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# Influence of grazing on the activity pattern and temporal niche of two dominant rodent species in Alxa desert

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Grazing by large herbivores can potentially affect interspecific interactions between small herbivores by reducing the ecological fitness of animals. Desert rodents are important components in desert ecosystems and indicators of environmental change. Grazing reduces food resources, but rodents can decrease interspecific niche overlap by adaptive behavior. However, the key factors driving rodent behavioral activities and coexistence in the Alxa desert remains unstudied. We monitored population density and behavioral activities of Midday gerbil (*Meriones meridianus*) and northern three-toed jerboa (*Dipus sagitta*) in a grazing exclusion experiment in Alxa desert, Inner Mongolia, China, in 2017. We assessed the relationship between environmental factors (such as plant height, density, coverage, rainfall and temperature) and the behavioral activities of two coexisting rodent species. The results showed that: (1) In summer, grazing significantly reduced the activity time of gerbil and jerboa compared to that in grazing exclusion areas (gerbil:  $F=5.98$ ,  $p<0.05$ ,  $\eta^2=0.22$ ; jerboa:  $F=8.57$ ,  $p<0.01$ ,  $\eta^2=0.28$ ). Grazing reduced the temporal niche overlap with an obvious shifting of activity peaks between two species. (2) Grazing exclusion enhanced the temporal niche overlap between the two rodent species due to greater food availability which relieved inter-specific competition in each season. (3) Grazing strengthened the sensitivity of rodents to environmental changes in all seasons. These results indicated that grazing affected competition between the rodent species by altering vegetation conditions, which in turn affected the temporal niche and activity patterns of rodents.

## KEYWORDS

desert, rodent, grazing exclusion, activity pattern, temporal niche, coexistence mechanisms

## 1. Introduction

Animal behaviour underlies many critical ecological functions, including nutrient cycling, primary productivity, pathogen transmission and habitat provision (Gribben et al., 2009; Barber and Dingemans, 2010; Palkovacs and Dalton, 2015; Fernandes et al., 2020; Rahelinirina et al., 2021). While every species is inherently linked to ecosystem function, keystone species or ecosystem engineers are far more critical for overall ecosystem function than other species (Wilson et al., 2020). Desert rodents are important components in desert ecosystems and indicators of environmental change (Wu et al., 2016). Human-induced habitat fragmentation has a clear impact on rodents' behavioral fitness (Goulson and Nicholls, 2022). As one of the most extensive land uses worldwide (Wang et al., 2019), grazing causes habitat loss and reduces wildlife (Loggins et al., 2019), which directly contributes to the reduction of biodiversity. In addition, the behavior of species and their interspecific relationships are altered through the influence of indirect and cascading effects (Azevedo et al., 2018). Grazing may change plant quality and food availability for small mammals, and subsequently may affect their population size, survival, body mass and reproduction (Li et al., 2016). The predation risk hypothesis states that trampling by livestock alters the height and coverage of vegetation, making it easier for predators to hunt, and that prey has greater ability to perceive predation risks in sparse, low vegetation (Pereira et al., 2012). Previous studies have shown that animal behavior changed only when human interference reached a certain threshold level. When animals believe that human activities are neither threatening nor beneficial, chronic or repeated interference can promote animal adaptability and tolerance (Smith et al., 2019).

Human activities, such as overgrazing, can reduce the ecological fitness of animals, and potentially affect interspecific interactions (Li et al., 2021). In this context, how to achieve regional coexistence through ecological niche allocation has become a hot issue in conservation biology and animal ecology in recent years (Bu et al., 2016). Temporal niche allocation for sympatric species is one of the main mechanisms supporting stable species coexistence (Sunarto et al., 2015). Animals can adjust their niche width and range through adaptation or behavioral changes to maximize benefits (Kronfeld-Schor and Dayan, 2003). Recently, a growing number of studies have suggested trade-offs in foraging ecology is a mechanism supporting coexistence (Ziv et al., 1993; Brown, 1996). Different activity patterns mean different evolutionary adaptations. Taxonomically close species possess similar activity patterns (Daan, 1981). Temporal partitioning may occur between distantly related species or even within various functional groups (Shuai et al., 2014). Both theoretical and empirical evidence support the hypothesis that interference competition stimulates temporal niche partitioning between sympatric species (Carothers and Jaksić, 1984; Ziv et al., 1993; Navarro-Castilla et al., 2017; Cepeda-Duque et al., 2021).

Direct human presence and indirect impacts on the surroundings of animals could alter their behaviour *via* changing population densities, top-down effects, bottom-up effects and effects on the physical environment (Wilson et al., 2020). Interspecific competition of sympatric species affects their spatiotemporal activities (Odden et al., 2010; Ayala et al., 2021). In addition, many other biotic and abiotic factors may shift individual activity patterns. Such factors include predation risk (Yuan et al., 2017a; Loggins et al., 2019), intraspecific competition (Alanärä et al., 2001), food availability (Tang et al., 2020) and population size (Cui et al., 2015). However, the relative importance of multiple factors acting on rodent species coexistence and the drivers underlying the activity patterns of sympatric species remain unstudied.

Midday gerbil (*Meriones meridianus*) and northern three-toed jerboa (NTJ), *Dipus sagitta* are typical nocturnal dominant rodent species, and coexist in the Alxa desert in China (Wu et al., 2016). They are omnivorous species with similar food habits (Yuan et al., 2018; Yang et al., 2020), and compete for food in the same habitats (Li et al., 2020). Midday gerbil is a quadrupedal forager with food-hoarding habits, while NTJ is a bipedal wanderer with larger home range, and does not store food (Zhao, 1964; Song and Liu, 1984; Shuai et al., 2016). The two species seem to compete, because of similar diets and nocturnal activity. However, they are sympatrically distributed in Alxa desert. These facts seem to violate the niche hypothesis. The climate in the desert is arid and food resources are extremely limited, so there is limited room for compromise in the nutritional niche between Midday gerbils and NTJ. However, the reasons for coexistence of the two species remain unknown. Is the coexistence of the two rodent species caused by rational nighttime allocation? Reasonable time allocation is of great significance to the survival and reproduction of animals (Ebensperger and Hurtado, 2005). Therefore, we hypothesized that: (1) There is strong competition between Midday gerbil and NTJ, and they coexist through temporal niche partitioning. (2) In grazing areas, lower food availability would prolong the activity time of rodents, and decreased vegetation coverage and the expansion of bare land would be beneficial to NTJ, while the vigilance behavior of Midday gerbils in grazing areas would increase. Meanwhile, the NTJ would reduce feeding behavior and increase vigilance in grazing exclusion areas because of dense vegetation. (3) Grazing exclusion would change the key pathways affecting temporal niche and behavioral patterns between sympatric Midday gerbil and NTJ.

## 2. Materials and methods

### 2.1. Study area

This study was conducted in southern Alxa Desert, Inner Mongolia, China, (E104°10'–105°30', N37°24'–38°25'). Our study area has a continental climate with cold and dry winters and warm summers. Annual precipitation ranges from 75 mm to 215 mm,

about 70% of which falls from June to September. The soil is grey desert soil and grey brown soil. The vegetation is sparse, and the plants are mainly xerophytic, super xerophytic and halophytic shrubs. Midday gerbil, NTJ, desert hamsters (*Phodopus roborovskii*) and Mongolian five-toed jerboa (*Orientallactaga sibirica*) are dominant small-mammal species (Yang et al., 2020). Other natural enemies include Eurasian eagle owl (*Bubo bubo*), Marbled polecat (*Vormela peregusna*), and Corsac fox (*Vulpes corsac*; Yuan et al., 2018).

In the study area, we established an experimental area using a randomized block design with 3 blocks and 2 treatments (Yuan et al., 2018), grazing exclusion (3 repeated plots) and grazing (3 repeated plots). Each block covered 240 ha and each treatment unit was 60 ha. The distance between each replicate plot is 300–1,000 m. The grazing exclusion area began to be fenced in 1997, and in the grazing plots grazing began in 1995 with a grazing intensity of 1.03 sheep/ha (Yuan et al., 2017a). Before the exclusion areas were set up, the treatment blocks experienced the same grazing events. Grazed and grazing exclusion plots were enclosed by standard sheep fencing (110 cm high) that prevented livestock movement in or out of plots. Other small mammals and natural enemies were allowed to enter and leave the study area freely. We conducted rodent surveys, plant community surveys, and infrared camera monitoring in May, July, September, and October in 2017. According to the local climatic conditions, we defined May as spring, July as summer, September as autumn, and October as early winter.

## 2.2. Rodent population density survey

A 7 × 8 trapping grid (1-ha) at a 15-m inter-trap distance was established at the center of each plot (60 ha). We placed one wire-mesh live trap (42 cm × 17 cm × 13 cm, Guixi Rodent Equipment Co. Ltd.) at each trap station. Traps were baited with fresh peanuts and checked twice (morning and afternoon) each day. We recorded the species name, sex, reproductive status, capture location, and weight (to the nearest 0.10 g) of the captured individuals. Each captured individual was marked with a passive integrated transponder (PIT; 2.12 mm × 8 mm, Guangzhou Ruimai Intelligent Technology Co. Ltd.) tag with a unique identification number (ID) injected under the pelage. In order to prevent rainfall and other sudden events, a wooden box (15 cm × 10 cm × 10 cm) was placed in the live trap to protect the rodents entering the cage (Yuan et al., 2018). The species and quantity of rodents captured every day in each plot were counted. We live-trapped rodents for four consecutive days in each season. The relative population of captured rodents was calculated according to the hundred cage capture rate (Wu et al., 2016).

## 2.3. Vegetation sampling

We randomly selected three 100 m<sup>2</sup> plots within each treatment unit to sample shrubs in each season. Within each

100 m<sup>2</sup> plot, we randomly placed three 1 m<sup>2</sup> quadrats to sample grasses and forbs. We measured the height, cover, density, abundance and biomass of shrubs and herbs (Yuan et al., 2018).

## 2.4. Camera trapping

After the rodent survey, the live trap was retrieved and an infrared camera trap experiment was conducted in the same grid. Before camera trapping, five points were randomly selected in each grid. We placed fresh peanut bait at 18:00 daily, checked and weighed the remaining peanuts at 06:00 in the next morning. We then chose the point with the highest number of harvested peanuts, and set up one infrared camera (ERE-E1B, Shenzhen Ereagle Technology Co. Ltd) at the selected point in each grid. In total, there were three camera points in both the grazing exclusion and grazing areas. The camera was fixed at a distance of 30 ~ 40 cm from the ground, so that it could monitor the feeding, handling and vigilant behavior of rodents as much as possible. Camera monitoring continued from 18:00 to 06:00. Camera trapping was conducted for four consecutive days each month. To effectively observe the foraging behavior of rodents, peanuts (about 10 g) were selected as attractants. Other studies on mammals have shown that the use of attractants does not affect abundance and density estimates, distance moved or activity patterns (Preez et al., 2014; Braczkowski et al., 2016). We recorded the shooting time of each video, species, appearance time, departure time, rodent behavior, and duration time of each behavior.

## 2.5. Statistical analyses

We used the overlap package in R 4.1.2, which was developed specifically for the visualization and activity patterns analysis for camera trapping data. Activity patterns were performed using kernel density estimates which describe the probability of a camera-trap event occurring at any given time (Linkie and Ridout, 2011). We then ran the procedure developed by Ridout and Linkie (2009) to determine the overlap coefficient of activity patterns between different rodent species. Overlap was defined as the area under the curve formed by taking the minimum of the two kernel density estimates at each point in time (Ridout and Linkie, 2009). We used  $\Delta 4$  for large samples (>75 camera records; Azevedo et al., 2018), and the  $\Delta 1$  estimator was used when the number of events was less than 50. Confidence intervals were generated using the basic0 estimation for 10,000 bootstrapped samples (Meredith and Ridout, 2017).

A rodent ethogram during foraging was obtained from previous observations (Shang, 2005; Wang et al., 2015; Table 1). We calculated the ratio of a given behavior duration to the total activity time in 1 day, and the duration of the active period (Azlan and Sharma, 2006; Bach et al., 2017). All the data involved in this paper have been Shapiro - Wilk tested, in which activity pattern ( $p > 0.05$ ,  $n = 12$ ) and population density ( $p > 0.05$ ,  $n = 12$ ) all

TABLE 1 Rodent ethogram.

Activity	Definition
Foraging	During the movement process, a series of actions such as crawling to search for food through smell, smelling the ground and vegetation, etc.
Feeding	In standing, sitting, squatting or lying down positions, grabbing food with both front claws to assist in gnawing and chewing food.
Storage	Taking food away from the feeding point and bringing it back to the nest or finding temporary shelter.
Vigilance	Observing the surrounding environment in a standing, sitting or squatting position, often accompanied by head twisting, for longer than 3 s.; or interrupting ongoing behaviors (such as running, feeding, foraging, etc.) and quickly leaving the feeding point.
Fighting	Behavior of two individuals biting, threatening, chasing, fleeing, trembling, avoiding, etc.

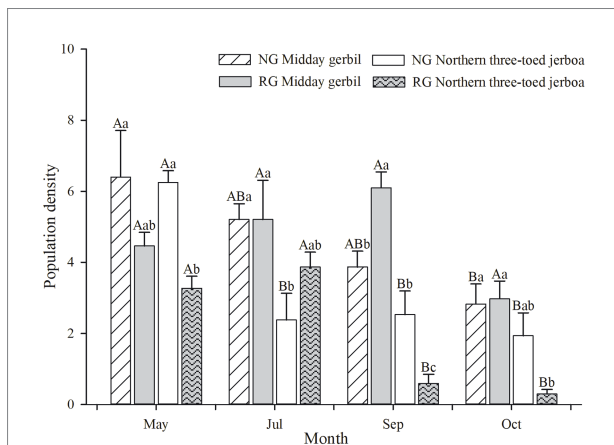


FIGURE 1

Seasonal changes in population densities of Middy gerbil, northern three-toed jerboa. NG represent the grazing exclusion area, RG represent the grazing area. Different capital letters (A and B) indicate that the population density of rodents varied significantly between seasons; different lowercase letters (a and b) indicate significant differences in population density of rodents in the same season.

conform to the normal distribution. In addition, the activity duration have been normalized ( $\log(n+1)$ ) prior to the analysis. Activity duration and patterns under different grazing treatments and seasonal difference was analyzed with the two-way repeated measures ANOVA using SPSS Statistics. SigmaPlot 12.0 was used for the plot.

We used random forest (RF) to evaluate the relationship of environmental factors with the duration of each behavior. RF analysis was performed to identify the major driving factors and to estimate the importance of the variables. We used percentage increases in mean squared error (MSE) of variables, where a

higher MSE% value implied a more important variable. Analysis was conducted using the “rfPermute” package in R (Jiao et al., 2021). Calculation of the correlation coefficient and the visualization of the heat map are all realized through “link ET” (Huang, 2021).

### 3. Results

A total of 6,629 videos were shot over the study. The total shooting time was 4,917 min, and the total duration of rodent activity was 1,448 min. Five rodent species, including Middy gerbil, NTJ, desert hamsters, Mongolian five-toed jerboa, and Alashan ground squirrel (*Spermophilus alaschanicus*) were captured by the cameras.

#### 3.1. Population density

There were significant seasonal differences in the population ( $F_{(3,44)}=9.42$ ,  $p<0.01$ ,  $\eta^2=0.36$ ). In the grazing exclusion plots, the population density of Middy gerbil decreased from spring to early winter ( $F_{(3,44)}=12.34$ ,  $p<0.001$ ), and NTJ population in spring was significantly higher than in other seasons ( $F_{(3,44)}=20.64$ ,  $p<0.001$ ). The population density of Middy gerbil was significantly higher than that of NTJ in summer ( $F_{(3,44)}=3.391$ ,  $p<0.05$ , Figure 1).

In the grazing area, there was no significant difference in the population density of Middy gerbil in different seasons ( $F_{(3,44)}=0.44$ ,  $p>0.05$ ), and the NTJ populations in spring and summer were significantly higher than in autumn and early winter ( $F_{(3,44)}=52.36$ ,  $p<0.001$ ). The population density of Middy gerbil was significantly higher than that of NTJ in autumn ( $F_{(3,44)}=23.874$ ,  $p<0.001$ , Figure 1).

Grazing exclusion promoted higher NTJ population density than in the grazing treatment, both in spring ( $F_{(3,44)}=4.314$ ,  $p<0.05$ ) and autumn ( $F_{(3,44)}=23.874$ ,  $p<0.001$ ). Grazing exclusion induced higher population density of Middy gerbil than that in the grazing area in early winter ( $F_{(3,44)}=6.086$ ,  $p<0.01$ , Figure 1).

#### 3.2. Daily activity pattern

The activity time of the two species had a large overlap, and there were seasonal differences in the daily activity pattern. In spring, the niche overlap index of Middy gerbil with NTJ was higher than other seasons, both in the grazing exclusion and the grazing areas ( $\Delta$ grazing exclusion = 0.8994,  $\Delta$ grazing = 0.9549). The activity peak of the two species was concentrated at 20:00. Grazing promoted higher activity intensity of both species compared to the grazing exclusion area (Figures 2A,E). In summer, the niche overlap index of the two species was 0.8890 in the grazing exclusion area (Figure 2B). Grazing induced a clear

staggered peak pattern in the daily activity rhythm pattern of the two species, and the overlap index of two species was 0.6329 (Figure 2F). In autumn, the niche overlap index of the two species was 0.8496 in the grazing exclusion area. There was an obvious staggered activity peak pattern in the grazing area ( $\Delta=0.7957$ , Figures 2C,G). In early winter, the overlap index of the two species was 0.7195 in the grazing exclusion area (Figure 2D). There was a staggered peak pattern in the grazing area and the niche overlap index of the two species was 0.8329 (Figure 2H).

### 3.3. Activity duration of rodent species

There were significant seasonal differences in the activity duration of Midday gerbil and NTJ (Midday gerbil:  $F_{(3,44)} = 11.87$ ,  $p < 0.001$ ,  $\eta^2 = 0.35$ ; NTJ:  $F_{(3,44)} = 12.26$ ,  $p < 0.001$ ,  $\eta^2 = 0.358$ ). In the grazing exclusion area, Midday gerbil had the longest activity duration in spring and autumn ( $F_{(3,44)} = 2.94$ ,  $p > 0.05$ ,  $\eta^2 = 0.31$ ), while the NTJ activity duration reduced in early winter ( $F_{(3,44)} = 7.39$ ,  $p < 0.01$ ,  $\eta^2 = 0.53$ ). In the grazing area, Midday gerbil and NTJ were active longer in spring and autumn than that in other seasons (Midday gerbil:  $F_{(3,44)} = 6.55$ ,  $p < 0.01$ ,  $\eta^2 = 0.49$ ; NTJ:  $F_{(3,44)} = 4.52$ ,  $p < 0.05$ ,  $\eta^2 = 0.40$ ). In summer, the Midday gerbil and NTJ activity duration was significantly longer in the grazing exclusion area than in the grazing area (Midday gerbil:  $F_{(1,22)} = 5.98$ ,  $p < 0.05$ ,  $\eta^2 = 0.22$ ; NTJ:  $F_{(1,22)} = 8.57$ ,  $p < 0.01$ ,  $\eta^2 = 0.28$ ; Figure 3).

### 3.4. Time allocation pattern

In the grazing exclusion area, Midday gerbil showed significant foraging behavior in spring and summer ( $F_{(3,44)} = 6.82$ ,  $p < 0.01$ ), storing behavior in autumn and early winter ( $F_{(3,44)} = 10.48$ ,  $p < 0.01$ ), and most fighting behaviour in autumn ( $F_{(3,44)} = 7.89$ ,  $p < 0.01$ ; Table 2). NTJ allocated significantly more time for foraging behavior in spring than that in early winter ( $F_{(3,44)} = 5.60$ ,  $p < 0.01$ ), and showed notable vigilance in spring ( $F_{(3,44)} = 5.20$ ,  $p < 0.01$ ). There were no significant seasonal differences in storing, feeding and fighting behavior of NTJ among seasons (Storing:  $F_{(3,44)} = 0.86$ ,  $p > 0.05$ ; Feeding:  $F_{(3,44)} = 0.51$ ,  $p > 0.05$ ; Fighting:  $F_{(3,44)} = 2.14$ ,  $p > 0.05$ ; Table 3). In the grazing area, Midday gerbils showed significant foraging behavior and vigilance behaviour in spring and summer (Foraging:  $F_{(3,44)} = 13.47$ ,  $p < 0.01$ ; Vigilance:  $F_{(3,44)} = 3.89$ ,  $p < 0.05$ ), storing behavior in autumn ( $F_{(3,44)} = 4.69$ ,  $p < 0.01$ ), and feeding behavior peaked in spring ( $F_{(3,44)} = 9.64$ ,  $p < 0.01$ ; Table 2). In the grazing area, NTJ showed more vigilance behavior in spring ( $F_{(3,44)} = 4.66$ ,  $p < 0.01$ ), and no seasonal differences in their other behaviors (Foraging:  $F_{(3,44)} = 2.42$ ,  $p > 0.05$ ; Storing:  $F_{(3,44)} = 1.15$ ,  $p > 0.05$ ; Feeding:  $F_{(3,44)} = 0.76$ ,  $p > 0.05$ ; Vigilance:  $F_{(3,44)} = 2.16$ ,  $p > 0.05$ ; Table 3).

In spring, the vigilance behavior of NTJ in the grazing exclusion area was significantly longer than that in the grazing

area ( $F_{(1,22)} = 4.95$ ,  $p < 0.05$ ). In summer, the storing behavior of NTJ in the grazing exclusion area was significantly longer than that in the grazing area ( $F_{(1,22)} = 4.63$ ,  $p < 0.05$ ; Table 3). In autumn, the fighting behavior of Midday gerbil in the grazing exclusion area was significantly longer than that in the grazing area ( $F_{(1,22)} = 5.99$ ,  $p < 0.05$ ; Table 2). In early winter, Midday gerbils spent more time on foraging, storing, vigilance and fighting behaviors in the grazing exclusion area than in the grazing area (Foraging:  $F_{(3,44)} = 5.58$ ,  $p < 0.05$ ; Storing:  $F_{(3,44)} = 9.42$ ,  $p < 0.01$ ; Vigilance:  $F_{(3,44)} = 4.83$ ,  $p < 0.05$ ; Fighting:  $F_{(3,44)} = 11.63$ ,  $p < 0.01$ ; Table 2).

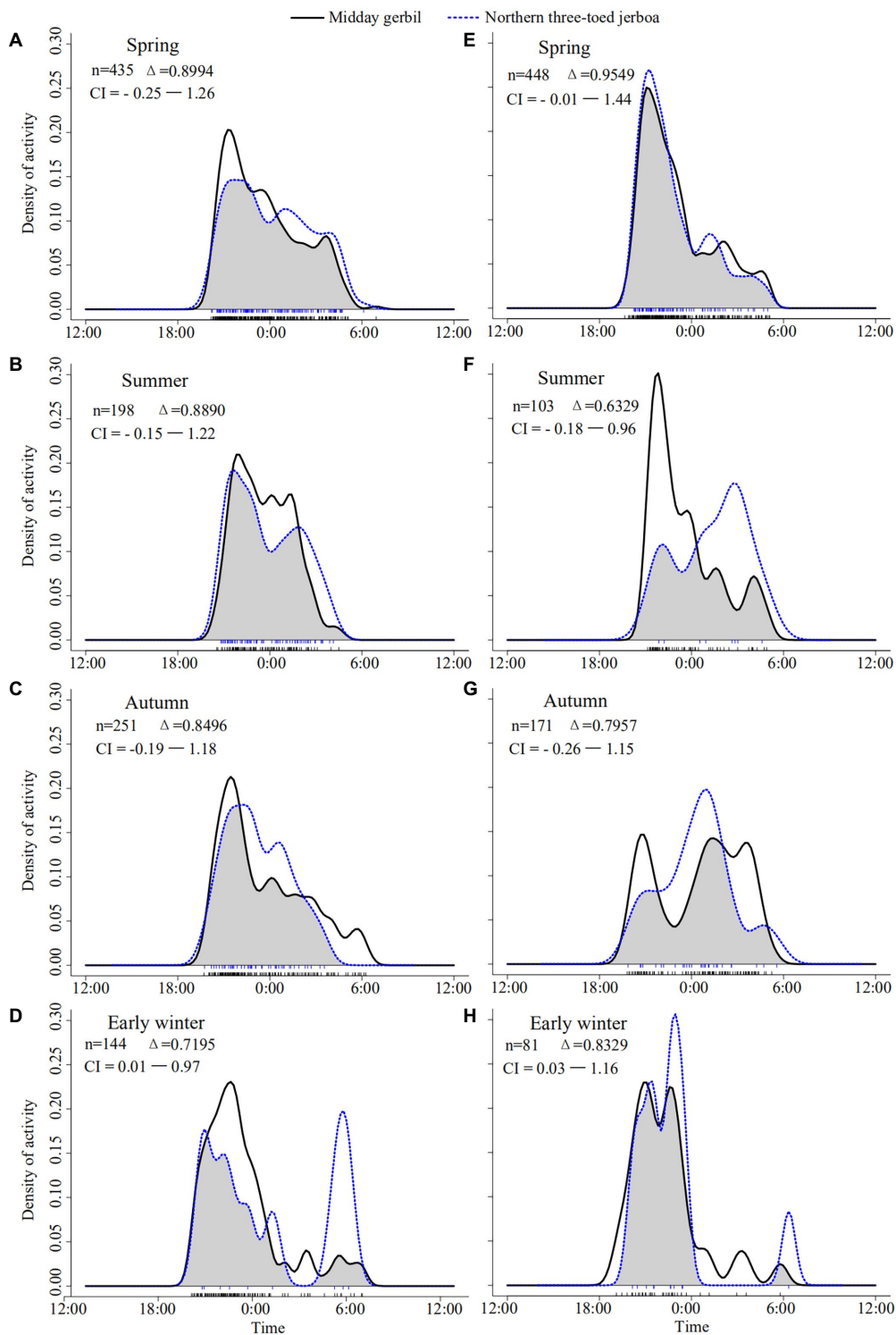
### 3.5. Influencing factors on rodent behavior

Environmental humidity (Hum) and precipitation (Pre) reduced the activity overlap of the two dominant rodent species in the desert area (Grazing:  $R_{Hum} = -0.38$ ,  $p < 0.05$ ;  $R_{Pre} = -0.58$ ,  $p < 0.001$ ; Grazing exclusion:  $R_{Hum} = -0.67$ ,  $p < 0.001$ ;  $R_{Pre} = -0.55$ ,  $p < 0.001$ ; Figure 4). In the grazing exclusion area, environmental factors had non-significant influences on the daily activity rhythm overlap index (Overlap), vigilance behavior of Midday gerbil (M.Vig), and the foraging behavior (D.For), vigilance behavior (D.Vig) and activity duration (D.Dur) of NTJ. In the grazing exclusion area, the key factor affecting animal behaviors was NTJ population density ( $R_{Overlap} = 0.95$ ,  $p < 0.001$ ;  $R_{M.Vig} = 0.51$ ,  $p < 0.001$ ;  $R_{D.For} = 0.40$ ,  $p < 0.01$ ;  $R_{D.Vig} = 0.46$ ,  $p < 0.001$ ;  $R_{D.Dur} = 0.44$ ,  $p < 0.01$ ; Figure 4A). In the grazing area, environmental factors had non-significant influences on the daily activity rhythm overlap index (Overlap), the behaviors of Midday gerbils (M.For, M.Sto, M.Fee, M.Vig, M.Fig, M.Dur), and the foraging and storing behaviors of NTJ (D.For, D.Sto). Key factors affecting the activity overlap of species were shrub density and coverage. The key factor affecting the behaviors of Midday gerbils was their population size ( $R_{M.For} = 0.48$ ,  $p < 0.001$ ;  $R_{M.Sto} = 0.54$ ,  $p < 0.001$ ;  $R_{M.Fee} = 0.52$ ,  $p < 0.01$ ;  $R_{M.Vig} = 0.43$ ,  $p < 0.01$ ;  $R_{M.Fig} = 0.43$ ,  $p < 0.01$ ;  $R_{M.Dur} = 0.48$ ,  $p < 0.01$ ). The population density of Mongolian five-toed jerboa was the key factor affecting vigilance behavior of NTJ ( $R_{D.Vig} = 0.31$ ,  $p < 0.05$ ). Grass density was a key factor affecting the storing behavior of NTJ ( $R_{D.Vig} = 0.48$ ,  $p < 0.001$ ). Grass height was a key factor affecting the vigilance behavior and activity duration of NTJ ( $R_{D.Dur} = 0.34$ ,  $p < 0.05$ ). Rodent activities in grazing areas are affected by more biotic and abiotic factors than activities in grazing exclusion areas (Figure 4B).

## 4. Discussion

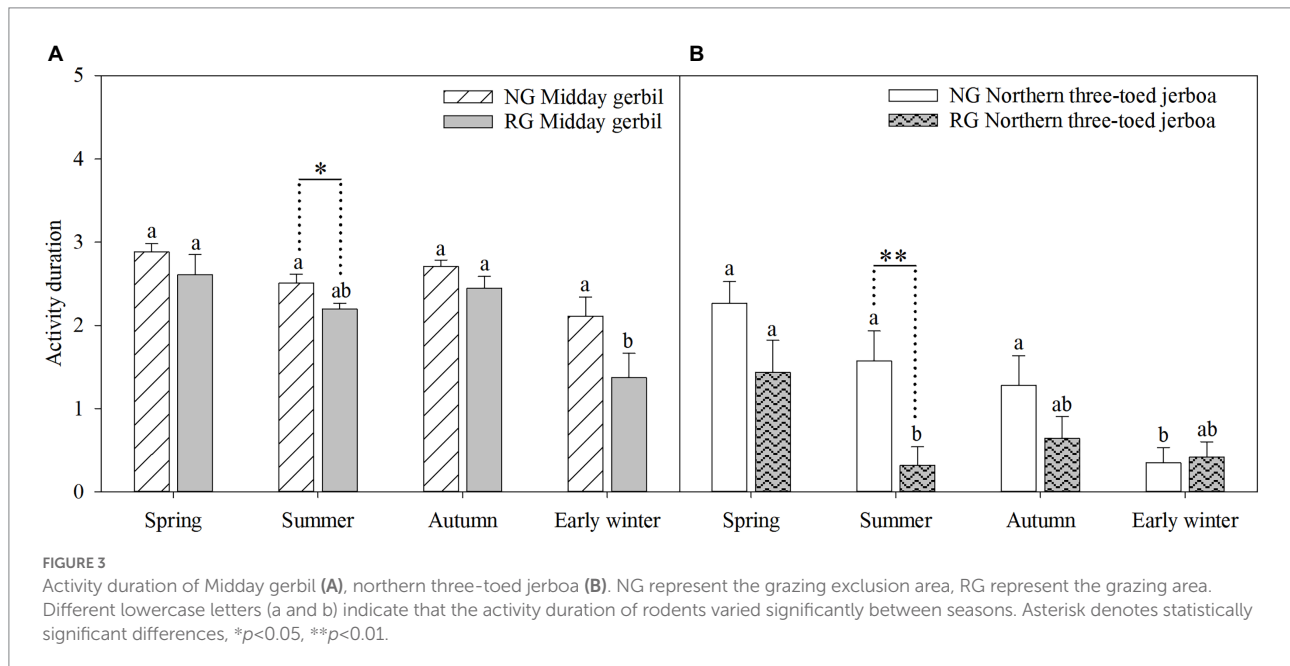
### 4.1. Coexistence strategies of two rodent species

The activity rhythm overlap index reflects the degree of competition and temporal niche separation between two



**FIGURE 2**

Daily activity patterns of Midday gerbil and northern three-toed jerboa. The gray area shows the overlap between activities of the two species and the notches at the bottom of each image illustrate the density of camera-trap events. (A–D) represent the daily activity patterns of Midday gerbil and northern three-toed jerboa in the grazing exclusion area in May, July, September and October, respectively. (E–H) represent the daily activity patterns of Midday gerbil and northern three-toed jerboa in the grazing area in May, July, September and October, respectively. The number of independent camera-trap records (*n*), classification of daily activity patterns, estimates of coefficients of overlapping ( $\Delta$ ) of Midday gerbil with northern three-toed jerboa and 95% confidence intervals (CI) are given in each plate.



species (Sunarto et al., 2015). The activity patterns of Middy gerbil and NTJ in the grazing exclusion area showed high similarity in different seasons, and the separation degree in the temporal niche between two species was low. Studies in the same study area showed that food availability in the grazing exclusion area was significantly higher than that in the grazing area (Yang et al., 2020). Middy gerbils and NTJ have a similar diet, but higher food availability alleviated the pressure of food competition. Thus, despite high temporal niche overlap of Middy gerbil with NTJ in the grazing exclusion area, they can coexist in the grazing exclusion area due to sufficient food and the lack of large competitors such as livestock. In the grazing areas, the activity patterns of Middy gerbil and NTJ begin to stagger significantly in summer, with a separation of the temporal ecological niches of the two species. This is because summer is a critical period for the growth and development of individual herbivores and determines breeding success (Wang et al., 2021). Interspecific competition among animals is particularly intense in summer, and the presence of competitors can influence the behavioral patterns of species (Ritchie and Johnson, 2010). In contrast, temporal niche separation of species usually occurs in situations where alternative mechanisms of coexistence cannot operate (spatial and trophic niche; Harrington et al., 2009; Anna et al., 2015). To reduced competition, Middy gerbil and NTJ have adopted a strategy of temporal niche separation to achieve coexistence. Therefore, hypothesis (1) was supported, as desert rodents with similar a diet used a strategy of temporal (grazing areas) niche separation to reduce niche overlap and achieve coexistence.

## 4.2. Time allocation for the two dominant rodent species

There were seasonal differences in the activity duration of Middy gerbil and NTJ. Their activity durations were significantly higher in spring. In spring, rodents have a higher energy requirement caused by limited food availability (Yang et al., 2020), lower ambient temperatures (Sun, 2006), and frequent reproduction behavior (Wei et al., 1996; Topilko et al., 2022). In summer, the activity duration of Middy gerbil and NTJ was significantly curtailed, and the high temperatures reduced the animals' foraging efficiency (Plessis et al., 2012). Moreover, food was sufficiently abundant to meet rodents' energy needs and there was no need to let itself under the risk of predation. Desert rodents maximize their foraging efficiency by reducing the time spent outside their burrows to reduce water loss (Hut et al., 2012) and predation risk, which facilitates their adaptation to arid desert environments (Ji et al., 2021). Due to the higher predation risk from low vegetation coverage for quadrupedal gerbils in the grazing area (Pereira et al., 2012), the activity duration of Middy gerbil in the grazing area in summer was significantly lower than that in the grazing exclusion area. In autumn, there were differences in the activity allocation of the two dominant rodents, because they had different overwintering patterns (Shuai et al., 2016; Yuan et al., 2018; Yang et al., 2020). Middy gerbils are non-hibernators, so they increased food storing behavior and showed confrontation behavior in autumn. NTJ are hibernators (Zhao, 1964). Because they need to store body fat reserves prior to hibernation, and fighting behaviour can be energy draining, so fighting behaviour

TABLE 2 Difference analysis of time distribution ratio of Midday gerbil.

Behavior	Month		Grazing exclusion (mean±SE)	Grazing (mean±SE)	Grazing disturbance	
Foraging	Simple Effects	May	57.705 ± 3.462 Aa	58.438 ± 2.889 Aa	$F_{(1,22)} = 0.026, p > 0.05$	
		July	59.530 ± 9.099 Aa	65.166 ± 7.165 Aa	$F_{(1,22)} = 0.237, p > 0.05$	
		September	24.150 ± 3.484 Ab	33.058 ± 7.215 Ab	$F_{(1,22)} = 1.236, p > 0.05$	
		October	38.846 ± 7.640 Aab	13.689 ± 7.431 Bb	$F_{(1,22)} = 5.572, p < 0.05$	
		Season	$F_{(3,44)} = 6.818, p < 0.01$	$F_{(3,44)} = 13.472, p < 0.01$		
	Repeated Measures	Season	$F = 17.562, p < 0.001, \eta^2 = 0.444$			
		Grazing	$F = 0.288, p > 0.05, \eta^2 = 0.013$			
		Season × Grazing	$F = 2.912, p > 0.05, \eta^2 = 0.117$			
Storage	Simple Effects	May	25.356 ± 3.949 Ab	21.899 ± 3.261 Aab	$F_{(1,22)} = 0.456, p > 0.05$	
		July	13.347 ± 3.486 Ab	27.289 ± 8.095 Aab	$F_{(1,22)} = 2.502, p > 0.05$	
		September	57.235 ± 7.371 Aa	46.962 ± 8.961 Aa	$F_{(1,22)} = 0.784, p > 0.05$	
		October	40.561 ± 7.476 Aa	11.029 ± 6.059 Bb	$F_{(1,22)} = 9.418, p < 0.01$	
		Season	$F_{(3,44)} = 10.477, p < 0.01$	$F_{(3,44)} = 4.690, p < 0.01$		
	Repeated Measures	Season	$F = 10.474, p < 0.001, \eta^2 = 0.323$			
		Grazing	$F = 2.473, p > 0.05, \eta^2 = 0.101$			
		Season × Grazing	$F = 3.968, p < 0.05, \eta^2 = 0.153$			
Feeding	Simple Effects	May	6.879 ± 1.539 Aa	11.580 ± 3.549 Aa	$F_{(1,22)} = 1.476, p > 0.05$	
		July	7.386 ± 3.965 Aa	0.822 ± 0.729 Ab	$F_{(1,22)} = 2.651, p > 0.05$	
		September	9.176 ± 6.185 Aa	0.108 ± 0.108 Ab	$F_{(1,22)} = 2.149, p > 0.05$	
		October	1.223 ± 0.965 Aa	0.094 ± 0.094 Ab	$F_{(1,22)} = 1.356, p > 0.05$	
		Season	$F_{(3,44)} = 0.826, p > 0.05$	$F_{(3,44)} = 9.642, p < 0.01$		
	Repeated Measures	Season	$F = 2.845, p > 0.05, \eta^2 = 0.115$			
		Grazing	$F = 2.007, p > 0.05, \eta^2 = 0.084$			
		Season × Grazing	$F = 2.147, p > 0.05, \eta^2 = 0.089$			
Viligance	Simple Effects	May	9.715 ± 1.248 Aa	7.668 ± 1.098 Aa	$F_{(1,22)} = 1.517, p > 0.05$	
		July	3.032 ± 1.170 Ab	6.569 ± 3.033 Aa	$F_{(1,22)} = 1.184, p > 0.05$	
		September	6.540 ± 1.519 Aab	3.004 ± 1.254 Aab	$F_{(1,22)} = 3.223, p > 0.05$	
		October	2.206 ± 0.899 Ab	0.188 ± 0.188 Bb	$F_{(1,22)} = 4.825, p < 0.05$	
		Season	$F_{(3,44)} = 7.887, p < 0.01$	$F_{(3,44)} = 3.893, p < 0.05$		
	Repeated Measures	Season	$F = 8.792, p < 0.05, \eta^2 = 0.286$			
		Grazing	$F = 0.784, p > 0.05, \eta^2 = 0.034$			
		Season × Grazing	$F = 2.279, p > 0.05, \eta^2 = 0.094$			
Fighting	Simple Effects	May	0.344 ± 0.106 Ab	0.415 ± 0.162 Aa	$F_{(1,22)} = 0.134, p > 0.05$	
		July	0.039 ± 0.026 Ab	0.155 ± 0.134 Aa	$F_{(1,22)} = 0.712, p > 0.05$	
		September	2.899 ± 1.095 Aa	0.201 ± 0.132 Ba	$F_{(1,22)} = 5.985, p < 0.05$	
		October	0.497 ± 0.146 Ab	0.000 ± 0.000 Ba	$F_{(1,22)} = 11.628, p < 0.01$	
		Season	$F_{(3,44)} = 5.626, p < 0.01$	$F_{(3,44)} = 1.900, p > 0.05$		
	Repeated Measures	Season	$F = 5.441, p < 0.05, \eta^2 = 0.198$			
		Grazing	$F = 7.049, p < 0.05, \eta^2 = 0.243$			
		Season × Grazing	$F = 5.430, p < 0.05, \eta^2 = 0.198$			

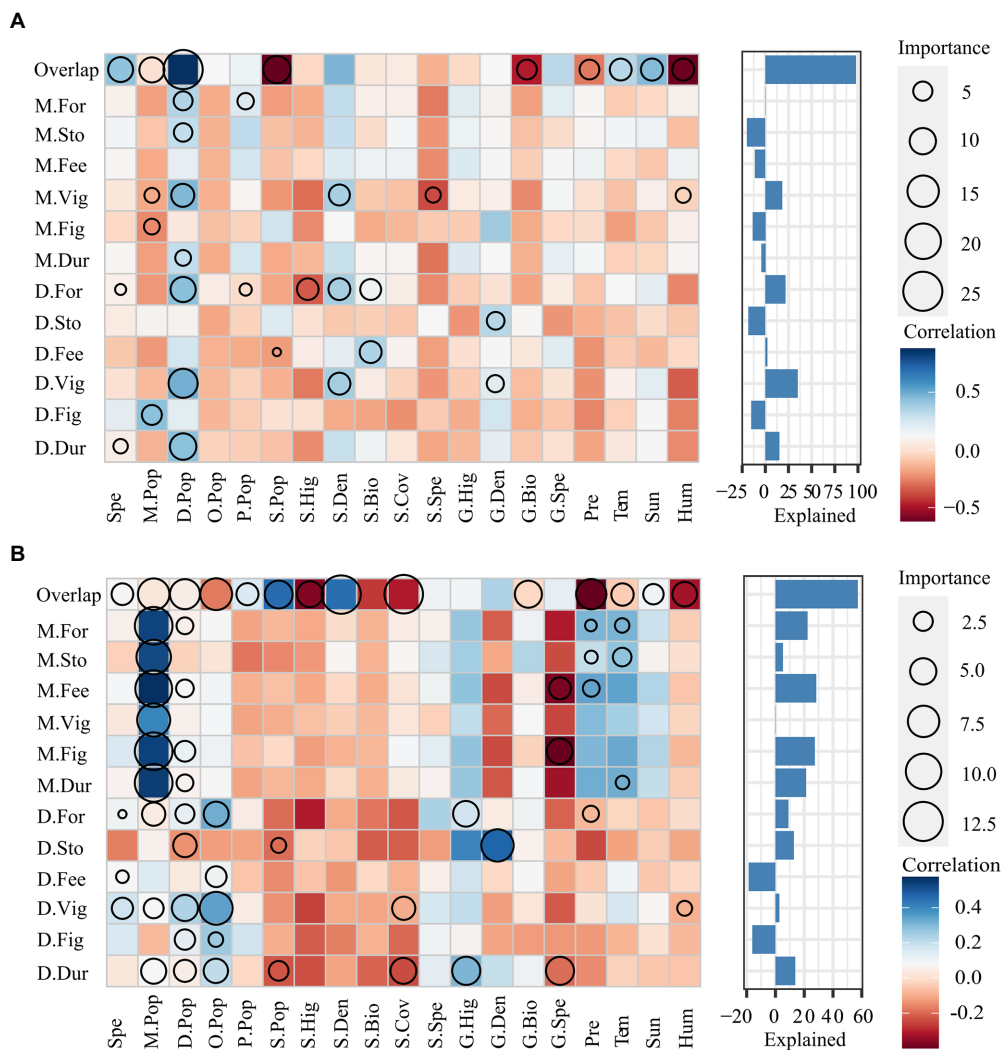
Different uppercase letters (A and B) indicate differences in grazing practices, and different lowercase letters (a and b) indicate significant seasonal differences. Bold values indicate the significant difference.



TABLE 3 Difference analysis of time distribution ratio of northern three-toed jerboa.

Behavior	Month	Grazing exclusion (mean±SE)	Grazing (mean±SE)	Grazing disturbance	
Foraging	Simple Effects	May	57.602±8.447 Aa	47.388±10.708 Aa	$F_{(1,22)} = 0.561, p > 0.05$
		July	32.119±11.180 Aab	13.086±9.210 Aa	$F_{(1,22)} = 1.727, p > 0.05$
		September	24.050±10.301 Ab	39.270±12.309 Aa	$F_{(1,22)} = 0.899, p > 0.05$
		October	6.674±4.250 Ab	18.657±9.561 Aa	$F_{(1,22)} = 1.312, p > 0.05$
		Season	$F_{(3,44)} = 5.598, p < 0.01$	$F_{(3,44)} = 2.418, p > 0.05$	
	Repeated Measures	Season	$F = 6.818, p < 0.01, \eta^2 = 0.225$		
		Grazing	$F = 0.005, p > 0.05, \eta^2 = 0.000$		
Season × Grazing		$F = 1.554, p > 0.05, \eta^2 = 0.066$			
Storage	Simple Effects	May	3.665±1.193 Aa	2.353±1.984 Aa	$F_{(1,22)} = 0.321, p > 0.05$
		July	0.419±0.195 Aa	0.000±0.000 Ba	$F_{(1,22)} = 4.626, p < 0.05$
		September	1.011±0.536 Aa	0.798±0.581 Aa	$F_{(1,22)} = 0.072, p > 0.05$
		October	6.702±6.036 Aa	0.000±0.000 Aa	$F_{(1,22)} = 1.233, p > 0.05$
		Season	$F_{(3,44)} = 0.864, p > 0.05$	$F_{(3,44)} = 1.152, p > 0.05$	
	Repeated Measures	Season	$F = 0.969, p > 0.05, \eta^2 = 0.042$		
		Grazing	$F = 1.456, p > 0.05, \eta^2 = 0.062$		
Season × Grazing		$F = 0.950, p > 0.05, \eta^2 = 0.041$			
Feeding	Simple Effects	May	20.730±6.616 Aa	13.565±4.758 Aa	$F_{(1,22)} = 0.773, p > 0.05$
		July	13.074±6.017 Aa	3.481±3.481 Aa	$F_{(1,22)} = 1.905, p > 0.05$
		September	23.061±10.035 Aa	8.961±4.263 Aa	$F_{(1,22)} = 1.673, p > 0.05$
		October	11.624±8.358 Aa	13.512±8.203 Aa	$F_{(1,22)} = 0.026, p > 0.05$
		Season	$F_{(3,44)} = 0.505, p > 0.05$	$F_{(3,44)} = 0.760, p > 0.05$	
	Repeated Measures	Season	$F = 0.742, p > 0.05, \eta^2 = 0.225$		
		Grazing	$F = 1.854, p > 0.05, \eta^2 = 0.078$		
Season × Grazing		$F = 0.528, p > 0.05, \eta^2 = 0.023$			
Viligance	Simple Effects	May	8.823±2.381 Aa	3.013±1.072 Ba	$F_{(1,22)} = 4.948, p < 0.05$
		July	4.380±2.313 Aab	0.034±0.034 Aa	$F_{(1,22)} = 3.532, p > 0.05$
		September	1.296±0.898 Ab	0.972±0.923 Aa	$F_{(1,22)} = 0.063, p > 0.05$
		October	0.000±0.000 Ab	1.164±0.935 Aa	$F_{(1,22)} = 1.550, p > 0.05$
		Season	$F_{(3,44)} = 5.204, p < 0.01$	$F_{(3,44)} = 2.163, p > 0.05$	
	Repeated Measures	Season	$F = 7.479, p < 0.01, \eta^2 = 0.254$		
		Grazing	$F = 3.958, p > 0.05, \eta^2 = 0.153$		
Season × Grazing		$F = 3.501, p < 0.05, \eta^2 = 0.137$			
Fighting	Simple Effects	May	0.847±0.353 Aa	0.347±0.138 Aa	$F_{(1,22)} = 1.739, p > 0.05$
		July	0.008±0.008 Aa	0.067±0.067 Ab	$F_{(1,22)} = 0.771, p > 0.05$
		September	0.584±0.460 Aa	0.000±0.000 Ab	$F_{(1,22)} = 1.607, p > 0.05$
		October	0.000±0.000 Aa	0.000±0.000 Ab	---
		Season	$F_{(3,44)} = 2.142, p > 0.05$	$F_{(3,44)} = 4.662, p < 0.01$	
	Repeated Measures	Season	$F = 3.156, p > 0.05, \eta^2 = 0.125$		
		Grazing	$F = 3.722, p > 0.05, \eta^2 = 0.145$		
Season × Grazing		$F = 1.145, p > 0.05, \eta^2 = 0.049$			

Different uppercase letters (A and B) indicate differences in grazing practices, and different lowercase letters (a and b) indicate significant seasonal differences.



**FIGURE 4**

Relationship of Middy gerbil and NTJ activities with environmental factors in grazing exclusion areas (A) and Grazing areas (B). The horizontal axis in the figure represents the predictor variable and the vertical axis represents the response variable. The size of the circle represents the importance of the variable. The larger the circle, the stronger the predictive effect of the predictor on the response variable. Different colors represent Spearman correlations. Red represents a negative correlation, blue represents a positive correlation, and the depth of the color represents the size of the correlation. The deeper the color, the stronger the correlation. The bar chart describes the total explanatory value of the predictor variable to the response variable. The variables are: degree of activity overlap of Middy gerbil and north three-toed jerboa (Overlap); Feeding behavior duration of Middy gerbil (M.Fee); Foraging behavior duration of Middy gerbil (M.For); Storage behavior duration of Middy gerbil (M.Sto); Vigilance behavior duration of Middy gerbil (M.Vig); Fighting behavior duration of Middy gerbil (M.Fig); Feeding behavior duration of northern three-toed jerboa (D.Fee); Foraging behavior duration of northern three-toed jerboa (D.For); Feeding behavior duration of northern three-toed jerboa (D.Sto); Vigilance behavior duration of northern three-toed jerboa (D.Vig); Fighting behavior duration of northern three-toed jerboa (D.Fig); Spe, Number of captured rodent species; Population density of Middy gerbil (M.Pop); Population density of northern three-toed jerboa (D.Pop); Population density of Mongolian five-toed jerboa (O.Pop); Population density of desert hamsters (P.Pop); Population density of Alashan ground squirrel (S.Pop); Average height of shrubs (S.Hig); Average shrub density (S.Den); Shrub biomass (S.Bio); Shrub coverage (S.Cov); Number of shrub species (S.Spe); Average height of grass (G.Hig); Average density of grass (G.Den); Grass biomass (G.Bio); Number of grass species (G.Spe); Precipitation (Pre); Temperature (Tem); Hours of sunshine (Sun); Humidity (Hum).

of NTJ) was significantly decreased in autumn. In early winter, the population density of NTJ in the grazing area decreased significantly, while in the grazing exclusion areas it remained at a high level. An increase in population size augments the movement distance and activity duration of mammals (Grove, 2012). The proportion of activity duration spent on each

behavior was significantly higher in the grazing exclusion area than in the grazing area. The time allocation strategies of the Middy gerbils and NTJ in the desert area varied with seasons, which not only facilitated their sympatric coexistence, but also enabled them to be in a favorable position with regard to natural selection.

### 4.3. Drivers of behavioral activity and coexistence

Synergies between land use and climate change have more profound negative impacts on biodiversity than single drivers (Brodie, 2016). Our results also demonstrate that rodents respond differently to grazing. Rodent activities in grazing areas had more influencing factors than in grazing exclusion areas. Livestock grazing made desert rodents more sensitive to environmental changes. Both environmental humidity and rainfall had a significant negative effect on the activity overlap of the two rodent species. Midday gerbil and NTJ had different responses to changes in ambient temperature and humidity. Midday gerbil are highly tolerant to rainfall, while NTJ are highly tolerant to high temperature (Wu et al., 2016). The different environmental tolerances of the Midday gerbil and NTJ reduced the overlap between their activities, and facilitated coexistence in the same domain. Our results did not support hypothesis 3, as the key pathways of the effects of grazing on the temporal niche changes and behavioral patterns of sympatric Midday gerbil and NTJ were inconsistent. Based on rodent natural histories, cattle grazing may favor bipedal heteromyids more than quadrupedal species (Jones and Longland, 1999; Wu et al., 2016) because of grazing-induced changes in vegetative structure (Pereira et al., 2012). NTJ and Mongolian five-toed jerboa require similar habitat conditions (Jones and Longland, 1999; Shuai et al., 2016). Therefore, the key factor affecting the activity duration of NTJ in grazing areas was interspecific competition with the Mongolian five-toed jerboa. Grazing expanded the NTJ home range (Yuan et al., 2017b), which then resulted in limited space available for the Midday gerbil in the grazing area. Therefore, the key factor affecting the Midday gerbil behaviors in the grazing area was intraspecific competition. In the grazing exclusion area, the available space for NTJ was limited, so it was most affected by intraspecific competition (Zhang et al., 2022). Therefore, the greatest impact of grazing exclusion on Midday gerbil activity was interspecific competition with NTJ. Previous studies showed that ungulate trampling altered habitat traits and indirectly affected intraspecific competition among rodents (Navarro-Castilla et al., 2017), and intensified intraspecific competition can lead to behavioral adaptation (Murray et al., 2006; Karanth et al., 2017). This is consistent with our results.

Rodent communities in nature are intrinsically dynamic, and some of the dynamics noted during the relatively short duration of our study differed systematically between grazing and grazing exclusion areas, indicating that these animals are sensitive to livestock grazing. There were seasonal differences in the activity pattern and temporal niche of the dominant rodent species in the desert area, and they adjusted their activity strategies according to the habitat characteristics. Grazing increased the competitive pressure on desert rodents, and long-term overgrazing is inevitably unfavorable to species

coexistence. Ranchers should formulate suitable grazing regimes based on grass yield to maintain healthy pastures, so that cattle have adequate forage.

### Data availability statement

The original contributions presented in the study are included in the article further inquiries can be directed to the corresponding authors.

### Ethics statement

The animal study was reviewed and approved by Research Ethics Review Committee of Inner Mongolian Agricultural University (NND2017012).

### Author contributions

XL and SY analyzed the data and wrote the manuscript. LLi, HZ, YJ, LLiu, RZ, SS, and FB collected data and samples in the field. XW and HF mapped out the manuscript. All authors contributed to the article and approved the submitted version.

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### Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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