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## Foraging behaviour in East Asian desert rodents and its implications on coexistence

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We studied the foraging behaviour of two sympatric rodents (*Meriones meridianus* and *Dipus sagitta*) in the Gobi Desert, Northwestern China. The role of the foraging behaviour in promoting species coexistence was also examined. We used giving-up densities (GUDs) in artificial food patches to measure the patch use of rodents and video trapping to directly record the foraging behaviour, vigilance, and interspecific interactions. Three potential mechanisms of coexistence were evaluated (1) microhabitat partitioning; (2) spatial heterogeneity of resource abundance with a tradeoff in foraging efficiency vs. locomotion; and (3) temporal partitioning on a daily scale. Compared to *M. meridianus*, *D. sagitta* generally possessed lower GUDs, spent more time on patches, and conducted more visits per tray per capita, regardless of microhabitat. However, *M. meridianus* possessed advantages in average harvesting rates and direct interference against *D. sagitta*. Our results only partly support the third mechanism listed above. We propose another potential mechanism of coexistence: a tradeoff between interference competition and safety, with *M. meridianus* better at interference competition and *D. sagitta* better at avoiding predation risk. This mechanism is uncommon in previously studied desert rodent systems.

**Keywords:** coexistence; foraging behaviour; gerbil; giving-up density; jerboa

### Introduction

The focus of studies on diversity maintenance is species coexistence (Chesson 2000). Stable coexistence often means mutual invasibility (i.e. each species can increase when rare) and requires that intraspecific competition be stronger than interspecific competition, which can be realized in many ways, e.g. food partitioning (Brown & Lieberman 1973; Schoener 1974; Bowers 1982), habitat partitioning (Brown & Lieberman 1973; Rosenzweig 1973), microhabitat partitioning (Leman & Rosenzweig 1978; Price 1978; M'Closkey 1982), seasonal variation of foraging efficiency among species or storage effects (Brown 1989; Brown et al. 1994; Chesson 2000), and frequency-dependent predation (Holt et al. 1994; Holt & Lawton 1994).

A mechanism of coexistence on a local scale normally requires an axis of heterogeneity and a tradeoff, such that each species can perform better than its competitors along some part of the axis (Kotler & Brown 1988). Mechanisms of coexistence are based, explicitly or implicitly, on the concept of niche, and the niche of a species often includes what, when, where, and how it eats. Foraging may also significantly affect the habitat use and activity patterns of individuals and often responds to intra- and interspecific interactions, and vice versa (Kotler & Brown 2006). Foraging theory thus connects an individual behaviour with population dynamics and opens a window into exploring mechanisms of coexistence (Kotler & Brown 2006).

Rodents are often sensitive to ecological factors and require high-energy intake due to their relatively high

metabolic rates (Halle & Stenseth 2000), and therefore are especially suitable for studies on the foraging behaviour. The giving-up density (the density of resources left behind in a resource patch following exploitation, hereafter “GUD”) framework proposed by Brown (1988) provides an especially effective method to reveal the foraging behaviour, patch use, biological interactions, and species coexistence. In the past decades, desert rodents in North America and the Middle East have proved to be successful models in this field, and several mechanisms of coexistence related to the foraging behaviour have been proposed and tested (Bowers 1982; Kotler 1984; Brown 1989; Kotler et al. 1993; Brown et al. 1994; Jones et al. 2001; Leaver & Daly 2001). However, studies in many other desert systems with different substrate and/or different species composition, such as the Gobi Desert in East Asia, have largely lagged behind (Kelt 2011), and comparative studies in this field on a global scale are thus hindered.

In this paper, we used the GUD method and camera video trapping of two sympatric rodents with similar diets and habitat use in the Gobi Desert to explore foraging behaviour's roles in promoting coexistence. Specifically, we evaluated the possibility of three coexistence mechanisms commonly found in desert rodent communities: microhabitat partitioning (Leman & Rosenzweig 1978; M'Closkey 1981; Price & Waser 1985; Brown 1989; Brown et al. 1994), spatial heterogeneity of resource abundance with a foraging efficiency vs. locomotion tradeoff (Brown 1986; Brown 1989), and temporal

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partitioning on a daily scale (Kotler et al. 1993; Ziv et al. 1993; Gutman & Dayan 2005).

## Materials and methods

### Measuring patch use and foraging behaviour

We used the GUD method (Brown 1988) to measure the rodent patch use. Underlying the GUD method is the elegant “ $H = C + P + MOC$ ” rule, which predicts that an optimal forager should cease foraging in a food patch with diminishing returns when its harvesting rate ( $H$ ) no longer exceeds the sum of metabolic costs ( $C$ ), predation costs ( $P$ ), and missed opportunity costs (MOC) of foraging (Brown 1988). Under this scenario, the GUD in a patch can be used to assess the foraging efficiency of the forager and therefore a measurement of a forager’s perceived costs. Higher GUD generally implies higher foraging costs and lower foraging efficiency. The GUD method is effective in titrating behaviour (Kotler & Blaustein 1995), relatively simple to employ, and has been frequently used in studies on desert rodents especially in North America and the Middle East.

We used supplemental methods including live-trapping, individual marking, and camera video trapping to identify each forager. In this manner, we could avoid problems that may arise from having more than one animal foraging in a tray. As Bedoya-Perez et al. (2013) suggest, the addition of cameras is a valuable solution for overcoming many potential limitations associated with the GUD framework. At the same time, video analysis can also provide us with other valuable information, such as foraging time, vigilance, and interactions between individuals.

### Study system

Our study system included the midday gerbil (*Meriones meridianus*, 45 g) and the three-toed jerboa (*Dipus sagitta*, 55 g), which are common species in many East Asian deserts. Both species are nocturnal (Song & Liu 1984) and possess inflated auditory bullae (an anti-predator adaptation). The desert hamster (*Phodopus roborovskii Satunin*) and the grey hamster (*Cricetulus migratorius*) are also present in our study area, but are relatively rare. Seeds of *Hedysarum scoparium* constitute a large part of both species’ diets in autumn. *M. meridianus* is a quadrupedal, central-place forager with food-hoarding habits, while *D. sagitta* is a bipedal wanderer with a much larger home range and generally does not store food. Like many other jerboas, *D. sagitta* is also known for its bipedal locomotory gait, which may increase its ability to travel long distances and chances of escaping predators in open microhabitats. *D. sagitta* hibernates in winter (usually from late October to early April), while *M. meridianus* does not. *M. meridianus* relies on the food collected in autumn to survive the tough times.

Based on the morphology and ecology of the two species, we tested three potential mechanisms of coexistence: (1) Microhabitat partitioning based on a tradeoff in the ability to forage efficiently in bush vs. open microhabitat.

If this is the case, one species should predominate in one microhabitat and possess a lower GUD in that microhabitat than the other species. For our system, we predict that *D. sagitta* and *M. meridianus* should possess a lower GUD relative to their competitor in open and bush microhabitats, respectively. (2) Spatial heterogeneity of resource abundance with a tradeoff in the ability to forage efficiently in a patch vs. the ability to travel easily between patches (efficiency vs. locomotion). Increasing body size or bipedality may make travel less costly, but at the expense of within-patch foraging efficiency (Kotler & Brown 1988). Accordingly, we predict that *M. meridianus* will leave a patch with lower GUD and *D. sagitta* will visit more patches per capita. (3) Temporal partitioning based on a tradeoff in foraging efficiently at high vs. low resource densities. In our experimental setting, resource densities in artificial patches decline and are replenished on a daily basis, resembling the environment faced by gerbils in the Negev Desert (Kotler et al. 1993; Ben-Natan et al. 2004). For this mechanism, we expect temporal partitioning on a daily scale between the two species, with the behaviourally dominant one foraging earlier than the subordinate one, or the species with faster foraging speed foraging earlier than the species with lower GUDs. These mechanisms, of course, are not mutually exclusive and may operate simultaneously. Other mechanisms, such as a seasonal rotation of foraging efficiency among species or temporal partitioning on an annual basis (Brown 1989), may also exist but are beyond the scope of this study.

We conducted our field study in Gaotai County, Gansu Province, northwestern China during August and September 2013. The Gobi Desert dominates the county, with shelter belts and woodlands spreading along the Heihe River. The substrate of this desert type is mainly coarse sand with a dark gravel cover. We selected eight desert sites near Baba village as our study area (39°48N, 99°70E). Each site was roughly rectangular (200 × 200 m<sup>2</sup>), spaced at least 200 m apart from each other. The vegetation of our study sites consists mainly of *H. scoparium*, a common shrub in northwestern China whose seeds are a favourite food for both rodents.

### Live-trapping

We first conducted live-trapping in all eight sites before experiments. In each site, we placed an 8 × 8 trapping grid, with roughly 25 m spacing between neighbouring stations. A locally made wire cage trap (12 cm × 15 cm × 30 cm) was placed at each trap station, and baited with fried peanuts. A piece of cotton was placed in each trap to keep the animals warm during the night. The live-trapping session lasted for five nights (2560 trapping nights). We opened traps at dusk (17:00–19:00 h) and checked traps at dawn (07:00–08:00 h). Each trapped animal was weighed, sexed, marked with black dye on the forehead, body sides, and tail in a unique pattern (if captured for the first time), and then released immediately. Of the 118 individuals captured (63 *D. sagitta*, 42 *M. meridianus*, and 13 *P. roborovskii*), 45 *D. sagitta* and 30 *M. meridianus* were adults (for *M. meridianus*, individuals ≥35 g; for *D. sagitta*,

individuals  $\geq 40$  g) and used as our subjects. At least 80% of individuals captured in each site were re-captured.

### Experimental procedure

Our experiments began immediately after the trapping session. We selected eight clear nights with similar temperature and illumination (half-moon) and carried out experiments on one site each night. The sequence of sites was randomly arranged, and the experiment on each site was preceded by one night to habituate animals to our experimental setup. *M. meridianus* and *D. sagitta* in our study area quickly habituated to our experiments and readily foraged in seed trays from their first encounter with trays. We selected eight stations (four under bushes and four in an open microhabitat) within each site, with spacing  $> 50$  m between any two stations. Between 19:00–19:30 h, we placed an aluminium tray (40 cm  $\times$  40 cm  $\times$  4 cm) filled with four litres of sifted sand at each station and thoroughly mixed 24 unhusked sunflower seeds (about 3 g) into the sand substrate. We used sunflower seeds because they were similar in size to seeds of *H. scoparium* and large enough for us to observe their consumption by individual rodents. An auto-triggered infrared video camera (Ltl 6210MM, Shenzhen Blueskyocean Technology Co., Ltd., China) was placed 1.5 m away from each tray in order to record animal activity. We collected all cameras and downloaded data the following morning.

We collected the following information from each camera: the identity of each individual that foraged in the tray; the start time and duration of each tray visit (during which the animal stayed in the tray longer than five seconds or performed successful harvesting); total time vigilant; the number of seeds carried away; and the number of seeds consumed during a visit. An individual was classified as vigilant if it stopped foraging and scanned or remained still with its head up. We found that most individuals focused their foraging in one seed tray, although jerboas often visited more than one tray in a night. For this reason, for an individual that visited more than one tray, we only analysed data for the tray in which it harvested the most seeds. We further calculated GUD (the number of seeds remaining in the tray when the individual ceased foraging), the number of visits per tray per capita, the number of seed trays visited per capita, the total time spent in the tray (to the nearest 0.1 s), the average harvest rate (the number of seeds harvested divided by the total time spent in the tray), the proportion of seeds carried away (the number of seeds carried away divided by the number of seeds harvested), and the proportional vigilance (total time vigilant divided by total time spent in the tray) for each individual. We also recorded direct one-on-one interactions between gerbils and jerboas and noted their outcomes.

### Statistical analysis

We conducted analysis of variance (ANOVA) to analyze behavioural data that passed normality tests (GUDs, the number of visits per tray per capita, the number of seed

trays visited per capita, the total time spent in the tray, the average harvest rate, and the proportion of seeds carried), with species, microhabitat, and grid as fixed factors. We acknowledge that Type I error rates can be inflated with repeated ANOVAs on the same subjects. This potential problem can be ignored in this instance because the fixed effect of species, which is our main interest, was highly significant in each analysis. For the two vigilance variables (total time vigilant and the proportional vigilance), we pooled data for both microhabitats for comparison due to the small sample size and conducted Mann–Whitney U tests for interspecific comparison. To compare the nocturnal activity patterns between *M. meridianus* and *D. sagitta*, we conducted independent-samples Kolmogorov–Smirnov tests for each microhabitat on the hourly distribution of frequency of visits per tray (for each species, all individuals recorded foraging in that microhabitat were pooled together) between the two species.

Based on Holling's (1959) disc equation, we used total foraging time (the total time spent in the tray minus total time vigilant) and GUDs to estimate the quitting-harvest rate (QHR) for each individual foraging in the bush microhabitat. In calculating QHRs, we followed the protocol provided by Kotler et al. (2010). We only calculated QHRs for each individual foraging in the bush microhabitat due to the limitation of sample size. We then plot the QHR against the GUD to generate harvest rate curves (the term "harvest rate curve" here means a curve reflecting the relationship between the QHR and the GUD rather than that between the QHR and time) for each species. For details of harvest rate curves, please see Supplemental data. All statistical analyses were conducted with SPSS 19.0.

### Results

We collected data on 59 recognizable focus individuals (bush microhabitat: 15 *M. meridianus* and 19 *D. sagitta*; open microhabitat: 8 *M. meridianus* and 17 *D. sagitta*) that foraged in 31 seed trays, for a total of 562 tray visits. *D. sagitta* (416 tray visits) was much more frequently recorded than *M. meridianus* (146 tray visits). The two species differed in microhabitat use (chi-square test:  $\chi^2 = 8.61$ ,  $df = 1$ ,  $P = 0.003$ ): *M. meridianus* was much less frequently observed in open microhabitat (45 tray visits) than in bush microhabitat (101 tray visits) while *D. sagitta* had no clear-cut microhabitat difference (bush: 230 tray visits; open: 186 visits). *D. sagitta* visited more trays per capita than *M. meridianus* in both microhabitats (bush:  $t = -3.67$ ,  $df = 32$ ,  $P = 0.001$ ; open:  $t = -3.96$ ,  $df = 23$ ,  $P = 0.001$ ; Table 1).

Species differed in GUDs ( $F_{1, 24} = 16.64$ ,  $P < 0.001$ ), with *M. meridianus* generally leaving patches at a higher GUD than *D. sagitta*, regardless of microhabitats (bush:  $t = 2.96$ ,  $df = 32$ ,  $P = 0.006$ ; open:  $t = 3.34$ ,  $df = 23$ ,  $P = 0.003$ ; Figure 1(A)). *M. meridianus* tended towards lower GUDs in bush than in open microhabitat, although this trend was not statistically significant ( $t = -1.66$ ,  $df = 21$ ,  $P = 0.112$ ). *D. sagitta* made more foraging visits to trays (bush:  $t = -3.78$ ,  $df = 32$ ,  $P = 0.001$ ; open:  $t =$

Table 1. Tray visits (mean values  $\pm$  1 SE) of the rodents *Meriones meridianus* and *Dipus sagitta* in different microhabitats.

Variables	Species	Bush habitat	Open habitat
Number of trays	<i>M. meridianus</i>	1.13 $\pm$ 0.09	1.00 $\pm$ 0.00
Visited per capita	<i>D. sagitta</i>	1.89 $\pm$ 0.17	2.06 $\pm$ 0.18
Number of visits	<i>M. meridianus</i>	6.70 $\pm$ 0.77	5.63 $\pm$ 0.65
Per tray per capita	<i>D. sagitta</i>	12.1 $\pm$ 1.10	10.9 $\pm$ 1.05

$-3.29$ ,  $df = 23$ ,  $P = 0.003$ ;  $F_{1, 24} = 15.76$ ,  $P = 0.001$ ; Table 1) and spent more time in a seed tray than *M. meridianus*, regardless of microhabitat (bush:  $t = 3.75$ ,  $df = 32$ ,  $P = 0.001$ ; open:  $t = 2.74$ ,  $df = 23$ ,  $P = 0.01$ ;  $F_{1, 24} = 16.07$ ,  $P = 0.001$ ; Figure 1(B)).

*M. meridianus* possessed a significantly higher average harvest rate than *D. sagitta* in bush microhabitat, while no interspecific difference was detected in open

microhabitat (bush:  $t = 4.34$ ,  $df = 32$ ,  $P = 0.001$ ; open:  $t = 0.86$ ,  $df = 23$ ,  $P = 0.40$ ;  $F_{1, 24} = 8.14$ ,  $P = 0.009$ ; Figure 1(C)). *D. sagitta* possessed a significantly lower mean harvest rate in bush than in open microhabitats ( $t = -2.72$ ,  $df = 34$ ,  $P = 0.01$ ; Figure 1(C)). Likewise, when foraging under bushes, *M. meridianus* left the patches with higher QHRs than *D. sagitta* (average  $QHR_{gerbil} = 0.031 \pm 0.0031$  vs. average  $QHR_{jerboa} = 0.018 \pm 0.0018$ ;  $F_{1,16} = 13.68$ ,  $P = 0.002$ ). Consistent with its food caching habit, *M. meridianus* carried proportionally more seeds away than *D. sagitta*, regardless of microhabitat (bush:  $t = 5.83$ ,  $df = 31$ ,  $P < 0.001$ ; open:  $t = 2.43$ ,  $df = 21$ ,  $P = 0.024$ ;  $F_{1, 22} = 16.78$ ,  $P < 0.001$ ; Figure 1(D)). Unlike gerbils that always acted as central-place foragers, *D. sagitta* never stored the seeds carried away, choosing instead simply to consume them in a nearby place.

*M. meridianus* and *D. sagitta* displayed significantly different patterns of activity in both microhabitats (Kolmogorov–Smirnov test:  $Z = 2.23$ ,  $P < 0.001$ ; Figure 2).

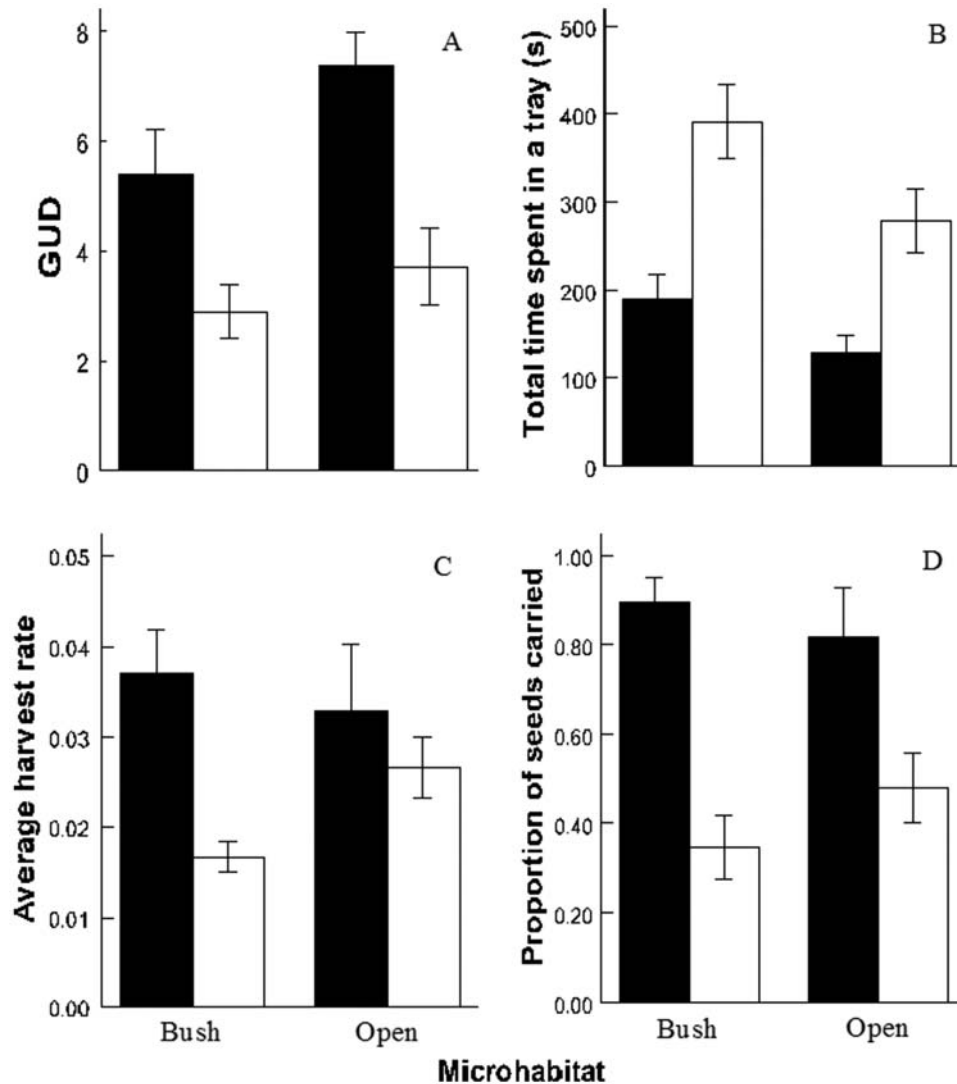


Figure 1. Comparison of the foraging behaviour between *Meriones meridianus* (black bars) and *Dipus sagitta* (white bars) in bush and open microhabitats: (A) average GUD (giving-up density, unit: item), (B) total time spent in a tray (unit: s), (C) average harvest rate (unit: item/s), and (D) proportion of seeds carried. Graphs show mean values  $\pm$  1 SE. The GUD is the number of seeds remaining in the tray when the individual ceased foraging. The average harvest rate is the number of seeds harvested divided by the total time spent in the tray.

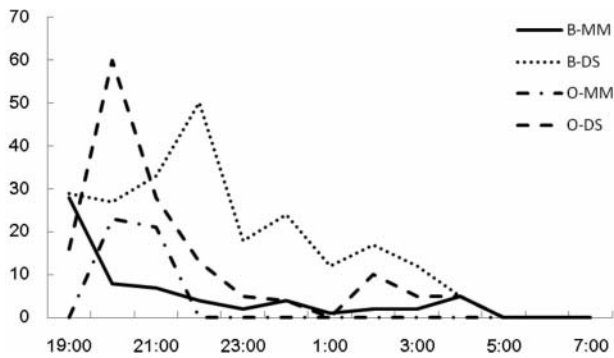


Figure 2. Nocturnal activity patterns of *Meriones meridianus* and *Dipus sagitta* in two microhabitats. Numbers on the horizontal axis represent local time and the vertical axis represents total visits per tray. B-MM, O-MM, B-DS and O-DS refer to *M. meridianus* in bush microhabitat, *M. meridianus* in open microhabitat, *D. sagitta* in bush microhabitat and *D. sagitta* in open microhabitat, respectively.

*M. meridianus* were only active early after sunset, while *D. sagitta* seemed to possess 2–3 peaks of activity throughout the night. However, both species were more active early in the night (19:00–23:00 h), and they seemed to be more synchronized in open microhabitats. In bush microhabitats, the two species showed more distinct activity patterns, with *M. meridianus* reaching its first peak immediately after sunset and *D. sagitta* reaching its first peak 3 hours later. On a finer temporal scale, *D. sagitta* started to forage earlier than *M. meridianus* in all but one seed tray. *M. meridianus* successfully drove *D. sagitta* away in each of the five one-on-one contests that we observed. However, *M. meridianus* never stayed in a tray longer than 2 minutes and *D. sagitta* soon resumed foraging after *M. meridianus* left the tray.

Only a small portion of rodents indicated apparent vigilance. No interspecific difference was detected in total time vigilant: *M. meridianus*  $11.4 \pm 3.70$  s ( $n = 10$ ) vs. *D. sagitta*  $27.6 \pm 7.34$  s ( $n = 4$ ),  $Z = -1.35$ ,  $P = 0.18$ ; or proportional vigilance: *M. meridianus*  $0.061 \pm 0.030$  ( $n = 10$ ) vs. *D. sagitta*  $0.067 \pm 0.014$  ( $n = 4$ ),  $Z = -0.57$ ,  $P = 0.57$ .

## Discussion

We designed our experiments to quantify the foraging behaviour of two species of desert rodents in the Gobi Desert in order to test three likely mechanisms of species coexistence. In regards to the foraging behaviour, *M. meridianus* and *D. sagitta* displayed three tactics for harvesting seeds: consuming food immediately in the tray, carrying food away for caching, and carrying food away to shelter for immediate consumption. *M. meridianus* generally acted as a central-place forager, and *D. sagitta* always consumed food immediately. This seems to be consistent with the jerboas in Asia and Africa generally adopting a dormancy strategy to survive winter (Kotler & Brown 1988) while gerbils may rely on food caches. However, why *D. sagitta* sometimes chooses to carry food away remains a question. They do so simply to move to a place of safety for consuming food, which may take

time and leaves the patch available for other potential competitors, hampering them from effectively protecting food resources. One possible explanation for this is that *D. sagitta* leaves a patch to avoid an interaction with *M. meridianus*, the dominant and more aggressive species. However, if this is true, *D. sagitta* should do so less frequently in open microhabitat where gerbils are less active and this is contrary to our results (Figure 1(D)). Another explanation is that *D. sagitta* leaves a patch in order to reduce sharing information of the food patch with intra- and interspecific competitors. If true, then *D. sagitta* should do so more frequently when foraging in open microhabitats with better illumination. Our results support this (Figure 1(D)). Furthermore, *D. sagitta* may recognize the contrast between the patch and the environment and treat it as a potential risk, and therefore moves away from the patch for consuming food in order to minimize the time exposed on the dangerous place. These explanations deserve further investigation.

While GUDs provide basic information on patch use, harvest rate curves may reveal more details on how individuals manage risk when foraging (Kotler et al. 2010; Embar et al. 2011; Embar et al. 2014). Figure 3 displays the harvest rate curves of these two species when in the bush microhabitat. Compared to *D. sagitta*, *M. meridianus* seems to be a less apprehensive forager, as it possesses a steeper harvest rate curve. However, *M. meridianus* manages to reduce predation risk by allocating less time to each patch harvesting food, as indicated by its higher GUDs.

As to the mechanisms of coexistence, the Gobi Desert system seems to be different from that in North America

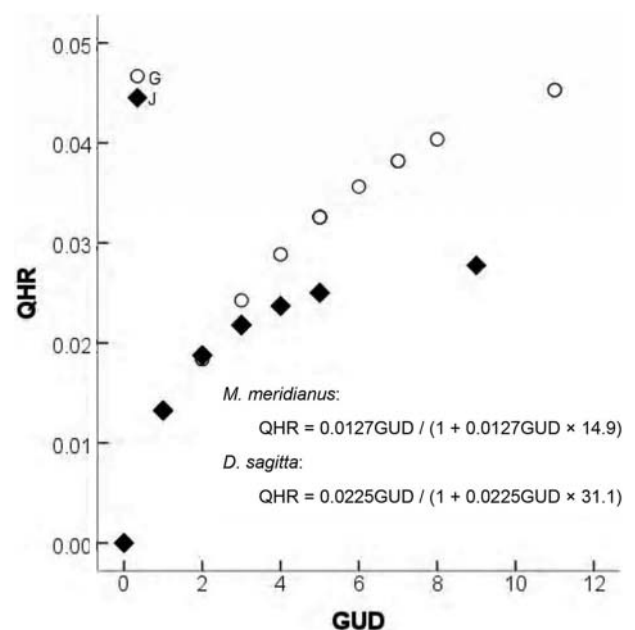


Figure 3. Harvest rate curves for individuals of *Meriones meridianus* (open circles) and *Dipus sagitta* (solid diamonds) foraging under bush microhabitat. Equations for the curves (based on Holling's disc equation) are also presented. Horizontal and vertical axes represent GUD (giving-up density) and QHR (quitting harvesting rate), respectively.

or in the Middle East (Brown 1989; Kotler et al. 1993; Brown et al. 1994). Judging from the activity level, *M. meridianus* prefers bush microhabitats and *D. sagitta* shows no clear preference. However, *D. sagitta* possesses a lower GUD in both microhabitats, which means that the two species cannot coexist simply through microhabitat partitioning. Similarly, *D. sagitta* foraged in more trays per capita, while still possessing lower GUD, which makes the “efficiency vs. locomotion” tradeoff unlikely. As to the third mechanism, the two species display somewhat different activity patterns. Although both prefer to forage early in the night, *M. meridianus* is a faster forager and therefore more efficient than *D. sagitta* at high resource density. Given that *M. meridianus* also possess advantages in interference, the two species may coexist on a resource that varies daily in density. In summary, it seems that only temporal resource partitioning is partly supported.

An alternative mechanism for coexistence is a tradeoff between interference competition and anti-predation ability. Interference competition has been widely recorded in rodent communities and may significantly affect coexistence and community structure (Frye 1983; Ziv et al. 1993; Gutman & Dayan 2005). In our study, *M. meridianus* wins all the direct fights against *D. sagitta*, which implies that *M. meridianus* is individually dominant to *D. sagitta*, although slightly smaller in size. Compared to *D. sagitta*, *M. meridianus* also spends much less time foraging and prefers to forage in bush microhabitats, which suggests that *M. meridianus* is more vulnerable and sensitive to predation risk, consistent with its morphology, smaller body, and higher GUDs. Meanwhile, *D. sagitta* may be more efficient in detecting predators and less susceptible to attack because of bipedal locomotion. A similar mechanism has been mentioned in studies on fox squirrels (*Sciurus niger*) and grey squirrels (*S. carolinensis*) that coexist in woodlands in the Midwestern United States. In that system, *S. niger* dominates in wood margins while *S. carolinensis* dominates in the interior. *S. carolinensis* is better at interference competition but more vulnerable to predation risk than its congener (Lanham 1998; Van der Merwe et al. 2005). The tradeoff between interference and safety along with environmental heterogeneity promotes habitat partitioning and coexistence between the squirrel species. This mechanism, however, is uncommon in previous studies on desert rodents.

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### Supplemental data

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