



Foraging behavior of the midday gerbil (*Meriones meridianus*): Combined effects of distance and microhabitat

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ABSTRACT

We used the giving-up density (GUD) method and direct observation to study the combined effects of travel distance and microhabitat on foraging behavior of the midday gerbil (*Meriones meridianus*), which often acts as a central place forager. We provided animals with artificial seed trays in which dry and unhusked pumpkin seeds were mixed with fine sand. Gerbils practiced an eat-and-carry strategy in patches of bush microhabitat that were far from central places (BF patches), and tended to carry all seeds back in the other three treatments. Resource protection, predation risk avoidance and the balance between future and present value of food items may contribute to the eat-and-carry strategy. When distance was held constant, GUDs in open patches were higher than in bush patches, which was consistent with most studies. When microhabitat was held constant, GUDs in nearer patches were normally lower than in farther patches. In most cases, gerbils preferred to carry more seeds back rather than consume them immediately. We concluded that this tendency was due to the gerbils balancing the factors of future value and present value, and individual fitness and inclusive fitness.

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1. Introduction

A foraging animal often needs to balance multiple priorities, among which the most often studied are energy intake and predation risk avoidance (Lima, 1985; Lima et al., 1985; Gilliam and Fraser, 1987; Hughes and Ward, 1993; Brown and Kotler, 2004). Under selection pressure, an animal should adopt a special feeding strategy to maximize its fitness or expected reproduction rate. In the past several decades, many models have been developed of optimal feeding strategy or patch use. However, many of these models assume that animals consume food immediately (Gerber et al., 2004), which is not true for many animals who tend to carry food back to nests or shelters for later use. Orians and Pearson (1979) introduced the Central Place Foraging theory (CPF) to deal with this problem. In the classic CPF model, distance between the food patch and the central place may affect foraging behavior including diets, load size and patch choice (Orians and Pearson, 1979). Later, Lima developed a simple multi-objective model to include effects of predation risk (Lima, 1985). His model predicts that, to balance between foraging efficiency and predation risk avoidance, an animal should tend to carry more foods back to the central place as (1) the distance between the central place and the

food patch decreases; or (2) the energetic value of food increases. These predictions were supported or partially supported by various studies (Lima, 1985; Lima et al., 1985; Valone and Lima, 1987). However, this model is based on the assumption that predation risk remains constant whether the forager is traveling or harvesting. Apparently, more often than not, this assumption is not met in reality. Though far away from central places, foragers may still tend to forage in relatively safe places, e.g., in bush or shrub microhabitats, which often possess rich food resources. In other words, a food patch may also serve as a refuge. Under such circumstances, the travel distance and the microhabitat structure of the foraging patch may have significant effects on predation risk and animals' decision making, and thus should be taken into consideration. As far as we know, few CPF model has been applied to the study of the combined effects of distance and microhabitat on foraging behavior (but see Druce et al., 2006), which are not taken into consideration even in the inclusive CPF model recently proposed by Olsson et al. (2008).

Moreover, as in many other CPF models, Lima's experiments with chickadees and squirrels provided free foods to animals, which meant that the harvest rate remained constant among bouts and animals could always harvest all foods in patches. However, in many actual cases, animals have to forage in depletable food patches, which yield diminishing returns. Brown developed a patch use model (the "H = C + P + MOC" rule, where H is the harvest rate, C is the metabolic cost rate, P is the predation risk, and MOC is the missed opportunity cost rate) to deal with this problem. According

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to Brown's model, an optimal forager should cease foraging activity in a patch when its harvest rate no longer exceeds the sum of metabolic costs, predation risk and missed opportunity costs (Brown, 1988), where both predation risk and missed opportunity costs are transformed into energy currency by using a marginal rate of substitution. This model, along with the giving-up density (GUD) method (Brown, 1988), has been widely used in research for more than a decade. Later the GUD method was used in studies on central place foraging. As one may expect, many studies confirmed the prediction that GUD increases as travel distance increases (Hughes and Ward, 1993; Kotler et al., 1999a; Druce et al., 2006; but see Kotler et al., 1999b) and they generally attributed this phenomenon to the level of predation risk perceived by foraging animals, which varied with distance between central places and foraging area.

In the present study, we used the GUD method and direct observation to study the foraging behavior of midday gerbils (*Meriones meridianus*) foraging in depletable patches with variable microhabitats and variable distances from a central place. Four combinations of microhabitat and travel distance were used: bush microhabitat with a long travel distance (a tray covered by shielding and at least 12 m away from burrows, treatment BF); open microhabitat with a long travel distance (an open tray at least 12 m away from burrows, treatment OF); bush microhabitat with a short travel distance (a tray covered by shielding about 2 m away from burrows, treatment BN) and open microhabitat with a short travel distance (an open tray 2 m away from burrows, treatment ON). Based on the classic CPF model and the previous field studies mentioned above, we predict that: (1) when microhabitat is constant, as travel distance increases, GUDs should increase and the proportion of seeds carried should decrease and (2) when travel distance is constant, gerbils foraging in bush microhabitat should utilize a patch more thoroughly (i.e., lower GUDs should result in seed trays) and carried back proportionally fewer seeds. Meanwhile, we are particularly interested in the foraging strategy used by gerbils foraging under BF treatment. We predict that when foraging in a BF patch, a gerbil should stay in the patch and consume in situ all the food he finds in the tray, for this strategy seems able to both maximize energetic intake and minimize predation risk.

2. Materials and methods

2.1. Animals

The midday gerbil (*M. meridianus*) is a medium-sized, mainly nocturnal rodent that is widely distributed in the East Asian desert. It often dominates in numbers in various kinds of desert and semi-desert microhabitats, and digs burrow systems near or under shielding bushes (Song and Liu, 1984). Midday gerbils mainly feed on seeds, leaves, stems and insects (Song and Liu, 1984; Ma et al., 1987). Although living in small groups, they generally forage solitarily and often search for food in open land at a distance from the dwelling systems. Compared to the Mongolia gerbil, the midday gerbil is less social and each individual seems to be more restricted in his territory (Shilova and Orlenev, 2004). Unlike hamsters or squirrels, midday gerbils do not possess pouches and this limits their carrying ability to some extent. However, like many other desert rodents, midday gerbils still have a habit of caching food, especially when confronting highly nutritious food, such as dry seeds, in late autumn (Ma et al., 1987). In our study area, midday gerbils living in one dwelling system (usually a family) were found to maintain a relatively large larder (sometimes more than 1000 g of food was cached in one hole) in their dwelling system (personal observation, unpublished). These characteristics make the midday gerbil a good object for the study of central place foraging and food caching.

2.2. Study area and habitat manipulation

In June and July 2007, we conducted the field study in Gaotai County of Gansu Province, northwestern China. Gobi constitutes the main body of the county, with shelter belts and woodlands spreading along the Heihe River. We selected a woodland and the surrounding Gobi desert in Baba Village as our study area. This woodland has been maintained for 24 years and is well protected from grazing and cutting. Trees within the woodland are normally 2–3.5 m tall, with 5–6 m spacing between them. The vegetation of the Gobi consists mainly of small clumps of *Ephedra przewalskii* Stapf, which are normally 40–60 cm in height. Along with the midday gerbil, the desert hamster (*Phodopus roborovskii* Satunin), grey hamster (*Cricetulus migratorius* Pallas) and three-toed jerboa (*Dipopus satitta* Pallas) also dwell in the study area but are relatively rare. Previous trapping records indicate that the midday gerbil is the dominant rodent species in this area, and gerbils generally dwell in the woodland and forage at night both in the woodland and the Gobi (personal data, unpublished). During our experiments, nocturnal temperature ranged from 18 to 23 °C and relative humidity ranged from 37 to 48%. According to our previous observation, the main predators of gerbils in this region are eagle owl (*Bubo bubo*) and little owl (*Athene noctus*). A domestic cat (*Felis silvestris catus*) was also found wandering near the study area but with much lower frequency (only once during our field work).

Our study was carried out at four rectangular sites (about 100 m × 20 m) located in the Gobi, with one long side adjoining the woodland. According to previous trapping data, these sites all possess a moderate density of active dwellings of gerbils. Within the four sites, most of the dwelling systems were found near the edge of the woodland. The interval between any two sites was ≥ 100 m. We removed all the clumps in the sites, which we thought might be used by gerbils as temporary shielding. To create "bush" microhabitats, we used a plastic box (55 cm × 55 cm × 25 cm) to cover the seed tray. The box had only one side open (for entrance of rodents and observation) and was covered with vegetation cut from the Gobi to mimic the natural bush shelter. Dry and unhusked pumpkin seeds were used as artificial food in our study. Each seed tray (45 cm × 45 cm × 2.5 cm) contained 15 pumpkin seeds which were thoroughly mixed in 4 L sand.

2.3. Animal preparation and pilot observation

To obtain experimental subjects, we conducted live trapping for 3 d in the four sites. During the live trapping, we placed and baited 10 Sherman traps in each site every night. We captured a total of 13 adult midday gerbils (9 males and 4 females). All the individuals were weighed and given a unique mark with permanent hair dye immediately after capture, and then taken back to our laboratory for later experiments. Using a digital camera, we recorded the exact location of capture of each individual as well.

We conducted a 1-week pilot observation 1 d after release to confirm the location of the dwelling system used by each marked animal. Six seed trays were provided in each site. These trays were arranged in two parallel lines (three trays in each line). One line was 2 m away from the woods and the other was 12 m away. Each night, three of the six trays were randomly placed in the "bush" microhabitats and the other three were placed in open microhabitats, with at least 15 m spacing between them. This arrangement allowed gerbils to become familiar with the study area, the seed trays, the four treatments (i.e., BF, OF, BN, and ON) and the presence of the observers. We started our pilot observation at 20:30 (right after sunset), using 4 × 50 infrared binoculars and headlights. We recorded the behavior of each individual using an MP3 recorder at least 10 m from the nearest tray. We could only monitor two sites simultaneously due to limitations of manpower, so every night we

randomly selected two sites to watch first. After we finished observation at the first two sites, we quickly moved to the other two sites. Seed trays in each site were available only when we started observation.

During the pilot observation, 11 of the 13 marked individuals were observed regularly visiting our seed trays. Although there were other gerbils active in our study area and some of them were observed later in our experiments, they visited our food tray at much lower frequencies, which may be partly due to territoriality of midday gerbils. We selected our focus animals among those regular visitors. As previous studies suggest, body size (or body weight), age, sex and body condition may play important roles in shaping foraging behavior (Bachman, 1993; Vasquez, 1996; Reboreda and Fernandez, 1997). To eliminate these potential influences, we focused our observation on seven males with roughly similar weight (55–63 g). According to our pilot observation, each of these individuals possessed its own dwelling system. By the end of the pilot observation, we identified the exact positions of these dwelling systems. For these animals, all the entrances of the dwelling systems were located in the Gobi near the woodland. We did not find any evidence that the focus animals were disturbed by observers.

2.4. Formal experiments

We initiated our formal experiments 2 d after the pilot observation. Formal experiments included three rounds for each focus animal, and each round consisted of four nights (one treatment for each animal per night). Each night we provided one tray to each focus animal. For each individual in each round, the order of the four treatments was randomly determined. Based on the pilot observation, we placed the seed tray within the area of dwelling systems of focus animals to make sure that all trays were in the region that the focus animals were active and frequently observed. Between two consecutive rounds there was a break of at least 2 d to ensure independence among rounds. During the breaks, we did not provide seed trays and did not know exactly the behavior and the location of these focus animals. However, once our experiments resumed, the focus gerbils were attracted to seed trays again immediately. We then inferred that the breaks might not cause significant effects to these gerbils. To eliminate the effects of lunar phase on animal behavior, the whole experiment was conducted under mediate illumination (nearly half moon).

During the pilot study, we found that gerbils were seldom active until 21:00–21:20, so at the formal observation phase, we started observation at 21:00 to focus animals one by one. Two investigators conducted observations on one animal at a time. During observation the behavior of the focus animal was recorded by using an MP3 recorder. To make sure that only the focus animal had access to the seed tray, the other investigator sat near the observer and chased other individuals away from the seed tray in case needed. This action, however, could frighten the focus animal and cause unpredictable effects. Fortunately, we did not have to perform chasing frequently since in most cases only the focus animals appeared in our observation. We (4 people of 2 groups participated in the formal experiments) could only monitor two animals simultaneously due to limitations of manpower, so every night we randomly selected two focus animals to watch first. After that, we provided seed trays to another two animals and repeated the observation procedure until all the focus gerbils were observed. We ended observation when all the food items in the focus seed tray had been removed or the subject had been out of vision since its last emergence for more than 15 min. Approximately 3–4 h were generally required to complete observation for all seven individuals in one night. We collected the following information in the formal experiment:

- (1) *GUDs*. The original meaning of GUD is the instantaneous food density in a seed tray when an animal gives up foraging. Because all the seed trays in this study were of the same size and the seeds selected for our experiment were roughly equal in weight, we used the number of seeds left in a seed tray to represent GUD for convenience.
- (2) *Details of food handling*. We recorded by direct observation the number of seeds eaten in a patch (N_e) and the number of seeds carried away (N_c). In our study, $GUD + N_e + N_c = 15$, and gerbils could only handle one pumpkin seed in one handling event with an apparent break in between. Therefore, the value of N_e and N_c were easily obtained. Among the seeds carried away, we further classify two distinct scenarios: (1) seeds carried away and handled in adjacent area and (2) seeds carried back to dwelling systems.

2.5. Statistical analysis

We conducted repeated measures ANOVA ($p = 0.05$) with post-hoc analysis (Turkey HSD tests) on GUD, N_c and the ratio of N_e to N_c in the four treatments. We then employed two-way ANOVA ($p = 0.05$) to test the effects of travel distance and microhabitats on these variables. All the statistic works were conducted by using SPSS 13.0 for Windows.

3. Results

3.1. Food handling

Carrying behavior was always recorded whenever an animal foraged in a seed tray. Each gerbil typically carried one or two seeds away in one bout. Number of foraging bouts of an individual per night ranged from 4 to 10. Time spent in each tray per bout ranged from 11 to 158 s and time duration between two consecutive bouts ranged from 31 to 137 s. All the seeds carried away were transported back to dwelling systems. In some cases (especially when foraging in BF trays), gerbils also chose to consume some seeds immediately in trays.

Gerbils always ate a few seeds before carrying some seeds back (mean $N_e = 3.43 \pm 2.56$ per trial, 21 trials) when foraging in BF trays. Such a strategy (namely eat-and-carry) was also observed in the other three treatments, but with much lower frequency (BN: 7 trials; ON: 3 trials; OF: 1 trial), and the ratio of N_e to N_c was much lower (Fig. 1). All the consuming behavior happened before carrying, and the last items harvested in a patch were always carried back to central places.

Generally, microhabitat has significant effect on food handling (Table 1). When foraging in near patches, gerbils carried back significantly more seeds from BN patches than from ON trays. Travel distance also greatly affects food handling. When microhabitat was held constant, gerbils always carried back significantly more seeds from patches nearer to central places than from those far from central places (Table 2). However, no significant difference in N_c was found between BF and OF patches (Table 2).

Distance and microhabitat also strongly affected tradeoff between immediate consuming and food transportation (Table 1). Average ratio of N_e to N_c in BF treatment was significantly higher than in OF, ON or BN treatments (Table 2).

3.2. GUD

Both microhabitat and travel distance significantly affected GUDs (Table 1). No significant interaction effect was detected, however. On average, GUD was highest in the OF trays ($GUD_{OF} = 9.050 \pm 1.560$ per trial, 17 trials), followed by those

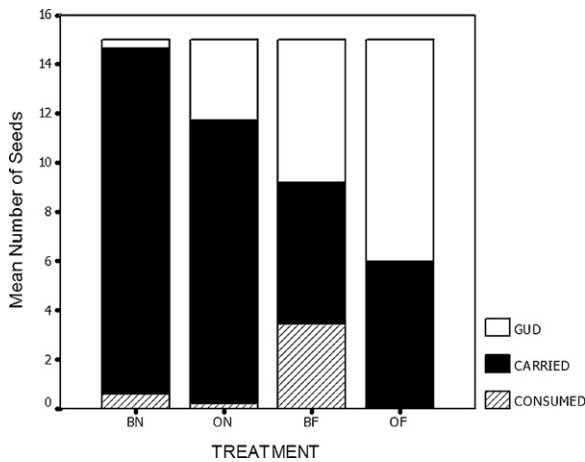


Fig. 1. Food handling in four treatments. Open bars represent the average GUDs under various treatments. Filled bars represent the average number of seeds carried back by an individual per trial, under various treatments. Shaded bars represent the average number of seeds immediately consumed by an individual per trial, under various treatments.

in the BF, ON and BN trays, respectively ($GUD_{BF} = 5.810 \pm 1.861$ per trial, 21 trials; $GUD_{ON} = 3.286 \pm 1.454$ per trial, 21 trials; $GUD_{BN} = 0.381 \pm 0.590$ per trial, 21 trials). When the distance is constant, gerbils tend to forage seeds more intensively (lower GUDs) in patches with better shielding (Table 2). When the microhabitat is constant, gerbils tend to forage more intensively (lower GUDs) in patches nearer to dwelling systems (Table 2).

4. Discussion

Travel distance and microhabitat have long been documented as important factors in shaping foraging behavior (Smith et al., 1979; Lima, 1985; Ash and Roberts, 1992; Hughes and Ward, 1993; Nakatsuyama and Fujita, 1995; Kotler et al., 1999a,b; Ovadia et al., 2001). Our results supported our second prediction but not our first prediction. When travel distance was held constant, gerbils foraging in bush microhabitats generally conducted lower GUDs and carried away proportionally fewer seeds. However, the effects of travel distance on foraging efficiency seemed to be a little more complex. When foraging in bush microhabitats, gerbils generally left seed trays far from central places with higher GUDs and carried back less seeds proportionally. However, when foraging in open microhabitats, gerbils carried away proportionally

Table 1
Repeated measures ANOVA for GUD, N_c and the ratio of N_e to N_c in the four treatments.

	df	Mean square	F	p
N_c				
Intercept	1	6557.430	2177.014	<0.001**
Microhabitat	1	31.093	10.323	0.004**
Distance	1	945.664	313.953	<0.001**
Microhabitat \times Distance	1	29.716	9.865	0.005**
Ratio of N_e to N_c				
Intercept	1	3.542	24.128	<0.001**
Microhabitat	1	2.376	16.183	0.001**
Distance	1	2.539	17.297	<0.001**
Microhabitat \times Distance	1	2.043	13.916	0.001**
GUD				
Intercept	1	1689.603	864.032	<0.001**
Microhabitat	1	177.146	90.589	0.004**
Distance	1	607.203	310.512	<0.001**
Microhabitat \times Distance	1	0.071	0.037	0.850

Note: **** = very significant.

Table 2
Comparisons among GUD, N_c and the ratio of N_e to N_c in the four treatments.

(I) Treatment	(J) Treatment	Mean difference (I–J)	Std. error	P
N_c				
BN	ON	2.52381	0.46931	<0.001**
	BF	8.28571	0.46931	<0.001**
	OF	8.16527	0.49615	<0.001**
ON	BF	5.76190	0.46931	<0.001**
	OF	5.64146	0.49615	<0.001**
BF	OF	-0.12045	0.49615	0.995
Ratio of N_e to N_c				
BN	ON	.020934	.040634	0.955
	BF	-.307805	.040634	<0.001**
	OF	.028518	.042958	0.910
ON	BF	-.328739	.040634	<0.001**
	OF	.007584	.042958	0.998
BF	OF	.336323	.042958	<0.001**
GUD				
BN	ON	-2.90476	0.44415	<0.001**
	BF	-5.42857	0.44415	<0.001**
	OF	-8.67787	0.46954	<0.001**
ON	BF	-2.52381	0.44415	<0.001**
	OF	-5.77311	0.46954	<0.001**
BF	OF	-3.24930	0.46954	<0.001**

Note: **** = very significant.

more seeds from OF patches than from ON patches. However, when we consider absolute number of seeds rather than ratio, gerbils generally carried away more seeds from ON trays than from OF trays. We then conclude that the relatively low ratio of N_e to N_c for OF patches was caused by the fact that when foraging in most risky patches (i.e., OF patches in the present study), gerbils spent extremely little time consuming food. These findings indicate that midday gerbils made decisions on when to give up based on both the distance of the food resource from the central place and the microhabitat or shelter conditions. Our results are consistent with those of previous studies (Brown, 1988; Hughes and Ward, 1993; Druce et al., 2006) and can be reasonably explained as a trade-off between energy intake and avoidance of predation risk.

Our study addressed the question: what decision would an animal make when it forages in a patch far from a central place but with good shelter conditions? The results of this study indicate that under this scenario, an animal would be more willing to consume immediately inside the patch, rather than to immediately carry foods back. In most cases, gerbils ate some seeds right away in the BF trays (i.e., a safe foraging place, but with a long travel distance) before carrying seeds back. Two interesting things should be noted in regard to this strategy: (1) the animals chose to eat first rather than carry back all the seeds they found and (2) after consuming some seeds, they still carried back some of the leftovers rather than going on to consume them immediately.

More than one mechanism could contribute to the "eating first" tendency. Again, predation risk avoidance seems to be an important factor. In our study area, avian predators were major threats to rodents. Therefore, when travel distance is relatively long (in the present study, gerbils carrying food back to dens have to travel through open area, predation risk during food transportation is therefore important), it is reasonable to predict that gerbils should decrease exposure to predator by staying in a covered patch than frequent traveling between dens and trays. This is because as travel distance increases, both predation risk and energetic cost should increase during carrying bouts. This was supported by the fact that average ratio of N_e to N_c in BF trays was significantly higher than in open trays (Table 2). Gerbils get benefits from higher energy intake and decreased risk by consuming more food in the site right away. The results are in accordance with the predictions

of Lima's efficiency maximization-risk avoidance-tradeoff model (Lima, 1985).

Resource protection may also contribute to the "eating first" tendency. Food in patches far from central places may be more accessible to other neighboring individuals. During the pilot observation, on three occasions we observed two individuals from different dwelling systems sequentially harvesting in one patch. When a gerbil carried some food away, the leftovers in the patch were exposed to other individuals wandering nearby. The farther the food patch is, the higher risk of pilferage might be. At the early phase of foraging in the BF trays, seed density is relatively high, and so are the risk of pilferage and the benefit of protection. Under this scenario, a foraging animal would tend to stay in a patch longer and consume more food before leaving.

As mentioned above, compared to staying in BF patches, carrying food back might bring gerbils much higher predation risk and energetic cost. It seemed that animals would be able to realize both energetic maximization and risk minimization by consuming all the seeds found in these trays. Why, then, did gerbils still choose to carry some food back after consuming some seeds? Notice that in our study, gerbils generally preferred to carry food back rather than eat them right away (for each treatment, average ratio of N_e to N_c is less than 1, Fig. 1). This preference of carrying was also observed in a field study conducted by Ovadia et al. (2001). In that study, high predation risk in field may be a reasonable explanation for this preference. In the present study, however, gerbils also foraged in bush microhabitats. Under this scenario, carrying food back may not appear to be beneficial for gerbils.

Should this be caused by a limited appetite? During both the pilot and the formal study, we found that midday gerbils seldom leave their burrow systems for food before 21:00, possibly because of the relatively high temperature in this season. Meanwhile, natural food of high energetic value was scarce in our sites, and all the focus gerbils were easily attracted by our seed trays and seemed to rely heavily on our pumpkin seeds when available. Most gerbils did not spend much time harvesting other natural food once pumpkin seeds were provided. In another experiment in June 2005, we found that in 15 min, a midday gerbil of normal size (previously deprived of food for 8 h) could consume 12–15 pumpkin seeds (personal observations, unpublished data). This number was significantly higher than the amount of seeds consumed in the present study. Based on these facts, we conclude that limited appetite should not be a good reason for the preference of carrying.

The reason, we guess, lies at least partly in the extra benefits provided by food caching. Caching behavior is well-documented as an adaptive strategy used to compensate for a highly variable environment or resource supply (Smith and Reichman, 1984; Vander Walls, 1990), which is also the case in our study area. An important factor affecting animals' decision making in caching is the trade-off between the present value and the future value of food items. Although the balance between present and future value was proven to significantly affect foraging behavior (Kotler et al., 1999a), it was not included in most CPF models (e.g., Orians and Pearson, 1979; Schoener, 1979; Lima, 1985; Olsson et al., 2008). In addition, cached food may also be used to feed cubs or sharing with kin (Spitzer and Brazeau, 2003), while food consumed directly contributes to the forager's own fitness, only. Obviously, food caching helps animals to take other factors (e.g., long term energy intake and inclusive fitness) into consideration, as well as predation risk and instantaneous energy intake. In our study, compared to natural food provided by plants in sites, the dry and unhusked pumpkin seeds are highly nutritious and imperishable, and therefore very suitable for caching. Under this scenario, it seems reasonable that even in bush patches (most suitable for immediate consumption), gerbils still carried back the majority of seeds they found, although this behavior was more or less depressed by increased distance.

Besides food handling, the energetic state of individuals may also significantly affect their harvest rates (Kotler et al., 1999a) and foraging strategies. As to the "H=C+P+MOC" rule proposed by Brown, the costs of predation risk increase as the present value of food decreases (Brown, 1992; Kotler et al., 1999a). After consuming some seeds, gerbils should be less willing to take a risk to continue to forage in patches far away from dwelling systems. This "saturation effect" has been well-documented in previous studies (Kotler et al., 1999a; Morris and Davidson, 2000; Olsson et al., 2002; Brown and Kotler, 2004), and may also contribute to the relatively higher GUDs in the BF patches. However, further experiments are needed to support this assumption.

In our study, we used dry and unhusked pumpkin seeds instead of millets or sunflower seeds often used in many field works. Compared to the other two types of food, pumpkin seeds are much larger and therefore may cause larger burden (and therefore higher energetic cost) during food carrying. However, during our observations, we did not see any significant difference of locomotive pattern and moving speed caused by food carrying. So this negative effect on carrying seemed to be very small, if any. On the other hand, larger size may suggest longer handling time, which has been testified in another experiment carried out later (personal observation, unpublished data). As indicated by Lima's model (Lima et al., 1985) and some experiments (Nakatsuyama and Fujita, 1995; Whishaw and Tomie, 1989), when exposed to predators, longer handling time would increase predation risk during *in situ* food handling and therefore should depress the tendency of immediate consuming (or relatively stimulate the tendency of food carrying). Meanwhile, for a food searcher relying mainly on vision (this is true for many desert rodents), large size of seeds may shorten the searching time and therefore affect the loading function and the curve of diminishing return. Further experiments are still needed to testify and quantify these potential effects of food size.

As mentioned above, we used a criteria of termination in formal experiments (i.e., the observation on one individual per night was ended if all the food items in the focus seed tray had been removed or the subject had been out of vision since its last emergence for more than 15 min) to save time. This protocol may be problematic since the focus animal may intend to resume its foraging after observation ends. However, as our study suggests, time elapsed between two consecutive bouts is much shorter than 15 min (ranged 31–137 s), which suggests that gerbils are less likely to resume foraging after such a long interval. We then considered that our criteria of termination would not bring significant effects to our results, if any.

When facing various travel distance, animals may adopt various strategies to maximize their fitness. In an experiment on the caching behavior of kangaroo rats, Daly et al. (1992) found that for kangaroo rats, the principal determinant of the initial disposition of discovered food was its distance from the day burrow: food found within about 10 m was mainly larder hoarded, although food found farther afield was usually dispersed immediately in shallow caches. In our study, instead of scatter hoarding, gerbils used an eat-and-carry strategy as an alternative to balance several priorities. Several reasons may contribute to this. Firstly, compared to scatter hoarding, larder hoarding is generally more economical, less time consuming and requires less memory load if the larder is defended or well hidden (Smith and Reichman, 1984; Daly et al., 1992). For midday gerbils in the present study, underground larders appeared to be easily defended. Under this scenario, gerbils may not need to resort to scatter hoarding for food protection. Secondly, our study was conducted in the Gobi, whose surface is tougher than sandy desert, and therefore it was more difficult for rodents to dig holes for temporary caching. Thirdly, travel distance in our study may not have been long enough to stimulate scatter hoarding. Further studies are needed to identify the underlying mechanisms.

Ethical approval

We honour any reasonable request for materials or methods needed to verify or replicate this study and to make available, upon request, any data sets upon which published studies are based. Our experiments conform to the 'Guidelines for the use of animals in research' (published in *Animal Behaviour* (1991, 41, 183–186)). All persons related to this study gave their informed consent prior to their inclusion in the study.

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