

# Activity strategy and activity pattern of Siberian jerboa (*Orientallactaga sibirica*) in the Alxa desert region, China

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## Abstract

Seasonal changes in activity patterns are an essential survival strategy for rodent species. Here, we studied the activity patterns and activity strategy of Siberian jerboa (*Orientallactaga sibirica*) in the Alxa desert region, which is a critical process for understanding the living habitats and behavioural ecology of xeric rodents. An experiment with three plots was conducted to monitor the activity time (the duration of the active period) and frequency of Siberian jerboa using infrared cameras at Alxa field workstation in 2017, Inner Mongolia, China. The relationships between the activity time and frequency, biological factors (perceived predation risk, food resources, and species composition), and abiotic factors (temperature, air moisture, wind speed) were analysed with Redundancy Analysis (RDA). The results showed that: 1) In spring, relative humidity mainly affected activities. In summer temperature, relative humidity and interspecific competition mainly affected activities. In autumn, relative humidity and perceived predation risk mainly affected activities. 2) The activity pattern of the Siberian jerboa changed in different seasons. Activity peaks of Siberian jerboa were found to be bimodal during spring and summer, and trimodal during the autumn, and activity time and frequency in autumn were significantly lower than in spring. 3) Animals possess the ability to integrate disparate sources of information about danger to optimize energy gain. According to the demand for food resources, the jerboa adapted different responses to predation risks and competition in different seasons.

**Key words:** Activity pattern, Activity strategy, Infrared camera, Jerboa

## Introduction

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Different activity patterns of animals indicate various evolutionary adaptations. Each population has its time allocation that is best suited to local conditions. Individuals allocating in the optimal time to other activities have the most significant advantage in natural selection (Daan 1981; Kronfeld-Schor & Dayan 2008). **Animals Activity activity** pattern is a comprehensive adaptation to the periodic changes of various environmental conditions, including adaptation to non-biological conditions such as light, temperature, humidity, and food need, intra-species community relations, and natural enemies (Halle 2000). Influencing factors may include predation risk (Orr 1992; Fenn & Macdonald 1995), competition (Alanara & Metcalfe 2001; Kronfeld-Schor & Dayan), food availability (Orpwood *et al.* 2006), reproductive status (Schrader *et al.* 2009), nutritional status (Metcalfe and Steele 2001), habitat (Wasserberg *et al.* 2006), and physical factors (Fraser *et al.* 1993). Temperature can affect animal activity patterns, and the effects of temperature on behaviour and its interactions with other factors have been experimentally studied (Levy *et al.* 2007). Some research results indicated that the activity period of animals would change with the change of seasonal temperature (Lee *et al.* 2010), and activity periods may also vary between microhabitats with different wind speeds (Melcher *et al.* 1990). These results indicate that temperature and wind speed influence animals' activity patterns. Results also confirmed that air moisture is particularly essential for animals living in warm or hot environments, due to the influence of air moisture on heat balance (Shuai *et al.* 2014; Kausrud *et al.* 2008). Food resource is the primary factor influencing activity pattern changes of rodents, and studies have concluded that ecological factors directly related to energy demand affected the animals' activity pattern (Denis 1980). Predation risk may be another ecological factor affecting animal activity patterns (Claire & Leiner, 2017). Although there are many findings related to factors that influence animal activity patterns, most studies of activity patterns have tended to focus on only one aspect, and have failed to consider the relative importance of other factors (Shuai *et al.* 2014; Kei & Motokazu 2017). Species composition of the rodent community also influences rodent nocturnal activity patterns, that is, the presence or absence of potential competitors (Elke *et al.* 2013). Among many factors, what is the factor that affects the activity of the Siberian jerboa?

Studies of rodent activity patterns in desert areas have found that they change with the seasons (Gregory *et al.* 2001; Richman & Kent 1973). For example, Golden spiny mice (*Acomys russatus*) shown diurnal activity patterns with a midday peak in winter and a bimodal pattern (with peaks in morning and afternoon) during summer (Shkolnik, 1971; Kronfeld-Schor & Dayan 2008). It has been speculated that the less typical diurnal pattern demonstrated by *A. russatus* is due to competitive displacement (Kronfeld *et al.* 1996). The kangaroo rat (*Dipodomys merriami*) responded to the cold winter by decreasing its activity from a November high (Richman & Kent 1973). Seasonal shifts in activity patterns have also been observed in studies of other rodent species, analysis of daily activity rhythm has shown that the number of peak periods of activity is higher during high-temperature seasons than that in low-temperature seasons. Research of monthly activity rhythm has been demonstrated that activity was higher in high-temperature months than in low-temperature months. For example, the activity pattern

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**Nocturnal activity and habitat selection of Hotson Jerboa, *Allactaga hotsoni* Thomas, 1920 (Rodentia: Dipodidae)**

Mastureh Darabi, Zohreh Zeini, Abdolreza Karami, Ali Kaveh

1. **Notes on habitat affinities of the Hotson's Jerboa, *Allactaga hotsoni* Thomas, 1920 (Rodentia: Dipodidae) from Isfahan province, Iran**

Mansureh Khalatbari; Morteza Naderi

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**Nocturnal activity of Iranian jerboa, *Allactaga frouzi* (Mammalia: Rodentia: Dipodidae)**

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of Verreaux's sifaka (*Propithecus verreauxi*) was bimodal during the low-temperature winter period, which reduces energy loss, and unimodal with more extended activity periods in high-temperature summer (Erkert & Kappeler 2004). Activity peaks of Japanese flying squirrel (*Pteromys momonga*) were bimodal in the temperate seasons and trimodal in the cold seasons. As a survival strategy, this species reduces their active time in the cold season to reduce energy consumption caused by long-term exposure to low temperatures (Lee *et al.* 2010). Hence, when external environmental factors change with the season, some rodents will also change their activity pattern. When the external biological and abiotic environment changes, the transformation of animal activity patterns is essentially a choice of survival strategies, and animals usually adjust their activity times and frequency to cope with these changes (Delany 1972).

A pattern has emerged in some studies, abiotic environmental factors such as temperature often provide a range within which the rodents can be active. Within this range, the quantity or quality of food will determine the surface activity (Bartholomew and Cade 1957). A relatively new literature system starting from Emlen (1966), MacArthur, and Pianka (1966), now called the optimal foraging theory, attempts to explain and predict many aspects of animal foraging behaviour. Most of the hypothesis of this theory is that the foraging behaviour and adaptability of animals are maximized through natural selection, but subject to certain restrictions. The optimal foraging theory predicts that risk-taking decisions should vary with the perceived threat level. (Kelly *et al.* 2020). This theory means that animals have to face trade-offs when they encounter predators when foraging. When biological factors change, such as food resources and predation risk, the survival strategy that animals usually adopt may also vary. In evolution, the animal's response to predator pressure may be to remove itself from the predator's foraging microhabitat (predator avoidance mechanism), or to reduce the probability of successful predation within the predator's perceptual domain (anti-predator mechanism). Predator avoidance mechanisms are typical patterns of behaviour exhibited by animals, such as occupying (e.g., cover or dense vegetation), changing their foraging habitats (spatial avoidance), or adjusting their activity periods (temporal avoidance). A variety of morphological and behaviour traits represent antipredator mechanisms (Brodie 1991). The ability of animals to bear the risk of predation is related to their own characteristics. An animal with a higher basal metabolism is more sensitive to the risk of predation. When animals forage under conditions of food shortage, they will change strategy from risk-aversion to risk-proneness (Wei *et al.* 2004).

The Siberian jerboa (Michaux & Shenbrot 2017) is one of the pests widely distributed in the desert and semi-desert of Alxa, every year from early September into hibernation, emergence from hibernation in late March or early April of the following year (Li & Han 1990; Zhou *et al.* 1992). Siberian jerboa is usually active in the evening and before dawn, and is not easily found during the day (Liang & Xiao 1982; Dong *et al.* 2006). What is the activity pattern of the five-toed jerboa? What are the impact factors? Does the Siberian jerboa change its activity pattern with the seasons? And what is the reason for this shift? What kind of survival strategies are involved in this transition?

Based on the above, to explore whether Siberian jerboa had the same seasonal

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variation as some other rodents, and what was the driving factor for this variation, and the survival strategies involved in this transition. We selected biological factors (perceived predation risk, food resources, and species composition of rodent community), and abiotic factors (temperature, air moisture, wind speed) as possible influencing elements for the jerboa activity patterns.

In order to answer these questions, we proposed the following hypotheses: (1) In spring, after a long hibernation period, energy supply is incredibly important, and food resources may be an essential factor influencing the activity pattern of Siberian jerboa. In summer, high temperatures may limit the activity of the jerboa, but to compensate for this thermal constraint, wind speed, and air humidity also play essential roles in summer. In autumn, to store the energy needed during the long hibernation period, food resources may be an essential factor influencing the activity pattern of jerboa. (2) There were seasonal changes in the activity patterns of the Siberian jerboa. The dominant factor driving this shift may be competition or temperature. (3) The mechanism driving this shift is risk-taking decisions should vary in response to perceived levels of threat.

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## Materials and methods

### Study area

This study was conducted in the southern part of Alxa Zuo Qi at the eastern edge of the Tengger Desert, Inner Mongolia, China (E104°10'-105°30', N37°24'-38°25') from April to October in 2017. The area has a continental climate with cold and dry winters and warm summers. Annual temperatures range is from -36 to 42 °C with a mean of 8.3 °C. Annual precipitation range is from 45 to 215 mm, but about 70 percent falls from June to September. The potential evaporation range is from 3000 to 4700 mm, and the annual frost-free period is 156 days. The Siberian jerboa is a common species in the study site, and it is distributed throughout the study site. Approximately 5-15% of the ground is covered with shrubs, forbs, and some gramineous plants. Shrubs mainly consist of *Zygophyllum xanthoxylon*, *Nitraria tangutorum*, *Caragana brachypoda*, *Ceratoides latens*, *Oxytropis aciphylla*, *Artemisia sphaerocephala*, and *Artemisia xerophytica* with *Reaumuria soongorica* as the dominant species. The major grasses/forbs species are *Cleistogenes squarosa*, *Pegandum nigellastrum*, *Cynanchum komarovii*, *Salsola pestifer*, *Suaeda glauca*, *Bassia dasyphylla*, *Corispermum mongolicum*, *Artemisia dubia*, and *Plantago lessingii* (Yuan et al., 2018). Coexistent rodent species include Dipodidae (*Orientallactaga sibirica*, and *Dipus sagitta*), Cricetidae (*Meriones meridianus*, *Cricetulus barabensis*, and *Phodopus roborovskii*) and Sciuridae (*Spermophilus alaschanicus*). The natural enemies of rodents in the area are corsac (*Vulpes corsac*), eagle owls (*Bubo bubo*), and snakes (*Agkistrodon halys*). According to our field observations, snakes, eagle owls, and foxes are active at night. According to the climate characteristics of the test site, spring is from March to May, summer is from June to August, autumn is from September to November, and winter is from December to February of the following year.

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### Camera trapping

We deployed camera traps in three plots, each approximately 1 hm<sup>2</sup> in area, each

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separated by more than 500 meters. We deployed a survey infrared camera (Infrared monitor E1B, Lianyungang Jinsheng Technology Co., Ltd., China) at each plot. All cameras worked in May (Spring), July (Summer), and September (Autumn) each year. Since the Siberian jerboa is a nocturnal rodent, the cameras worked from 19:00 to 07:00 the next day, divided into 12 time periods (i.e., 19:00-20:00, 20:00-21:00, and so on). Cameras functioned for four successive days each month, totalling 36 trap nights. Each camera was placed on a stake approximately 30 cm above the ground and faced towards a lure 1.5-2.0 m away. Vegetation in the camera's line of sight was cleared to prevent false triggers. The lure was peanut (*Arachis hypogaea*) that rodents may feed on. Before the experiment, we did a pre-experiment on the placement of the infrared cameras. Infrared cameras were randomly placed in the territory of the Siberian jerboa to find out where this rodent is active, and we chose places where the Siberian jerboa is active. The camera parameters were set to shooting mode (video), and the video recorded for 2 min when triggered, with no quiet period between trigger events. We checked the performance of the camera and replaced the battery and storage card when collecting data every morning. The captured videos were downloaded to a computer, and each camera was assigned a point number. We identified each wildlife video, enter information on each wildlife video into an Excel table according to the camera number and appearance time, in order to avoid repeatedly counting the activity information of the same animal in a short time. Multiple videos of the same animal within 30 minutes are entered as one record. We identified each photo of an animal to species, recorded the time and date, and rated each photo as a dependent or independent event. We defined an independent event as (1) consecutive photographs of different individuals of the same or different species, (2) consecutive photographs of individuals of the same species taken more than 0.5 hours apart, (3) nonconsecutive photos of individuals of the same species (O'Brien *et al.* 2003; Duquette *et al.* 2017). We watched the video and recorded the duration of each appearance of jerboa, add up the period of each appearance of Siberian jerboa the animal within 60 min, which register the activity time. (O'Brien *et al.* 2003). We recorded the appearance of jerboa, and ~~record~~ the activity frequency. And recorded the total cumulative time of vigilance in every 60 min. Vigilance behaviour is defined as a series of physical action response behaviours exhibited by animals in response to existing or potential risks in the surrounding environment (Wang *et al.* 2015). It can be divided into the following cases: 1) Tweet: when danger is detected, a sitting, standing, or squatting posture is used to look directly at the threat and a series of screams are emitted to warn other members of the same species; 2) Alert: interrupt the ongoing behaviour (such as running, feeding, foraging, etc.), take the squat posture, static, or accompanied by a rapid head twist to observe the surrounding environment, to determine whether there is danger around, generally for no more than 3s; 3) Watching: Observe the movement of the surrounding environment by standing, sitting, or squatting, and the field accompanied by the head writhing for a longer time than 3s; 4) Avoiding: When danger is detected, or a call is heard, interrupt the ongoing behaviour (such as running, feeding, foraging, etc.), and quickly run back to the cave, sometimes accompanied by a cry of alarm.

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## Abiotic factors

Climatic data are all from "Luanjingtan Weather station of Alax ", and the average distance from the study area is 5.5 km. The climatic data can reflect the local environmental conditions in study plots (Wu *et al.* 2016). We collected hourly temperature, relative humidity, and wind speed data from China Meteorological Administration (<http://www.cma.gov.cn/>) for the same four days that the camera operated each month.

## Biological factors

### Food resource

We conducted vegetation sampling in three plots in May, July, and September in 2017. We randomly placed three 100-m<sup>2</sup> square sampling plots on each treatment unit to sample shrubs and randomly placed three 1-m<sup>2</sup> quadrats in each 100-m<sup>2</sup> square plot to sample grasses and forbs. In a shrub sample of 100-m<sup>2</sup>, three shrubs of each species were randomly selected, measure their crowns, and an appropriate amount of the aboveground part was taken. After drying, the dry weight was weighed. In the herb sample of 1-m<sup>2</sup>, measure their height, and cut all kinds of herbs and dry them, then weigh the dry weight (Yuan *et al.* 2018). We estimated aboveground standing biomass of shrubs, grasses, and forbs by species. It is well-known that Siberian jerboa feed on green parts of plants, underground parts of plants, seeds, and insects in approximately equal proportion (Shenbrot *et al.* 2008). The same species distributed in different regions may also have different diets. An additional experiment on feeding behaviour observations of Siberian jerboa was conducted in 2017 to determine the food resources in the study sites. The experiment was conducted as follows. Jerboas were live-trapped for each season (spring, summer, and autumn) from the desert habitat at a distance from the study sites and fasted for 8 h before placing them into the cages at dusk. A total of 14 jerboas were used (two males, and two females in May, three males and two females in July, three male and two female jerboas were captured in September), weighing on average 95.80g, SD =17.74g. Each jerboa was randomly assigned to one cage. We provided each plant species to each subject in 100 mm petri dishes placed in a randomized array with one species per dish. We fed jerboas every 3 hours, 2- 3 times per night. Ten to twelve plant species were fed each time. The plant species fed to each jerboa was the same on the same night, but plant species were arranged randomly for each jerboa. We collected the remaining plants (including those cached throughout the cages) and plant remnants, separated and weighed them by species, when putting the new plant species in. The same plant species with same weight were placed outside of the cages as a control group to determine water loss. We calculated species composition of consumed plants by subtraction:  $Y = A - \frac{B}{1-E}$ , where  $Y$  is mean food consumption,  $A$  is mean initial weight,  $B$  is mean remaining weight,  $E$  is mean diriage.

Preference index (PI) was calculated according to the daily food consumption of each plant by the formula:  $PI = \frac{RI}{RB}$ , where  $PI$  is mean preference index,  $RI$  is mean mass percentage of a plant's consumption in total food consumption,  $RB$  is mean mass

percentage of a plant in total feed. The plant species from food resource was chosen or calculating the total food biomass and preference food biomass. Preferred foods were selected using the preference index (Batzli & Pitelka 1983). Preferred food biomass represents the food resources in the habitat.

#### *Perceived predation risk*

Vigilance time, vigilance frequency, and vigilance alert distance are three indicators for assessing the perceived predation risk level of small rodents (Wan 2019). Vigilance behaviour is one of the most essential countermeasures against predation, which depends heavily on the perceived predation risk (Lima 1987). Studies have shown that when the risk of predation increases, an animal's time-allocation strategy changes, reducing the risk of predation by increasing alertness, reducing foraging and other behaviors, and vice versa. Therefore, there is a theory that there is a trade-off between the alertness of animals and the activity intensity of other behaviors, such as foraging. This theory is called the predation risk allocation hypothesis (Wei *et al.* 2004; Steven & Peter 1999). This theory means that the higher the risk in the habitat, the greater the proportion of vigilance in total activity. To assess perceived predation risk, we measured the proportion of vigilance frequency in total activity frequency. We evaluated the perceived predation risk of Siberian jerboa by vigilance behavior, and verify the feasibility of this idea from two perspectives. One is to use vegetation structure to verify. Another is to exclude the influence of other factors on vigilance behavior.

Studies have shown that safety for small mammals is correlated with some measure of vegetation density, such as shrub coverage or grass height (Jacob & Brown 2000; Morris & Davidson 2000). Changes in vegetation may change an animal's perceived risk by increasing a potentially risky structure (Hagenah *et al.* 2009). In fact, fine-scale changes to the vegetation structure have been shown to alter the fear levels of prey, regardless of the abundance of predators (Wheeler & Hik 2014), and influence prey's perceived predation risk more than actual predator cues. Reductions in ground cover, grass height, and horizontal structure would increase rodents' perception of risks (Banasiak & Shrader 2015; Shrader *et al.* 2008). We used grass height and shrub coverage to assess predation risk. The calculation formulas are as follows.

$$AH = \frac{(LH+MH+SH)}{3} \quad (1)$$

*AH* represents the average height (cm) of a shrub species. *LH*, *MH*, and *SH* represent the height (cm) of large, medium, and small plants of the shrub species.

$$C = \frac{3.14 \times SR^2 \times Den}{100 \text{ m}^2} \times 100\% \quad (2)$$

*C* represents the average coverage per unit area of a shrub species (%), and *SR* represents 1/2 (m) of the average canopy width of the shrub species.

$$TC = \sum_{i=1}^S C_i \quad (3)$$

*TC* represents the total coverage per unit area of the shrub (%), *S* represents the number of species, and *C<sub>i</sub>* represents the coverage per unit area of the *i*th shrub (%).

In addition, it should be pointed out that the vigilant behavior of animals is related to the risk of predation and the trade-off between vigilant and predation. Besides it is



also affected by other factors, such as animal sex, age (Randall *et al.* 2020; Xia *et al.* 2011), population size (Xia *et al.* 2011; Tchabovsky *et al.* 2001), individual position in the group, and environmental characteristics (Bekoff *et al.* 1995). Therefore, the vigilant behavior of animals is the result of the comprehensive effect under the influence of multiple factors (Bekoff *et al.* 1995). We excluded the coexisting nocturnal rodent from its vigilance behavior.

Spearman correlation analysis was used to analyze perceived predation risk, shrub coverage, and grass height (Table 1). Perceived predation risk was significantly negatively correlated with shrub coverage and grass height in spring and summer ( $P < 0.01$ ). Perceived predation risk was significantly negatively correlated with grass height ( $P < 0.01$ ), and negatively correlated with shrub coverage. From the perspective of vegetation structure, we speculate that vigilance behavior can represent the perceived predation risk of Siberian jerboa to some extent. Therefore, we measured the perceived predation risk of Siberian jerboa by the ratio of vigilance to all behaviors.

Spearman correlation analysis was used to analyze vigilance frequency and the population relative number of rodents in different seasons. The results showed no significant correlation between the vigilance frequency and the other three species of rodents co-existing in the same area. The influence of the population size of the Siberian jerboa on its vigilance behavior was also excluded (Table 2).

Through the above proof, it is feasible to evaluate the perceived predation risk of Siberian jerboa by vigilance behavior.

#### *Species composition of the rodent community*

Rodents were live trapped for 4 consecutive days at 4-week intervals from April to October in 2017. Trapping was not run during winter (from November to March). Traps were baited with fresh peanuts, and checked twice (morning and afternoon) each day. Considering that the average survival time of jerboa was greater than that of other non-jerboa species in our study areas. The life span of jerboa is longer than 2 years, and the average life span of non-jerboa species is shorter than 2 years. The electronic chips be used to a life span of 2 years. Each captured jerboa individual was sexed, marked with a 1.5 g aluminum leg ring (0.4 cm diameter) with a unique identification number (ID) attached to the left hind foot, and weighed to the nearest 1 g. Each captured non-jerboa individual was sexed, marked with an electronic chip with a unique identification number (ID). The capture station, The sex, eapture station, body weight, and reproductive condition of each eapture individuals were recorded. Males were considered in reproductive condition if they had scrotal testes. Females were considered reproductive if they possessed enlarged nipples surrounded with white mammary tissue, or a bulging abdomen. In order to avoid accidental death, traps were closed on extremely warm or rainy days, and trapping time was extended after extremely warm or rainy days to ensure 4 days of trapping in each month (Wu *et al.* 2016). To assess the effectiveness of the aluminum leg rings, whether the leg rings are lost, we conducted a pre-experiment in 2018 and 2019. In April and May 2018, the leg rings and electronic chips were used to mark the jerboa simultaneously, and the loss of the leg rings and the electronic chip was recorded in September of the same year. At the beginning of this pre-experiment, we captured 21 *Dipus sagitta* individuals and 15 *Orientallactaga*

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*sibirica* individuals in 2018. In September of 2019, 6 *Dipus sagitta* individuals and [seven](#) *Orientallactaga sibirica* individuals were recaptured. And there was no loss of leg rings or chips.

In this study we calculated the population relative number of rodents with a hundred cage capture rate (Wu *et al.* 2016). Its calculation formula is:

$$P = \frac{N}{H \times n} \times 100\% \quad (4)$$

$P$  is the capture rate;  $N$  is the number of captured individuals;  $H$  is total number of cages;  $n$  is the number of consecutive days.

Among the rodents co-existing with the Siberian jerboa, the nocturnal species is the *Dipus sagitta*, *Phodopus roborovskii* and *Meriones meridianus*. Add up the relative numbers of the three species as the number of coexisting species.

### Statistical analyses

Activity time (the duration of the active period), activity frequency, predation risk, and food resources in different seasons were analysed by one-way ANOVA using SAS 9.0 software. Before we do the one-way ANOVA, the data involved in this paper have been Shapiro-Wilk tested, all conform to the normal distribution (Table 3). Spearman correlation analysis was used to analysed perceived predation risk, shrub coverage, and herb height. This analysis is implemented in SPSS 21.0.

Multivariate analysis was performed with CANOCO 5 to explore the relationship between environmental factors (biological and abiotic factors) and activity time and frequency over the different seasons using Redundancy Analysis (RDA). To determine whether to use linear or unimodal based numerical methods, detrended correspondence analysis (DCA) with detrending by segments was first conducted to analyse the data on activity time and frequency in 2017 and evaluate the gradient length of the first axis. A Monte Carlo permutation test based on 499 random permutations was conducted to test the significance of the eigenvalues of the first canonical axis.

## Results

### Food resources

According to the preference index in different seasons, food resources varied between seasons. There were 12 species of plants favoured by Siberian jerboa in spring, 18 species favoured in summer, and 20 species favoured in autumn. There were differences in the feeding habits of the jerboa in different seasons (Table 1). There were significant differences in food resources in different seasons. Preferred food biomass in autumn was significantly higher than that in spring and summer ( $F_{2,24}=15.67$ ,  $P<0.0001$ ). Total food resource in spring was significantly less than that in summer and autumn ( $F_{2,24}=18.16$ ,  $P<0.0001$ ). Total food resource was significantly higher than preferred food biomass in different season (Spring  $F_{1,16}=5.04$ ,  $P=0.040$ ; Summer  $F_{1,16}=38.50$ ,  $P<0.0001$ ; Autumn  $F_{1,16}=8.91$ ,  $P=0.0093$ ) (Fig.1).

### Activity time and activity frequency

In spring and summer, the activity time of the jerboa was longer than that was in autumn ( $F_{3,33}=5.64$ ,  $P=0.0078$ ). There were two significant activity peaks in the daily activities, which appear at 21:00-00:00 and 02:00-04:00, respectively, and were

significantly different from other non-peaks times (Spring  $F_{11,132}=4.81$ ,  $P<0.0001$ ; Summer  $F_{11,132}=2.86$ ,  $P=0.0022$ ). The difference between the two activity peaks is not significant (Spring  $F_{4,55}=0.83$ ,  $P=0.5100$ ; Summer  $F_{4,55}=0.87$ ,  $P=0.4876$ ). There were three peaks of activity time in the autumn, which appear at 20:00-21:00, 23:00-00:00 and 04:00-05:00, respectively, and were significantly different from non-peaks times ( $F_{11,132}=2.23$ ,  $P=0.0165$ )(Fig.2A).

There was a significant difference between the activity frequency of the jerboa among three seasons ( $F_{2,33}=10.67$ ,  $P=0.0003$ ). There were two peaks of activity frequency in spring and summer. In spring appear respectively at 21:00-00:00 and 01:00-04:00, and were significantly different from non-peaks times ( $F_{11,132}=3.71$ ,  $P<0.0001$ ). In summer appear respectively at 21:00-23:00 and 02:00-05:00, and were significantly different from non-peaks times ( $F_{11,132}=3.84$ ,  $P<0.0001$ ). There were three peaks of activity time in the autumn, which appear at 20:00-21:00, 23:00-00:00, and 04:00-05:00, respectively, and were significantly different from non-peaks times ( $F_{11,132}=3.87$ ,  $P<0.0001$ ). (Fig.2B).

There was a significant difference between the total activity time each season. The total activity time in autumn was significantly shorter than in spring and summer. ( $F_{2,33}=5.64$ ,  $P=0.0078$ ) (Fig.2C). There was a significant difference between the total activity frequency in each season, following the order: spring> summer> autumn. ( $F_{2,33}=1.67$ ,  $P=0.0003$ ) (Fig.2D).

#### Perceived predation risk

In spring, vigilance behaviour occurred mostly during 05:00-06:00. In summer, vigilance behaviour occurred most during 20:00-21:00. In autumn, vigilance behaviour occurred most during 04:00-05:00 (Fig.3A, Fig.3B, Fig.3C). There were significant differences in the proportion of vigilance behaviour in total activity among periods in spring and autumn (Spring  $F_{11,110}=5.70$ ,  $P<0.0001$ ; Autumn  $F_{11,103}=2.93$ ,  $P=0.0021$ ), but no significant differences during summer ( $F_{11,85}=1.64$ ,  $P=0.1008$ ).

There was a significant difference in daily vigilance behaviour frequency in different seasons ( $F_{2,33}=4.05$ ,  $P=0.0268$ ). Perceived predation risk in spring was significantly higher than in autumn (Fig.3D).

#### Species composition of the rodent community

Among the rodents co-existing with the Siberian jerboa, the nocturnal species is the *Dipus sagitta*, *Phodopus roborovskii*, and *Meriones meridianus*. There was no difference in the catch proportion of *Dipus sagitta* and *Meriones meridianus* between the seasons (*Dipus sagitta*  $F_{2,6}=1.11$ ,  $P=0.3902$ ; *Meriones meridianus*  $F_{2,6}=0.41$ ,  $P=0.6812$ ). There was a significant difference in the catch proportion of Siberian jerboa between the seasons ( $F_{2,6}=4.85$ ,  $P=0.0558$ ). There was a significant difference in the total number of coexisting species between seasons ( $F_{2,6}=7.25$ ,  $P=0.0251$ ) (Table 5).

#### The relationship between environmental factors and activity pattern in different seasons

##### The relationship between environmental factors and activity pattern in spring

Analysis of relationships between different factors and activity time showed that the cosine value of the line segment representing activity time and temperature, food resource was positive. The cosine value of the line segment representing activity time

and predation risk was 0, so there was no correlation between activity time, and perceived predation risk. The cosine value of the line segment representing activity time, wind speed, relative humidity, and intraspecific competition were negative. Thus, there were negative correlations between activity time, wind speed, relative humidity, and intraspecific competition. The line segment representing temperature and relative humidity was longer, so temperature and relative humidity had a more significant impact on activity time.

The analysis relationships between environmental factors and activity frequency showed that the cosine value of the line segment representing active frequency and temperature and intraspecific competition was 0, so there was no correlation. A positive correlation was found between activity frequency and predation risk, food resources and interspecific competition, and a negative correlation between activity frequency and relative humidity and wind speed. Among these factors, relative humidity had more significant impact on activity frequency, and this factor explained a larger proportion of variation in activity frequency.

Relative humidity significantly affects the activity of Siberian jerboa in spring (RH  $F=12.2$ ,  $P=0.002$ ) (Fig. 4).

#### *The relationship between environment factors and activity pattern in summer*

There were negative correlations between activity time and relative humidity, temperature, wind speed, food resources, interspecific competition, intraspecific competition, and perceived predation risk. Among these factors, the lines representing relative humidity and temperature were longer, indicating that their influence on the activity time was relatively more important.

There were negative correlations between activity frequency and each factor. Among them, temperature and relative humidity had more significant explanatory value, and had greater impacts on activity frequency.

Temperature and relative humidity had significant impacts on the activity of this rodent species in the summer (T  $F=11.4$ ,  $P=0.002$ ; RH  $F=29.4$ ,  $P=0.002$ ; InterC  $F=4.4$ ,  $P=0.028$ ) (Fig.5).

#### *The relationship between environment factors and activity pattern in autumn*

There were positive correlations between activity time and temperature and predation risk, food resources, and intraspecific competition. There were negative correlations between activity time and wind speed and interspecific competition. There was no correlation between activity time and relative humidity. Among these factors, temperature, relative humidity, wind speed, and perceived predation risk had more considerable explanatory value, and their impact on activity frequency was more significant.

There were positive correlations between activity frequency and temperature and perceived predation risk. There was a negative correlation between activity frequency and relative humidity and wind speed and food resource.

Relative humidity, and perceived predation risk had significant impacts on the activity of this rodent species in the autumn (RH  $F=6.5$ ,  $P=0.010$ ; PR  $F=33.5$ ,  $P=0.002$ ) (Fig.6).

## Discussion

Choosing a period to perform basic survival and breeding activities involves a trade-off between the costs and benefits associated with environmental and biotic demands, such that individuals usually tune their activities to the most favourable period in a day (Refinetti 2008), and through this way individuals try to maximize their fitness. The Siberian jerboa had two similar peak periods in spring and summer, which were 21:00 -00:00 and 02:00 to 04:00. The activity time and frequency in autumn were very low, and there were three activity peaks. Our results are similar to those of a previous study of the ecological habits of Siberian jerboa (Liang *et al.* 1982). However, their research showed that the Siberian jerboa had a high intensity of activity in September. This difference may be due to different conditions in the experimental sites (Dong *et al.* 2006). This suggests that the species is adaptable to different environments. The optimal response of an organism to change in its environment is to minimize the cost to it through some kind of adaptive response (Wootton 1990). Activity peaks of Siberian jerboa were bimodal during the spring and summer, and trimodal during the autumn. Studies have shown that rodents change the number of peaks of activity depending on the temperature of the seasons (Erkert & Kappeler 2004; Levy *et al.* 2007). In this region, the temperature in autumn was lower than in summer, and reducing activities in the cooler autumn can minimize exposure in cold environments in order to save energy consumption (Cotton & Parker 2000). However, the temperature in autumn was similar to that was in spring, or was even slightly higher than in spring. So why was there a difference in the number of activity peaks? This may be attributed to differences in the factors that affected the activities in different seasons.

Our results showed that the factors affecting activities were different in different seasons. In spring, relative humidity mainly affected activities. In summer, temperature, relative humidity, and interspecific competition mainly affected activities. In autumn, wind speed, relative humidity and perceived predation risk mainly affected activities. Although the relationship between temperature and activity time was negative in summer, the fundamental mechanism was the same as in the other two seasons. Each species has its optimal temperature range (Rezende *et al.* 2003). In summer, temperatures were higher than in spring and autumn, exceeding the jerboa's temperature range. In different seasons, relative humidity had a negative impact on jerboa activities, which indicated that relative humidity was an important factor affecting the activity of this species. Other studies have shown that relative humidity promotes rodent activity in arid and semi-arid areas (Brodie *et al.* 1991). This was contrary to our findings. Studies have shown that the effects of humidity on animals vary, this may be due to the different ecological habits of each species (Zhang *et al.* 2006). The Siberian jerboa is a hibernating species (Zhou *et al.* 1992). The activity of hibernating species is negatively related to humidity (Zhang *et al.* 2006). This difference in different seasons indicates that this species' activity in different seasons is not affected by a single factor. Still, a combination of multiple factors, and the elements were various in different seasons. These results support our hypothesis. Therefore, seasonal differences in the number of activity peaks can be attributed to the activity

being affected by different factors in different seasons. Although some studies have suggested that the number of peak periods is affected by temperature (Kei & Motokazu 2017), this is somewhat different from our results. The possible reason is that we considered the influence of multiple factors, while previous studies only considered the impact of single element (Ricardo *et al.* 2011). There are many findings related to factors that influence animal activity patterns. Most studies of activity patterns have tended to focus on only one aspect, and have failed to consider the relative importance of other factors (Shuai *et al.* 2014; Kei & Motokazu 2017). Ecological and behavioural relationships between small mammals, especially rodents, are well documented. It is reasonable to suspect that these factors may significantly affect the overall utilization of the local environment (Delany 1972). Changes in animal activity patterns are adaptations to the general atmosphere, so changes in activity patterns may be influenced by multiple factors, not just one (Rant 1978). Therefore, it is vital that numerous factors must be taken into considered when analysing variation or change in animal activity patterns.

Research shows that temperature and relative humidity in different seasons play essential roles in influencing the activities of this rodent. In addition to factors that work together in different seasons, under the influence of external abiotic factors, this rodent also responds to changes in biological factors. It was found that food resources, perceived predation risk, and competition (Interspecific and intraspecific competition) played different roles in activities in different seasons. Just as optimal foraging theory predicts that risk-taking decisions should vary in response to perceived levels of threat (Emlen 1966; Pianka 1966; Kelly *et al.* 2020). In spring, Siberian jerboa came out of hibernation one after another, and after a long hibernation period, they need food to supplement their energy. At this time, food resource is an important factor for triggering activities. The increase in food resource leads to an increase in the time and frequency of activities in order to achieve the maximum use of food resources. The jerboa ignores the effect of perceived predation risk and intraspecific competition when seeking food resources and is thus risk-prone. Their foraging strategy in this season involved antipredator mechanisms and risk-proneness. In summer, when predation risk increases, their activity time and frequency decreased. The Siberian jerboa chose to avoid predation risk and competition. In summer, the adopted foraging strategy of the Siberian jerboa was risk-aversion and predator avoidance mechanisms, as reducing activity in the micro-habitat with high feeding pressure increases survival value (Clarks 1983). In autumn, the jerboa prepared to enter hibernation, and needed to store energy for the hibernation period. At this time, food resources guided the activities of this species. The decrease in food resource led to a reduction of activity time and frequency. The need for food made them ignore predation risks and interspecific competition. This season's campaign foraging strategy was the same as in spring, driven by the demand for food resources. In different seasons, the selection of food resources by Siberian jerboa was diverse, which indicates that it used the micro-habitat differently and selected habitat as an antipredator strategy. The demand for food in autumn has enabled it to expand the species of plants that can be selectively eaten, thereby allowing it to obtain more food resources at a level where the overall vegetation biomass of the habitat is not high.

Although there is no significant difference in the amount of food resources between spring and summer, why do they have different strategies when facing predatory risks? And why autumn food resources are abundant, it still chooses to face risks? When animals forage under food-deficient conditions, they generally switch from risk-aversion to risk-proneness. Therefore, some scholars have proposed the risk-sensitive foraging theory (McNamara & Houston 1990). Facing changes in food resources, *Ochotona curzoniae* increase ground activity time to make full use of and protect food resources (Zhang *et al.* 2005). Rodents reduce their exposure time and increase their activity frequency to reduce predation risk, which was one of the main countermeasures for adapting to high-risk environments (Yang *et al.* 2007). When a resource is necessary for an animal, even if the predation risk level increases, the animal still tends to take risks and acquire the resource (Barnard & Hurst 1987; Helfman 1984). This explains why spring and autumn adapted different strategies from in summer. Spring and autumn were more demanding for food resource acquisition. The adoption of this foraging strategy is driven by the demand for food resources, not by the amount of food resources. Thus, the request for food resource was an important influencing factor of overall activity during different seasons. Animals possess the ability to integrate disparate sources of information about danger to optimize energy gain (Chelsea *et al.* 2019).

## Conclusions

Based on the above, the factors affecting activities were different in different seasons. In spring, relative humidity mainly affected activities. In summer temperature, relative humidity, and interspecific competition mainly affected activities. In autumn, relative humidity and perceived predation risk mainly affected activities. The activity pattern of the Siberian jerboa changed in different seasons. The Siberian jerboa had two similar peak periods in spring and summer, and there were three activity peaks in autumn with lower activity time and frequency. Different factors affect animal activity at different levels. Abiotic factors (Temperaturetemperature, relative humidity and wind speed) acted on the daily activity level and mainly affected the number of peak periods of activity in different seasons. The demand for food resource affected the level of activity throughout the seasons. According to the amount of food resources, the jerboa adapted different responses to predation risks and competition in different seasons.

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