Foraging behaviour of a desert rodent community: habitat or moon – which is more influential?

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In this field study, we questioned how diverging vegetal coverage, temperature and moonlight influence the patch use indicated by the giving-up density (GUD) of a nocturnal small mammal community in sheltered and non-sheltered food patches. We investigated the foraging strategy of a widely spread community consisting of Desert hamsters (Phodopus roborovskii), Midday gerbils (Meriones meridianus), Northern three-toed jerboas (Dipus sagitta) and Long-eared hedgehogs (Hemiechinus auritus) in the Alashan Desert, China. The aim was to analyse foraging as a result of biotic and abiotic factors in undisturbed habitats, i.e. we did not manipulate any surrounding conditions and all animals were free ranging. Three habitats were investigated, named after the dominant species: Ammopiptanthus mongolicus, Corispermum sp. and Zygophyllum pterocarpum. The following results can be summarised: (1) we found no or only slight differences for the GUD within the habitats between open and sheltered places; (2) lunar illumination affected foraging during waxing and waning moon phases within the first part of the night; (3) ambient temperature and the presence of moonlight resulted in changes in the interspecific competition that impacted the GUD; and (4) we determined prominent differences amongst habitats within the four moon phases, especially between the more covered habitats Ammopiptanthus and Zygophyllum, in contrast to the Corispermum habitat with its sparse coverage ratio. In general, foraging effort was elevated in the more covered habitats. We found a preferred foraging activity in warm and dark parts of the night which may lead to elevated inter-individual competition resulting in higher GUDs. Warmer periods were preferred in nights with constant light conditions, although resource competition was again elevated. We concluded that the foraging strategy was mainly affected by habitat, whereas moonlight and temperature modulate the resulting GUD in undisturbed environments. The availability of vegetal shelters influences foraging only in detail.

KEY WORDS: habitat preference, GUD, species coexistence, patch use, temporal niche preference, behavioural plasticity.
INTRODUCTION

Life in harsh desert or semidesert climates is associated with several challenges including unpredictable food availability, low vegetal coverage (and therefore fewer plant shelters), and energy challenges due to high daytime temperatures and low humidity. One of the common survival strategies is nocturnality and a semi-fossorial way of life (Walsberg 2000). Our model species, the Desert hamster (Phodopus roborovskii) and Midday gerbil (Meriones meridianus), have adapted to their environment and living conditions by the above-mentioned activity pattern, use of subterranean burrows and reduced water loss due to highly concentrated urine (Sokolov & Mescherskii 1989; Walsberg 2000; Zhan & Wang 2004; Kelt 2011; Scheibler 2011). The latter is of importance due to limited availability of water that leads to lower water consumption. To compensate for this, the Desert hamsters and Long-eared hedgehogs (Hemiechinus auritus, the fourth species in this nocturnal community) consume insects. It is unknown whether the Midday gerbils or the Northern three-toed jerboas (Dipus sagitta, the third species) follow the same strategy. However, maintaining water balance is associated with being active in cooler periods of the day or avoiding the hot hours, but this is obviously limited by the increased energetic costs of warming. Zhan and Wang (2004) described the thermo-neutral zone of the Desert hamster to be between 25 and 33 °C. Notably, we did not measure this temperature in the course of the night, but only around sundown for our experiments, which were conducted during early summer (May and June).

In general, an animal’s behaviour and finally its survival are impacted by abiotic challenges of a dry habitat, as well as predation, and intra- or inter-specific competition (Schoener 1983; Penteriani et al. 2013; Scheibler et al. 2013). The actual risk of predation from snakes (Bouskila 1995) and meso-predators (Penteriani et al. 2013) varies in accordance with ambient light and season, suggesting that small mammal prey require flexible behavioural responses. Regarding this, we question if animals show universal adaptations towards regular alterations such as the lunar cycle. In the course of such a cycle, the visible moon disc size, moonrise and moonset vary regularly. Consequently, these repetitions would allow long- and short-term behavioural adaptation. For example, the nocturnal avian predators benefitted from additional lunar light during their hunting [barn owl (Tyto alba) Kotler et al. (1988); eagle owl (Bubo bubo) Penteriani et al. (2011)]. The same is described for tetrapodal groundhunting predators like hyenas that are more active on full-moon nights (Mukherjee et al. 2009).

Moonlight avoidance as a compensational strategy of nocturnal prey species has developed as a logical hypothesis (Clarke 1983; Price et al. 1984), even though investigators did not consistently observe moonlight avoidance amongst species (Daly et al. 1992; Zollner & Lima 1999; Kramer & Birney 2001; Griffin et al. 2005; Penteriani et al. 2013; Upham & Hafner 2013). A study by Zollner and Lima (1999) showed under controlled conditions a preference for brighter nights of white-footed mice (Peromyscus leucopus) instead of dark nights, which was explained by the importance of visual perception in that species. The finally observed activity pattern was then modified by the current predatory risk. In the current study, we described the slight influence by the moon on the activities of the Desert hamster resulting in a prolongation of activity during brighter nights, which we explained by elevated vigilance (Scheibler et al. 2014). However, as shown in previous studies, rodents are able to adapt their foraging to the predominant moon phase and prefer sheltered food patches associated with a lower predation risk on
moonlit nights (Bouskila 1995; Fanson et al. 2008; Gutman et al. 2011). Mandelik et al. (2003) reported that the Common spiny mouse (Acomys cahirinus) preferred to forage under and near boulders in a rocky environment, irrespective of the predominant moon phase. Thus, one of our research questions was whether animals would also prefer sheltered food patches in our habitats with only vegetal shelter and varying complexity, and whether we would observe in general habitat-specific foraging preference.

In order to quantify foraging effort, Brown (1988) defined the so-called giving-up density (GUD) as that density of seeds or other nutrition at which the animal will give up foraging at a particular patch. A central term is the harvesting rate (H), which relates to the sum of energetic costs of foraging (C), as well as the costs of predation risk (P), and the activity cost of missing other foraging opportunities (MOC). Additionally, the so-called interference cost (IC) describes elevated metabolic costs caused by disruption and competition between animals, and aggressive encounters. Interference can increase C (Kotler & Brown 1988) or IC can be added as a further summand (Bouskila 1995). Thus, C might be higher when there are more animals at a patch, which increases the possibility of competition and interference. The abandoned amount of feed at the food patch is consistent with the harvesting rate. The gain of energy from foraging then balances the energetic efforts of foraging, the costs for the predation risk at the food patch, and the costs for the missed participation in other fitness-promoting actions (such as reproduction). As soon as the sum of the energetic costs of C, P and MOC exceeds H, the animal will give up foraging. Abramsky et al. (1998) showed that, in a community of Allenby’s gerbils (Gerbillus allenbyi) and Greater Egyptian gerbils (G. pyramidum), the presence of a predator impaired activity to a greater extent than did IC.

In this study, we focused on the foraging strategy of a wild species community in an undisturbed environment. We applied the GUD paradigm of Brown (1988) on specific open living habitats as defined by Upham and Hafner (2013) in an activity-focused study. The lack of any experimental modification to the habitat or rodent community distinguishes our field study from other previous GUD studies (Gutman & Dayan 2001; Ziv & Kotler 2003; Kotler et al. 2010; Gutman et al. 2011).

Finally, we questioned whether GUD differences between moon phases are caused by changes in the animals’ activity pattern and/or altering foraging costs, as for example requested by Fanson et al. (2008), when they measured differences in GUDs between waxing and waning moon. Our aim was to shed light on the effective foraging paradigm of a nocturnal desert species community in natural field conditions with special focus on four elements: habitat, microhabitat, nocturnal illumination and ambient temperature.

MATERIAL AND METHODS

Field study sites

The field studies were carried out in May and June 2012 in the Autonomous Region of Inner Mongolia, China, near Jiaer Gale Saihan (37°53.224’N, 105°24.317’E, 1400 m above sea level; Fig. 1). The Alashan Desert is characterised by a semiarid continental climate with hot summers and cold winters. Precipitation is about 45–212 mm per year, and the temperature ranges between −35 °C in January and 40 °C in July (data purchased from the official Jiaer Gale Saihan weather station). The mean surface temperature in the shade during the study time was 23.7 ± 0.1 °C.
The ambient temperature was measured with an iButton placed in a shrub in the *Zygophyllum* habitat. It was positioned in a shrub that was 10 cm above the ground so as to prevent misrepresentation of the data by direct sunlight. The data were read with a 1-wire-network cable (DS1402D-DB8, Fuchs Elektronik, Weingarten, Germany) and the software 1-Wire-Viewer, version 0.3.15.50 (free download).

Fig. 1. — Area map of the experimental site showing photographs of the habitats and the shelter patches. Longitude and latitude are given in a larger font (37° north, 105° east); detailed position is given in arc minutes (') and seconds (") based on the sexagesimal system. The site of conducted pre-trials and camera observations are also depicted. The north and east fences are coarse-meshed cattle fences, which did not prevent any migration by the animals, thus not altering the undisturbed small mammal community composition. Black circles: food patch stations in the *Ammopiptanthus* habitat; white circles: food patch stations in the *Corispermum* habitat; black triangles: food patch stations in the *Zygophyllum* habitat; white triangles: pre-trial patch; black diamond: site of camera observations.
Sunrise was around 04:40 during the study time, while the sun set around 19:15. A summary of times for moonrise and moonset, duration of the light period and the appearance of the moon above the horizon, as well as for the illuminated area of the moon disc for the different observation periods, can be obtained from the websites of the US Naval Observatory (USNO 2012). The new moon was classified as a lit moon disc of 0–6%; during the waxing and waning moon phases the visible moon disc ranged from 30 to 65%. In the full moon phase, at least 95% of the moon disc was visible. Transition periods were not included in this analysis. There was mostly no or only minor cloud coverage, which did not diminish the moonlight substantially.

The habitat named “Ammopiptanthus” was located on a shallow dune (37°51.855’N, 105°20.032’E; Fig. 1). The dominating shrub Ammopiptanthus mongolicus was widely distributed until this area was used for grazing. Presently, the density of that species is comparably low. Nevertheless, it is still a preferred habitat, probably because of the high availability of seeds. The preference of this habitat is recognisable by numerous burrows. All other plants in this habitat were lower in height than the Ammopiptanthus shrubs (height up to 3 m). The other plants present in this habitat include Bassia dasyphylla, Corispermum sp., Salsola pestifer, Zygophyllum pterocarpum, and different grasses and herbs such as Agriophyllum pungens, Echinops gmelinii, Asteraceae eriocephalla or Oxytropis aciphylla.

Secondly, a habitat named “Zygophyllum” was selected, which was dominated by Zygophyllum pterocarpum (37°52.031’N, 105°20.271’E; Fig. 1). This habitat was the most representative one in the whole area; it was also characterised by numerous burrows which showed the high preference of the rodents for this habitat. We found Bassia dasyphylla, Corispermum sp., Echinops gmelinii, Atraphaxis bracteata, Agriophyllum pungens, Ceratoides latens and diverse grasses in this habitat. The vegetation height was up to 96 cm.

The third habitat – “Corispermum” – was characterised by a lack of taller plants (37°51.941’N, 105°20.193’E; Fig. 1). The ground was mostly covered with Bassia dasyphylla, Corispermum sp. and Salsola pestifer (up to height of 20 cm). However, since the shelter mainly consisted of dried-out parts from the genus Corispermum, it will be called “Corispermum”. In general, the ground coverage of this habitat was scarcely replenished by grasses, thistles and small shrubs like Echinops gmelinii, Salsola pestifer, Atraphaxis bracteata, Agriophyllum pungens, Ceratoides latens or Cynanchum komarovii. Although this habitat contained food plants, it was only slightly populated by the rodents. With its low cover ratio, it serves as a precursor for overgrazing.

Guidelines for the use of animals in research and the legal requirements of any national and institutional guidelines have been adhered to in this study. All experiments conducted were in concordance with the EU Directive 2010/63/EU for animal experiments. The work conforms to the provisions of the Declaration of Helsinki (Tokyo 2004).

In parallel experiments, the ratios of species within the community were determined with life traps. The single-capture life traps had a size of 20 by 15 by 30 cm and were built by a local manufacturer. Traps were baited with peanuts and were enriched with a wooden box in order to prevent danger from predators and weather impact by hyper- or hypothermia. Traps were closed during the daytime in order to prevent capture of diurnal species. Traps were opened during the nighttime and checked in intervals of 2–3 hr. Each of the four trap grids consisted of 56 life traps with a distance of 15 m in each direction. The position of transects was located using a global positioning system (GPS; Garmin Geo, Garmin Corporation, Olathe, USA). Trapping grids were at a distance of 100–350 m from the food patches. Trapping was conducted on nights different from those where GUD was determined, in order to prevent any impact. Animals of all three rodent species were marked with fur clipping to distinguish between new captures or recaptures and between males and females. Detailed trapping data are provided in Scheibler et al. (2013).

In this study period the species community was dominated by Midday gerbils (54%), followed by Northern three toed jerboas (31%), Desert hamsters (13%), and Long-eared hedgehogs (2%). Although the exact species at a particular feeding station could not be distinguished, our video observations and inspection of animal tracks indicated that all species used the food patches. Except for the jerboas, all of the investigated species are quadrupedal (69%).
Occasionally, some predators were observed [red fox (*Vulpes vulpes*), screech owls (*Strigidae*), snakes and stray dogs (*Canis lupus familiaris*)]. Their species-specific influence on foraging cannot be analysed because of the rare observations and their low population density.

**General procedure**

Commercially available plastic bowls served as food patches (8 cm height, 28 cm diameter and 2.8 L volume). They were filled with sifted local sand and dug in a way that the surface of the food patch was at ground level compared to the surrounding sand. Bowls were baited within the twilight hour after sundown by mixing the husked and chopped peanut pieces thoroughly with the sand in the bowls. This prevented the food patches from being foraged by birds or other diurnal animals. Finally, the remaining peanuts or parts of them were collected in closed plastic bags and weighed with an analytical balance (type H51, Sartorius AG, Goettingen, Germany) with a precision of 0.1 mg. The weighing procedure was performed in laboratories since the peanut pieces had to be cleaned of the adhesive sand with compressed air. Thus, the probes had to be stored between 3 and 7 weeks in plastic bags. In order to prevent any weighing errors due to loss of water and oils during storage, an extra experiment was conducted. Here, the peanut pieces were treated in the same way as in the field experiments, but were weighed once a week. We found out that the weight of the probes did not change after 3 weeks. Thus, no further time-correction factor had to be included when weighing the probes from the desert experiments.

**Pre-trials**

In order to determine the optimum initial density of peanuts for the GUD experiment and define an appropriate depth of the bowls serving as food patches, two preliminary tests were carried out (5-night duration per trial). We chose an area with a high frequency of local species and a short distance to the locations of the main experiment (see Fig. 1). Four bowls were set up at grade and with the same distance to each other without any shelter. For the determination of the initial density, either 1, 2, 5 or 10 g/L peanuts were thoroughly mixed with the locally sifted sand. In the second pre-trial the digging depth was analysed based on a density of 1 g/L for the depths 0, 2, 4, 6 and 8 cm. Each night, a different depth level was tested.

**Main experiment**

The three above-described habitats were selected to serve as study sites. A distance of 200–400 m was maintained between the particular habitats. Within those habitats, three locations were chosen for food patches. In each location, two plastic bowls (8 cm height, 28 cm diameter and 2.8 L volume) filled with local, sifted sand were installed and left in place for the whole study time. They were equipped with 2.8 g husked and chopped peanuts corresponding to an initial seed density of 1 g/L measured using a spring scale (PESOLA AG, Baar, Switzerland) with a precision of 0.1 g. One sand bowl was always placed under a dominating plant which served as shelter, and the other one was positioned in an open area without any adjacent vegetation (at an average of 2.2 m apart from each other; six food patches per habitat). Experiments were carried out between 20:00 and 09:00. The mean ambient temperature was 17.4 ± 0.1 °C during these night periods. All food patches were baited with chopped peanuts 3 nights before the main experiment began. Experiments were carried out on 5 consecutive nights within one moon phase, so there was a naturally created gap of 2 or 3 nights between the moon phases. The isolated geographic position meant a natural protection of that site from any artificial light of settlement which could have influenced the animals’ response to nightly illumination, as reported in previous studies (Mandelik et al. 2003).
Video recordings were conducted in a *Zygophyllum* habitat, maintaining a distance from the other food patches. During 2 nights of each moon phase, the video observation started at 21:00 and ended at 05:00. Peanut pieces were presented continuously in the course of the night. If the food patch was empty, new peanuts were provided. An infrared camera (ICD-45E, Ikegami Tsushinki Co., Ltd., Japan), two infrared lamps (850 nm, eneo, Korea), a digital recorder (Abus, Germany), and a monitor (Conrad, Germany) were used in the field. The energy source was a car battery (Chinese product). Videos were stored and later analysed with the following scheme: the number of animals of each species was documented for each minute, the means of moon phases were calculated and the percentages per hour based on all observations in all moon phases were presented in Fig. 2. Midday gerbils frequently returned to the food patch compared to the Desert hamsters, due to the lack of pouches. Therefore, Midday gerbils are slightly overrepresented (Fig. 2), i.e. the number of visits compared to the number of individuals is higher in contrast to that of the Desert hamsters. This may lead to a seeming contradiction with the above-mentioned composition of the species community.

![Graphs showing percentage of animal visits at the food patch in front of the camera in a Zygophyllum habitat, summary of all observations in four moon phases = 100%. Species are given as follows: Midday gerbils: black; Northern three toed jerboa: dark grey; Desert hamsters: grey; Long-eared hedgehog: light grey. Moonlit nights indicated by white bar at x-axis. Mean temperature is given by black line.](image_url)
Statistics

Statistical calculations were performed using SPSS 17.0 (SPSS Inc.). The normal distribution of all variables was tested with the Shapiro–Wilk (n < 50) or Kolmogorov–Smirnov test (n > 50). Since data of single groups or single parameters were not normally distributed including the focus parameter GUD even after data transformation, the appropriate non-parametric tests were conducted. In order to be consistent, only non-parametric tests were applied to compare the groups (Kruskal–Wallis-tests and Mann–Whitney U-tests, as post hoc tests respectively). Spearman correlations were calculated to indicate temperature effects. In general, an α-level of 0.05 was used declaring a statistical significance; the level of significance is indicated as follows; *: \( P < 0.05 \); **: \( P \leq 0.01 \); ***: \( P \leq 0.001 \). Values were given as mean ± standard error of mean (SEM).

RESULTS

Pre-trials

Concerning the initial density, no significant difference was found between the GUDs of the bowls set up with different initial feeding densities (Kruskal–Wallis test: \( df = 3, \chi^2 = 4.257, P = 0.2 \); 1 g/L: 0.081 ± 0.051 g; 2 g/L: 0.155 ± 0.104 g; 5 g/L: 0.116 ± 0.074 g; 10 g/L: 0.067 ± 0.027 g). An initial density of 1 g/L was chosen for the main experiment in order to prevent any influence on the experiments due to a high food supply.

The analysis of the digging depth of the rodent community showed lower GUDs for peanuts at 0, 2 and 4 cm depth in comparison to 8 cm, whereas the GUD of 6 cm depth remained indifferent (Kruskal–Wallis test: \( df = 4, \chi^2 = 12.137, P = 0.016 \); 0 cm: 0.015 ± 0.026 g; 2 cm: 0.008 ± 0.007 g; 4 cm: 0.034 ± 0.032 g; 6 cm: 0.249 ± 0.448 g; 8 cm: 1.950 ± 1.059 g; Mann–Whitney U-test: 0 vs 8 cm: \( U = 0.000, Z = -2.323, P = 0.029 \); 2 vs 8 cm: \( U = 0.000, Z = -2.309, P = 0.029 \); 4 vs 8 cm: \( U = 0.000, Z = -2.309, P = 0.029 \)). For the feeding depth with and between the lower depths of 0, 2 and 4 cm, no differences were determined. We concluded that it was possible for the rodents to find seeds at depths up to 6 cm in the sandy ground. Nevertheless, in the course of experiments we observed animals throwing lots of sand out of the bowls; thus, the sand density in the bowls never rose above 6 cm.

Microhabitat effect

In order to evaluate a habitat-specific impact of open versus sheltered food patches, an analysis was conducted based on the differences between shelter and open position per place and day, and per moon phase. Values above zero indicate a preference for the open patch; in contrast, values below zero point to a preference for the sheltered one. A general observation (see Fig. 3B) was made: animals used open food patches more intensively in the Corispermum habitat (0.037 ± 0.014 g) in contrast to the other two habitats (Ammopiptanthus: –0.012 ± 0.059 g; Zygophyllum: –0.020 ± 0.007 g), which was of special strength at waxing and full moon (Kruskal–Wallis test: \( df = 2 \); waxing moon: \( \chi^2 = 9.987, P = 0.007 \); full moon: \( \chi^2 = 6.453, P = 0.04 \)). During both moon phases, the habitat-specific impact of open versus sheltered food patches determined for the Corispermum habitat was higher than that of the Ammopiptanthus habitat (Mann–Whitney U-test, waxing moon:...
Fig. 3. — A: mean giving-up density (GUD) (± standard error of mean [SEM]) per moon phase (new moon: black; waxing moon: grey; full moon: white; waning moon: dark grey) of the three habitats *Ammopiptanthus* (A, potentially the most native vegetation), *Corispermum* (C, very dry, possibly due to overgrazing) and *Zygophyllum* (Z, most common, highly populated). B: shelter impact indicated by means (± SEM) of difference of GUD between shelter and open position; values above zero point to preference for open patch; and below zero to that for the sheltered one. Differences are indicated by asterisks with *P < 0.05, **P < 0.01, and ***P < 0.001.
U = 48.0, Z = -2.681, P = 0.007; full moon: U = 59.5, Z = -2.201, P = 0.03) and of the *Zygophyllum* habitat (waxing moon: U = 46.0, Z = -2.761, P = 0.005; full moon: U = 60.5, Z = -2.166, P = 0.03).

A direct comparison of GUD in open and sheltered food patches for the single habitats including splitting up by moon phases revealed only two of 18 possible differences. In the *Zygophyllum* habitat, a lower GUD was measured in the sheltered places (0.048 ± 0.036 g) than in the open ones (0.079 ± 0.046 g) during waning moon (U = 64.0, Z = -2.012, P = 0.045). During the waxing moon phase, a significantly lower GUD was found in the open patches (0.042 ± 0.063 g) compared to the sheltered ones of the *Corispermum* habitat (0.118 ± 0.103 g; U = 62.5, Z = -2.094, P = 0.04). For further analyses it was not distinguished whether the values were derived from open or sheltered food patches, because of the low impact.

**Lunar and temperature effect**

Differences in GUD were found between the moon phases within the habitats (Kruskal–Wallis test: df = 3: *Ammopiptanthus*: $\chi^2 = 25.329, P < 0.001$; *Corispermum*: $\chi^2 = 28.287, P < 0.001$; *Zygophyllum*: $\chi^2 = 36.299, P < 0.001$), and we determined constantly high GUDs in the waning moon within all habitats (see Fig. 3A and Supplemental material 1 for all values of means including post hoc statistics). The GUD in the waning moon phase was significantly higher compared to the other moon phases in the *Zygophyllum* and *Corispermum* habitats. No more difference could be determined between the other moon phases within those habitats. In the *Ammopiptanthus* habitat, the GUD during waning moon differed significantly from those in waxing and full moon. In this habitat, the animals also showed higher GUDs in the new moon than in the waxing and full moon phase.

In the next step the influence of ambient temperature was tested. We found positive Spearman correlations for the GUDs of the single habitats based on the mean ambient temperature of the whole day (24 hr) and the dark period of the night (activity period of the animals). In general, higher temperatures were associated with higher GUDs. This was of special importance for the *Ammopiptanthus* habitat, as the general observation of the whole day could be confirmed for the night period. All values are summarised in Table 1. Additionally, temperature curves were implemented in Fig. 2 for the dark phases. Although temperatures were slightly higher at the new moon, a temperature decrease is always recognisable until sunrise. Furthermore, during new, full and waning moon phases, more animals were observed at the food patch in the first and warmer phase of the night. A contrary observation was made during the waxing moon phase, when animals preferred the second, dark part of the night, although the temperature was lower here.

**Habitat effect**

In contrast to the position of food patches (microhabitat-effect), the impact by the (macro-) habitat was stronger (Fig. 3A, means provided in supplemental material 1; Kruskal–Wallis test: new moon: df = 2, $\chi^2 = 20.380, P < 0.001$, waxing moon: df = 2, $\chi^2 = 8.587, P = 0.014$, full moon: df = 2, $\chi^2 = 4.208, P = 0.122$, waning moon: df = 2, $\chi^2 = 16.496, P < 0.001$). Due to the above-mentioned lunar influence, the comparison of habitats was conducted for each moon phase separately with a post hoc Mann–
Most differences were found between the Corispermum and the Zygophyllum habitat (Mann–Whitney U-test: new moon: \( U = 167.0, Z = -4.197, P < 0.001 \); waxing moon: \( U = 278.0, Z = -2.572, P = 0.010 \); waning moon: \( U = 188.5, Z = -3.866, P < 0.001 \)). In addition, the high GUDs in the Corispermum habitat are remarkable. During the waxing moon and the waning moon phase, significantly higher GUDs were found in the Corispermum habitat than in the Ammopiptanthus habitat (waxing moon: \( U = 287.0, Z = -2.443, P = 0.015 \); waning moon: \( U = 246.0, Z = -3.016, P = 0.003 \)). The GUDs differed only in the new moon phase between the Ammopiptanthus and the Zygophyllum habitat (Mann–Whitney U-test: new moon: \( U = 211.0, Z = -3.548, P < 0.001 \)).

Overall, a general observation was an elevated food patch use in the Zygophyllum habitat in comparison to the Corispermum habitat. A weaker (macro-)habitat effect was observed between the Ammopiptanthus and the Corispermum habitats; here, the differences were only found during the waxing and waning moon phases. In addition, the remarkably high GUD values in the waning moon phase in all habitats are considerable.

### Table 1.

Summary of Spearman coefficients of correlation and \( P \)-values for the single habitats and in sum.

| Time period       | Spearman's Rho | Ammopiptanthus | Corispermum | Zygophyllum | Overall |
|-------------------|----------------|----------------|-------------|-------------|---------|
| Mean of the day   | Spearman's Rho | 0.433          | 0.219       | 0.214       | 0.287   |
| \( P \)           | < 0.001        | 0.016          | 0.019       | < 0.001     |         |
| Mean of the night | Spearman's Rho | 0.356          | 0.145       | 0.158       | 0.218   |
| \( P \)           | < 0.001        | 0.1            | 0.1         | < 0.001     |         |

**DISCUSSION**

In this current study, we found hints and evidences for influences on foraging efforts by habitat, moon, temperature and microhabitat of a wild-living nocturnal desert species community consisting of Midday gerbils (dominating species in the year of this study), Desert hamsters, Three-toed jerboas and Long-eared hedgehogs. This species community is common in dry regions of East Asia and therefore representative for those habitats (Wu & Fu 2005).

This study here was built upon our former field studies investigating activity patterns affected by intra- and interspecific interactions, moonlight and ambient temperatures. The logical next step was therefore to explore how those factors may influence foraging activity. For that purpose, GUDs were determined in three different habitats during one lunar cycle in May and June. Indeed, this makes our results only representative for the summer conditions. Nevertheless we want to mention that first, several repeated measurements represent the final data point for that specific lunar phase; second, these data were collected in a constant stable desert climate in a homogeneous landscape with respect to vegetation, soil, altitude and land use.
However, a vegetal shelter and an open place, both located in the same habitat, presented microhabitats. Distinct plant communities characterised habitats and determined not only the local environments but also a behavioural response. The distribution of shrubs, their height, and the distance between plants, the cover-ratio and the plant species – all these aspects create altering ecological niches in a harsh environment. The most common habitat, named *Zygophyllum*, offers advantageous conditions with shelters and food plants such as *Bassia dasiphylla*, *Ammopiptanthus mongolicus*, *Zygophyllum pterocarpum*, *Reaumures* sp., as well as insects and seeds of grasses (Bannikow 1954; Flint 2006; pers. obs.). The second habitat, *Ammopiptanthus*, is quite rare, although it is potentially natural vegetation. It provides the aforementioned foraging plants and the dominating tree-like shrub *Ammopiptanthus mongolicus*. For the animals, this habitat meant excellent conditions in terms of food plants and shelter conditions; however, the availability of this habitat has reduced. Open places and elevated aridity characterise the third habitat, *Corispermum*. It might also be the result of continuous grazing by sheep and goats and the associated disappearance of shrubs. Only low-growing herbs like *Bassia dasiphylla*, *Corispermum* sp. and *Salsola pestifer* were found here. These three habitats offered animals not only varying food availability, but also different amounts of shelter, which is of special importance in periods of nocturnal illumination.

Finally, the factors influencing rodent foraging appear to be complex and interdependent. One important factor is the availability of shelters. In general, sheltered places lower the risk of being discovered by a predator in two ways: first, the visual detection of the prey in an overgrown shelter may be difficult; second, the vegetal cover (like prominent branches) may mechanically deter the attack of a predator (Fanson et al. 2008). For example, Gutman et al. (2011) showed an avoidance of open food patches during moonlit nights for the nocturnal Golden spiny mouse. In contrast, the Desert hamster seems to intensify vigilance behaviour, which results in prolonged activity, but not in moonlight avoidance (Scheibler et al. 2014). Our results here are in concordance with that observation, as we did not determine any reduced foraging effort at open food patches during the full moon. Instead, concerning the moonlight avoidance strategy, our video observations showed a temporal strategy with a preference for food hoarding in dark phases of the night, during waning and waxing moon phases. We observed a common strategy with elevated foraging effort in the first half of the night at full and new moon with continuous illumination or darkness. Furthermore, during those lunar phases, our video observations indicate a preference for periods with warmer temperatures that coincides with the first part of the night, and is therefore a period with low energetic costs for the individuals (Chapell & Bartholomew 1981; Rezende et al. 2003; Hogan et al. 2011; Scheibler et al. 2014). Nevertheless, several alternative explanations can be applied beyond that and our observation is not unusual. Elevated foraging activity at the beginning of the dark period can repeatedly be found (Kotler et al. 1994; Fanson et al. 2008; Scheibler et al. 2013). The beginning of the night offers animals a time slot where all nocturnal species compete for seeds fallen during daytime which is a further strong factor for the activity observed (Ziv et al. 1993; Kronfeld-Schor & Dayan 1999). Additionally, individual and species-specific patterns for foraging are modulated by body size, individual number, social system and aggression level (Shkolnik 1971; Glass & Slade 1980; Kotler et al. 1994; Bouskila 1995; Gutman & Dayan 2001; Fanson et al. 2008; Scheibler et al. 2013). Although nocturnality per se can be seen as a predator-avoidance strategy (Walsberg 2000; Brown & Kotler 2004; Verdolin 2006), predation level itself varies
not only in the course of the night but also between nights due to lunar phases (Mukherjee et al. 2009; Packer et al. 2011; Penteriani et al. 2011, 2013; Embar et al. 2014a, 2014b). All these factors may lead to the higher number of animals observed especially at the beginning of the activity phase. Finally, such a similar foraging strategy across species may also result in raised competition between animals and aggressive encounters, which is associated with higher GUD by the IC. The IC represents elevated metabolic costs, caused by disruption and competition, which may be substantial at least for the inferior competitor (Bouskila 1995). Wasserberg et al. (2006) report such a nutritional partitioning in a gerbil community in arid habitats in Israel, indicating a more efficient foraging in the smaller Allenby’s gerbil (Gerbillus andersoni allenbyi). This is necessary because of a temporal avoidance strategy reducing energetic costs by aggressive encounters with the Greater Egyptian gerbil (Gerbillus pyramidum). In a former study, we observed a similar temporal resource partitioning for Desert hamsters coexisting with Midday gerbils (Scheibler et al. 2013), with the difference that the onset of activity was not altered, but the smaller Desert hamsters displayed a clear reduction of activity above ground.

A detailed analysis of microhabitat by macrohabitat (Fig. 3B) indicated that the use of open and sheltered food patches was influenced by the presence of shrubs (i.e. at least 40 cm in height). Although moonlight avoidance still appears logically as an anti-predator strategy (Bouskila 1995; Gutman & Dayan 2001; Fanson et al. 2008), Upham and Hafner (2013) presented a contradictory data set in a comprehensive and long-term study performed at 62 study sites across the Great Basin Desert of western North America. They only found moonlight avoidance in one genus – the Kangaroo rat (Dipodomys sp.) – and this in only single periods of time. No other rodent genus avoided moonlight. The locomotion pattern might provide an explanation for that diverging result. Bipedal and usually larger species in rodent communities like the bipedal kangaroo rat (Dipodomys), or in our case the Northern three-toed jerboa, show a diverging habitat use due to larger home range sizes and higher dominance because of their body size (Trombulak & Kenagy 1980; Thomson et al. 1996; Upham & Hafner 2013). For the kangaroo rats, moonlight avoidance but the preference for open areas is explainable by predator avoidance but interspecific dominance. In contrast, the night use of quadrupedal species differs and might show alterations in moonlight avoidance and preferences for open areas (O’Farrell 1974; Wondolleck 1978; Kotler et al. 2010; Scheibler et al. 2014). Besides lunar light with all its implications, the probability of aggressive encounters also may play a role. Therefore, the high individual number of Midday gerbils along with frequent visits at food patches and probably less frequent visits of Northern three-toed jerboas may explain why the microhabitat effect was lower in our study compared with observations by Thompson (1982) or Shuai and Song (2011). Additionally, we suppose that hamsters also benefited from these conditions and also had nearly undisturbed access to all food patches.

On the other hand, moonlight in the sense of additional light while foraging may provide a surplus for the foraging affectivity. It is therefore of importance for granivorous animals like Midday gerbils, who become active during dusk and would thus benefit from nocturnal illumination. This was reported for the closely related Mongolian gerbil (Meriones unguiculatus; Bytyqi & Layer 2005). The here hypothesised benefit by lunar light is of special importance, as gerbils dominated the species community we studied. This fact may explain the all-around low GUDs in the full moon.
In periods with changing moonlight, the situation appears more complex. We measured higher GUDs throughout the waning moon. This seems to be unexpected as in the waning moon phase the preferred first part of the night coincides with general appetence, low energy effort and darkness. The solution for that problem is IC, the interference cost. As presented in Figs 2 and 4, numerous individuals compete for food which increases IC. Together with a delayed foraging in the second part of the night (lower ambient temperatures, moonlight and lower probability for finding food) – this results in higher GUDs. Kotler et al. (1994) and Fanson et al. (2008) proposed similar observations of a foraging peak at the beginning of the night for rodent species.

Fig. 4. — A: example of lunar characteristics during the study period, lunar disc size in % (solid line), time that the moon is visible above the horizon in hours (dotted line) and time of moonrise in the course of the day (dashed line). B–E: mixed presentation of mean (± standard error of mean [SEM]) daily ambient temperature measured in an *Ammopiptanthus mongolicus* shrub 15 cm above ground (T, dashed line), moonlight (M, dotted line, schematic), number of animals present at food patch (n, solid line, schematic) and mean (± SEM) giving-up density (GUD, grey column).
A closer look at foraging in different habitats resulted in the following: we found no elevated foraging efficiency in the open or sheltered patches of the highly covered, potential natural *Ammopiptanthus* habitat. During the waning moon with moonrise after midnight, we measured a preference for sheltered places in the most common habitat *Zygophyllum*, while we determined a preference for the open food patches in the sparsely covered *Corispermum* habitat during the waxing moon phase. The latter one appears misleading, but we repeatedly observed especially Desert hamsters collecting seeds in this vegetation. Due to the agouti fur colour, these plants provide an adequate shelter, and animals easily disappear when they display freezing behaviour. Finally, this is an effective camouflage from more visually orientated mammalian or avian predators. Unfortunately, little is known about the local predators. Based on personal observations and animal tracks, we estimate red fox, screech owls and stray dogs are influential predators; snakes are relatively rare. Overall, a quantitative estimation of the predators is not possible.

The low density of snakes in our study site allows an explanation for the low microhabitat effect. Snakes have a preference for hunting in shrubs and places under boulders (Bouskila 1995), so their presence could have a contradictory influence on rodents, i.e. an avoidance of sheltered places in the absence of avian predators. We found only a low modification of food patch use by microhabitat. We suppose here the availability of subterranean shelters as possible explanation. Midday gerbils and Desert hamsters (the smaller species) used subterranean escape burrows as shelters; we found many such burrows in the *Ammopiptanthus* and the *Zygophyllum* habitat near the feeding stations. Escape burrows of gerbils have a simple structure without chambers, a short tunnel length and only two entrance holes (Flint 2006; Scheibler et al. 2006). Northern three-toed jerboas also used subterranean burrows, even though they usually escape using their very fast bipedal locomotion. Thus, burrows are of special importance not exclusively to escape from life-threatening climatic conditions. For example, Berger-Tal et al. (2010) observed modified foraging strategy in Allenby’s gerbils (*Gerbillus allenbyi*) with more foraging efforts near to their home burrow, if owls performed elevated hunting pressure. Shuai and Song (2011) described further evidence for this strategy for the studied Midday gerbil; they determined lower GUDs near the animals’ home burrows. In addition, the short distance between the (home) burrow of an animal and a food patch can lower the risk of predation, as avian predators typically detect and attack moving prey (Mandelik et al. 2003).

Furthermore, Fanson et al. (2008) concluded there is less foraging risk in a complex landscape leading to lower GUDs since the predation risk rises with increasing distance from shelters. Based on these observations and hypotheses, we postulate that if burrows are distributed throughout the area, the animals may no longer need to distinguish between a sheltered place and an open one – a burrow can also be seen as some kind of “shelter” and, thus, the vegetal shelter loses its uniqueness. The preference for open food patches in the low-covered habitat makes sense because this habitat was plain while the other two habitats showed hilly sections overgrown with plants such as *Caragana tibetica* and *Reaumures soongorica*. Such small hills can obstruct a predator’s sight over landscape scenery, thus preventing the small rodents from being discovered and offering them a near vegetal shelter. In contrast, an open area allows flight at an early stage, and, therefore, explains the observed behaviour.
Finally, our observations are explainable using existing hypotheses and models and are therefore widely comparable with findings from North America (e.g. Brown & Munger 1985; Upham & Hafner 2013), Africa (e.g. Fanson et al. 2008), Middle East (e.g. Kotler et al. 1994; Kronfeld-Schor & Dayan 1999) or Northwest Asia (e.g. Shuai & Song 2011) in terms of modulating factors for foraging effort. The studies mentioned herein were predominantly performed in the desert or dry areas that resulted in similar conditions regarding vegetation cover, land use, climate effects and food availability. Additionally, as shown by Kelt et al. (1996), for species communities on four continents, the rodent community chosen here can be classified as a representative one, which was our concern. Even though the reported higher GUDs during the waning moon phase may appear unusual, a closer analysis reveals the inter-individual competition factor as effective.

Jones et al. (2001) and Ziv and Kotler (2003) determined GUD patterns comparable to our results, although the dimensions of measurements were slightly different. Results observed in grassland obviously may differ; here, higher values were reported (Fanson et al. 2008). However, the desert species investigated herein not only look for food above ground but also dig very intensively. Additionally, desert species are highly adapted to conditions with unpredictable and limited food availability, which may be seen as a further factor for the effective use of food patches and, therefore, low GUDs.

**CONCLUSION**

This current study implies that moonlight affects foraging effort, but the observed behaviour goes beyond a modulation of vigilance behaviour in different lunar phases. Finally, although additional light means an increased predation risk for prey species, it also can mean a benefit if vision is the primary sensory system of the prey species (Prugh & Golden 2014). Therefore, for several species like the Midday gerbil, moonlit nights may explore in usually less preferred habitats and to forage more intensively in all profitable food patches. Moreover, one of our own previous studies (Scheibler et al. 2014) showed even a prolongation of the Desert hamster’s activity duration in brighter nights. We interpreted this as the result of the time needed for protecting their paths in the more risky moon phases, plus foraging activity. As shown by Trebatická et al. (2008), indirect predator contact is also able to affect spatial behaviour. Thus, the moon is only one factor that alters predation pressure on prey species and can also be seen as an indirect factor (Brown 1988). Furthermore, the reaction of a rodent species to predation risk depends also on the intensity of competition (Bouskila 1995). We assume that because of the high animal density, individuals were able to forage the trays within the first part of the night. For this reason, in the waxing moon phase, the animals had possibly finished foraging before moonset around midnight, and the dark, second part of the night did not influence the GUD experiments at all. The situation is different during the waning moon. Here, the first part of the night was not illuminated and preferred by several animals, resulting in elevated interference costs. A shift of foraging activity into the second part of the night was only observed in a low ratio which can be explained by the large drop in the surface temperature and, therefore, higher energy costs.

Beyond that, we suppose a stronger impact from the habitat, because differences are more consistent between the covered *Zygophyllum* and *Ammopiptanthus* in contrast to the sparsely covered *Corispermum* compared to those of different moon phases. The shelter effect triggers modified habitat use, especially as vegetal and
subterranean shelters both affect foraging behaviour. That is why the strength of vegetal shelters is reduced. Taking everything into account, we assign the highest impact on the foraging effort of a desert community to the habitat, whereas nighttime temperature, moonlight and, finally, the availability of shelters act as modifying factors.

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No potential conflict of interest was reported by the authors.

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