. dauricus*, in actuality, there was no significant correlation between capture frequencies of the 2 species (Pearson's $r = -0.167$, $P = 0.435$).

Microtus gregalis showed significant variation in activity patterns between Periods 1 and 2 ($P < 0.001$; Fig. 1). In Period 2, *M. gregalis* followed a bimodal pattern with 2 significant peaks occurring at morning and dusk. In Period 1, at least 3 peaks could be found, at night, dawn, and dusk.

Experiments.—Average ambient temperature decreased from Round 1 to Round 4 (Round 1: 16.82°C $\pm$ *SE* 1.13°C; Round 2: 10.86°C $\pm$ 1.17°C; Round 3: 10.11°C $\pm$ 1.11°C; Round 4: 5.84°C $\pm$ 1.50°C). A total of 1,252 trapping records were collected during our experiments, most of which belonged to *M. gregalis* (1,189 trapping records). There also were 53 trapping records of *S. dauricus* but no *S. dauricus* was captured in Round 4. There were 273 (63 individuals), 266 (58 individuals), 455 (71 individuals), and 379 (61 individuals) captures of *M. gregalis* in Rounds 1, 2, 3, and 4, respectively.

Examination of our data suggested that although *M. gregalis* always maintains some level of activity during the night, it can be viewed as a primarily diurnal species in our study area. The index of diurnality indicated that from autumn to winter, our experimental population of *M. gregalis* generally became more diurnal (control group: $I_D = 0.535$, 0.628, 0.678, and 0.821 in

Rounds 1, 2, 3, and 4, respectively; treatment group: $I_D = 0.552$, 0.790, and 0.642 in Rounds 1, 2, and 3, respectively). In each round and each treatment, the most prominent activity peak generally occurred in the afternoon, between 1300 and 1700 h (Fig. 2).

In Rounds 1–3, we found no significant differences in diel activity patterns of *M. gregalis* between treatments (Round 1: $P = 0.350$; Round 2: $P = 0.992$; Round 3: $P = 0.703$). However, seasonal effects on activity did exist (Kruskal–Wallis test: $P < 0.001$), and most pairwise comparisons of activity suggested significant between-round differences as well (Table 1). In Round 4, *M. gregalis* showed more intense and continuous activity than usual during the daylight hours.

Linear regression analysis indicated that in each round, ambient temperature was always significantly associated with the diel activity patterns of *M. gregalis* (Table 2; Fig. 3). This relationship is much more apparent in Round 4, in which ambient temperature accounted for a large portion of the variance in activity level. It can be inferred from Fig. 2 that *M. gregalis* follows a more unimodal activity pattern in Round 4. Meanwhile, the correlation coefficients indicated that the activity level of *M. gregalis* was least sensitive to ambient temperature in Round 1 (Table 2).

DISCUSSION

Interspecific competition has long been viewed as a possible driver of temporal niche shifts and temporal partitioning. However, direct experimental evidence for this idea is rare, and the relative importance of various ecological factors in

TABLE 1.—Pairwise comparison of diel activity patterns of *Microtus gregalis* between experimental rounds. *P*-values for Kolmogorov–Smirnov 2-sample tests are given (* $P < 0.05$; ** $P < 0.01$).

Round	2	3	4
1	0.031*	0.005**	0.110
2		0.198	0.001**
3			< 0.001**

TABLE 2.—The effect of ambient temperature on activity level (capture rate) of *Microtus gregalis*, assessed using linear regression (TEMP: ambient temperature; ** $P < 0.01$).

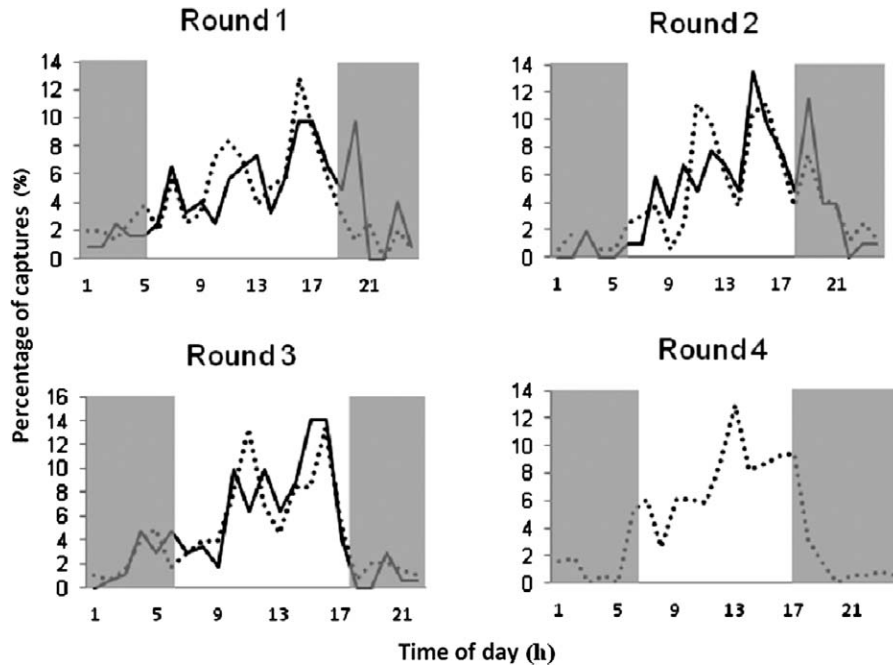|	Coefficient	SE	t-value	P	Adjusted R^2
Round 1					
Constant	0.770	0.392	1.960	0.054	
TEMP	0.109	0.028	3.856	< 0.001**	0.163
Round 2					
Constant	0.412	0.366	1.124	0.265	
TEMP	0.135	0.025	5.406	< 0.001**	0.284
Round 3					
Constant	1.532	1.048	1.480	0.143	
TEMP	0.342	0.076	4.504	< 0.001**	0.214
Round 4					
Constant	4.440	0.646	6.871	< 0.001**	
TEMP	0.414	0.046	8.958	< 0.001**	0.524

Fig. 2.—Activity patterns of *Microtus gregalis* during 4-round enclosure experiments in 2012. Dotted line: *M. gregalis* only; solid line: *M. gregalis* + *Spermophilus dauricus*. The shaded areas represented night hours. Timing of 4 rounds: Round 1—23–26 August; Round 2—6–9 September; Round 3—20–23 September; Round 4—6–9 October. Number of captures (*M. gregalis* only versus *M. gregalis* + *S. dauricus*): Round 1—150 versus 123; Round 2—162 versus 104; Round 3—284 versus 171; Round 4—379 versus 0.

affecting the timing of activity is poorly known. Our study is one of only a few that has compared the effects of interspecific competition and abiotic factors such as temperature on the activity patterns of rodents.

Previous studies dealing with interspecific competition between microtine species or between microtine species and other rodents have often produced somewhat puzzling results. For example, spatial rather than temporal segregation was observed between prairie voles (*Microtus ochrogaster*) and southern bog lemmings (*Synaptomys cooperi*), with the former considered the dominant species in one-to-one interactions (Danielson and Swihart 1987). However, in the same study area, Glass and Slade (1980) detected competition-induced temporal partitioning between prairie voles and cotton rats (*Sigmodon hispidus*), with *S. hispidus* being the dominant species. There seems to be no simple answer here. As Ziv and Smallwood (2000) suggested, even for a given limiting factor, there may exist several solutions to generate niche partitioning required for coexistence. Our study suggests that, although interference competition exists between *S. dauricus* and *M. gregalis*, the presence of *S. dauricus* does not seem to be important in shaping the diel activity patterns of the experimental populations of *M. gregalis*. It is too early, however, to definitively conclude that temporal niche segregation is not important in promoting the coexistence of these 2 species. In our experiments, several important parameters such as population density, sex ratio, and age all were held constant. However, timing of activity in voles is often sensitive to these characters (Halle 2000). One should note that natural populations of microtine species often suffer dramatic seasonal

or annual changes in density, which implies that the potential effects of density also be a factor. Future studies should take these complexities into consideration. Meanwhile, it is also crucial to find out the most significant limiting factor between these species.

Examination of our data suggests that, although not significantly affected by the presence of *S. dauricus*, the diel activity patterns of *M. gregalis* are highly variable seasonally, and that ambient temperature seems to be a possible ecological factor that contributes to this seasonal variation. Although a significant correlation alone does not necessarily mean a causal relationship, we believe that in our study, ambient temperature plays an important role in shaping activity patterns of *M. gregalis*. Previous studies suggest that small mammals tend to change their diel activity patterns to avoid extreme environmental conditions (Kenagy 1973; Bozinovic et al. 2000). The climate of the Hulunbuir meadow steppe is characterized by a dramatic daily variation in temperature and a long, harsh winter that normally lasts 6–7 months per year, in which temperatures often fall below –40°C. As winter approached, we found that ambient temperature became a more important correlate of activity patterns. During the early winter (Round 4 in this study), *M. gregalis* stores a large amount of food in preparation for the time when it is too cold to conduct extensive foraging (L.-Y. Shuai, pers. obs.). Even at this stage, the activity of *M. gregalis* seems to be greatly hampered by the cold weather during nighttime. In other words, ambient temperature appears to be a more important factor as winter approaches. This partially explains why our experimental population became more diurnal and its activity throughout the daytime grew more
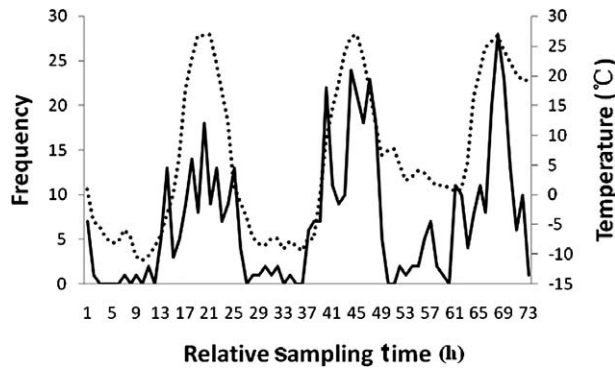
Fig. 3.—Relationship between ambient temperature and capture frequencies of *Microtus gregalis* during the Round 4 enclosure experiment in 2012. Data in 3 days (7–9 October) were used here. Temperature (dotted line) and capture frequencies (solid line) were plotted against relative sampling time (defined as length of interval between capture time and the launch time of Round 4).

continuous. However, consistent with Halle's study (Halle 1995) on root voles (*Microtus oeconomus*), ambient temperature alone explained only a portion of the variance in activity of *M. gregalis*. Ambient temperature in our study generally followed a unimodal diel pattern and therefore could not fully explain the ultradian components of activity patterns (especially in Rounds 1–3), suggesting that other important ecological factors remain. For example, the polyphasic activity pattern that is a characteristic of microtine species may represent a trade-off between eating and avoiding being eaten (Halle 2006). Moreover, the precise relationship between activity patterns and ambient temperature still deserves further laboratory studies.

Our study does not consider the effects of predation risk, another ecological factor that may affect activity patterns of *M. gregalis*. For microtine rodents in our study area, the main predators (Eurasian eagle-owl [*Bubo bubo*] and short-eared owl [*Asio flammeus*]) are nocturnal. There also are some diurnal raptors (steppe eagle [*Aquila nipalensis*]) and crepuscular predators (red fox [*Vulpes vulpes*]) but all are relatively rare in number (L.-Y. Shuai, pers. obs.). Although our trapping records indicate that our experimental population does not suffer significant mortality from predation, it has been suggested that even without actual mortality, the threat of predators alone still can cause significant stress on prey, thereby influencing behavior (Brown and Alkon 1990; Lank and Ydenberg 2003). We suggest that predation avoidance is possibly associated with the general diurnality of voles and also may influence the polyphasic pattern of activity (especially in warmer seasons when nocturnal predators are more abundant). However in the early winter (i.e., Round 4 in our experiments), *M. gregalis* becomes more diurnal and more continuously active, although the activity of the nocturnal predators has decreased dramatically. In this season, ambient temperature seems more likely to be a limiting factor than predation risk. Further studies, however, are needed to explore

the role of predation risk in shaping activity patterns and community structure of rodents in our study system.

In this study, we obtained the exact times that animals were captured by using digital timers attached to cages, an approach that has been utilized in several field studies (Bruseo and Barry 1995; Paise and Vieira 2006; Vieira et al. 2010). Compared to studies that use livetrapping without timers (Shkolnik 1971; Kenagy 1973; Daan and Slopsema 1978; Prochaska and Slade 1981), this method allows less frequent trap-checks, reducing disturbance of the study system while maintaining fine temporal resolution. It also could potentially bias results, however, because captured animals are not available for subsequent recapture, and the cages they occupy are not available to capture animals until the next trap survey (Hicks et al. 1998). Meanwhile, trapping and handling procedures also might have caused disturbance and stress on animals (Halle 1995). Our experimental design could not completely eliminate these potential limitations. However, we think they may not be a serious problem for 2 reasons. First, as Halle (1995) suggested, the main effect of trapping on activity of voles was a decrease in the total activity level rather than significant change in activity patterns. This may have been true in our experiments. Note that in Figs. 1 and 2, most activity peaks occurred in the middle of the interval between 2 trap-checks. This suggests that the curves mainly reflected ecological factors rather than simple trap-and-release events. Second, we implemented similar trap-check protocols for all enclosures and it is therefore likely that any systematic bias in detecting activity would have been largely eliminated when we compared treatments. However, this method would inevitably introduce some artifacts and the attenuated activity peaks during nighttime might be related to this limitation. In future studies, we will adopt alternative techniques such as radiotelemetry to acquire more accurate measurements of activity patterns.

The direct evidence provided by experimental approaches is necessary to solve major ecological problems. Many field studies focusing on desert rodent communities have yielded fruitful insights into community assembly rules and interspecific interactions. Our study on the effect of interspecific interactions and ambient temperature on diel activity patterns in *M. gregalis* represents a pioneering work in a little-studied region, the East Asian steppe. Although much further work is needed, these results represent a 1st step in understanding the various factors that govern the timing of daily activities of rodents.

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