

# Lunar and temperature effects on activity of free-living desert hamsters (*Phodopus roborovskii*, Satunin 1903)

Elke Scheibler · Corinna Roschlau · David Brodbeck

Received: 28 August 2013 / Revised: 17 December 2013 / Accepted: 19 December 2013 / Published online: 10 January 2014  
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**Abstract** Time management of truly wild hamsters was investigated in their natural habitat in Alashan desert, Inner Mongolia, China during summer of 2009, 2010, and 2012. Duration of activity outside their burrows, duration of foraging walks, and nocturnal inside stays were analyzed with the aim to elucidate impact of moon, ambient, and soil temperature. Animal data were determined using radio frequency identification (RFID) technique; for that purpose, individuals were caught in the field and marked with passive transponders. Their burrows were equipped with integrated microchip readers and photosensors for the detection of movements into or out of the burrow. Lunar impact was analyzed based on moon phase (full, waning, new, and waxing moons) and moon disk size. A prolongation of aboveground activity was shown with increasing moon disk size (Spearman  $\rho=0.237$ ;  $p=0.025$ ) which was caused by earlier onsets ( $\rho=-0.161$ ;  $p=0.048$ ); additionally, foraging walks took longer (Pearson  $r=0.037$ ;  $p=0.037$ ). Temperature of different periods of time was analyzed, i.e., mean of whole day, of the activity phase, minimum, and maximum. Moreover, this was done for the current day and the previous 3 days. Overall, increasing ambient and soil temperatures were associated with shortening of activity by earlier offsets of activity and shorter nocturnal stays inside their burrows. Most influential temperatures for activity duration were the maximum ambient temperature, 3 days before (stepwise regression analysis  $R=0.499$ ;  $R^2=0.249$ ;  $F=7.281$ ;  $p=0.013$ ) and soil temperature during activity phase, 1 day before ( $R=0.644$ ;  $R^2=0.283$ ;  $F=7.458$ ;  $p=0.004$ ).

**Keywords** Activity · Moon · Temperature · Desert hamster · Foraging

## Introduction

Life in extreme environments is closely associated with physiological and behavioral adaptations in organisms. One of them is the use of the time niche and its plasticity, because biotic and abiotic factors differ strongly on time scale. Especially in deserts, day temperature and humidity change in the course of a day which is partially caused by the lack of compensational effects due to vegetation. But beyond that, this characteristic sparse vegetation offers less shelter which promotes predation (Bozinovic and Gallardo 2006; Kelt 2011; Murray and Smith 2012; Scheibler 2011). These are some facts favoring nocturnality in several desert (rodent) species (Brown and Kotler 2004; Verdolin 2006; Walsberg 2000). Nevertheless, some species become active during daytime, for example, Chapell and Bartholomew (1981) investigated thermal energy in the antelope ground squirrel (*Ammospermophilus leucurus*) in extremely hot environments with ambient temperatures of up to 70 °C. These animals displayed short-term daytime activity, because thermal overload could be avoided as result of the factor shade, transient hyperthermia, the animal's resistance to heat flow, the gradient between body temperature and ambient temperature, body weight, color, shape, fur texture, solar radiation, soil temperature, and wind velocity. Between aboveground activity, animals returned to their burrow to cool down again. The risk of thermal overload is usually associated with water loss; here, food hoarding functions as further widespread water-saving strategy, since storage in underground chambers leads to a reduced water loss of plants, seeds, etc. because of the elevated humidity underground (Morton and MacMillen 1982). Beyond that, burrows have another important meaning—the antipredator function. While protection against predators during resting phase is given by their own burrow, foreign burrows are used as short-term shelter in the course of foraging walks or aboveground activity (Kinlaw 1999).

E. Scheibler (✉) · C. Roschlau · D. Brodbeck  
Department of Animal Physiology, Biological Institute, University of Stuttgart, Pfaffenwaldring 57, 70569 Stuttgart, Germany  
e-mail: elke.scheibler@bio.uni-stuttgart.de

Nevertheless, it has to be considered that the predation level itself depends on diverse factors like nocturnal illumination by the Moon. Although lunar light affects all nocturnal species, a pronounced impact can be assumed for desert species due to the earlier mentioned sparse vegetation and the poor shelter situation. Kotler (1984), Bowers (1988), and Rogovin et al. (1996) described reduced microhabitat use or increased giving up density in harvesting during full moon nights. Price et al. (1984) analyzed microhabitat use by life trap in sheltered and open places in the course of the moon cycle. They observed a preference of sheltered places in three of five rodent species during bright nights. Nevertheless, directly measured activity parameters of wild rodents are still missing. This is the purpose of this study as we adapted the radio frequency identification (RFID) system for the detection of animals in an experimental setup which allows us to determine the leaving and returning of individually marked and free-ranging desert hamsters (Scheibler et al. 2013).

However, even though nocturnal illumination depends on the moon phase, times of moonrise and moonset vary additionally. Owl monkeys (*Aotus azarai azarai*) (Fernandez-Duque and Erkert 2006), for example, use moonlit nights or parts of the night to forage and do this especially during periods of unfavorable temperatures; i.e., they avoid warm day periods and switch into bright nights. The question is “is this realized in desert hamsters?” Do we observe a switch of the preferred night periods? And what factors are decisive, is it the moon or is it temperature?

The latter question was our second issue, because the finally used temperature niche is bounded in lower ranges by an energetic deficit caused by thermogenesis and in upper ranges by the risk of hyperthermia. For example, the preferred range for the wombat (*Lasiorninus latifrons*) lies between 6 and 18 °C; beyond that, range activity is reduced (Hogan et al. 2011). However, the wombat is an herbivore of arid environments, while the here investigated model species forages insects and parts of plants. Insects are of special importance for the water balance of desert species because of their high water content (Reichman 1975; Walsberg 2000) and allow being active in wider ranges than it is for pure herbivores. The model species here is a psammophile one, but beyond that, insects are consumed in a ratio of up to 50 % (Bannikow 1954; Flint 2006; Judin et al. 1979; Ross 1994), indicating an adaptation for life in arid environments. Furthermore, Sokolov and Meschersky (1989) described water conservation mechanism by highly effective kidneys and the ability to increase urine concentration and to reduce water loss through skin and lungs if water availability was limited. Finally, the desert hamster excretes higher concentrated urine compared with the two further *Phodopus* species, the Campbell's dwarf hamster (*P. campbelli*) and the Djungarian hamster (*P. sungorus*), even under the same ambient conditions (Meschersky and Klishin 1990).

The here described model species *Phodopus roborovskii*, the desert hamster is the smallest species within the subfamily Cricetinae with a body mass between 12 and 20 g. These hamsters prefer sand soil for digging their burrows, where they rest during the daytime. Concerning sociobiology, only little is known; they show a sociotolerant way of life, living solitary or in pairs, or in pairs with their young (Ross 1994). Under natural conditions, we observed single animals per burrow or pairs, in rare cases, same gender use. Desert hamsters use habitats with sandy soil in semideserts and deserts in Northern China, in the Tuva region in Russia, in East Kazakhstan, and in west and south Mongolia (Flint 2006; Ross 1994; Smith and Xie 2008). It is a common species which can be observed in diverse rodent communities together with the Mongolian five-toed jerboas (*Alactaga sibirica*), northern three-toed jerboas (*Dipus sagitta*), Mongolian gerbils (*Meriones unguiculatus*), long-tailed dwarf hamsters (*Cricetulus longicaudatus*), and striped dwarf hamsters (*Cricetulus barabensis*), for example (Scheibler et al. 2013; Wu and Fu 2005; Zhang et al. 2009).

## Materials and methods

### Study sites

The study was performed in the Alashan desert in the autonomous region of Inner Mongolia, China, near Jiaer Gale Saihan (37°52'N, 105°20'E) during August and September 2009, in July and August 2010, and from April to June 2012. Alashan desert is a semidesert with vegetation coverage between 5 and 20 %. *Caragana tibetica*, *Cynanchum komarovii*, *Bassia dasyphylla*, *Zygophyllum pterocarpum*, and *Ammopipthantus mongolicus* with a vegetation height of up to 140 cm dominated the plant species communities. Continental climate is determined by hot summers associated with little precipitation (45–215 mm/year) and cold and dry winters (−35 °C in January up to 50 °C in July, mean annual temperature 8.3 °C; from the official weather station of Jiaer Gale Saihan, located 6.5 km away from the study site). Shallow hills, a sand horizon of at least 1-m depth and an elevation between 1360 and 1400 m above sea level characterized the study site. The field site was also agriculturally used as grazing area for sheep and goats. Only slight variation in species composition of the local vegetation was found because of the homogenous topography, land use, species communities, and sand horizon.

### Animals

The focus species of this study was the desert hamster (*P. roborovskii*); additionally, midday gerbils (*Meriones meridianus*) and northern three-toed jerboas (*Dipus sagitta*)

were trapped. Capture of animals was conducted with life traps (20×15×30 cm, single capture trap, local manufacturer), which were baited with peanuts and provided a wooden box in order to prevent danger by predators and weather impact by hyper- or hypothermia. In order to avoid capture of diurnal species and in order to reduce stress for the animals to a minimum, traps were opened only during the night and for intervals of 2 to 3 h. Life capture was essential since marking with microchips was necessary for the later described RFID measurements. Traps were placed at a distance of 15 m in each direction in an 8×7 trap transect. The position of transects was located using GPS (Garmin Gecko, Garmin Corporation, Olathe, USA). Animals of all three species were marked with fur cut to distinguish between new captures or recaptures and between male and female species, but animals of *Phodopus* were weighed and marked with passive transponders subcutaneously (ISO-compliant-transponder, ISO 11784/11785, 2×12 mm, 0.1 g; Tierchip Dasmann, Tecklenburg, Germany). The mean weight ( $\pm$ SEM) of male species was 16.9±0.5 g; the mean weight of female species was 14.8±0.5 g. All animals were released at the place of capture and then a single person followed the hamster to its home burrow, the position was determined with GPS and at least 2 h later the RFID-tunnel was placed.

In sum, 331 individuals of three species were trapped, and 451 recaptures were documented. Overall, 90 desert hamsters were trapped (2009, 37 (21, 16); 2010, 31 (18, 13); and 2012, 22 (7, 15)). None of the individuals marked in 1 year was recaptured in the following year or 2 years later, respectively. Furthermore, only adult or subadult animals were trapped and marked; smaller ones could leave the trap through the wire mesh. Guidelines for the use of animals in research, the legal requirements of Germany and China, and any institutional guidelines have also been adhered to in this study; measurements in China were notified the Grassland Office of Bayan Hot.

#### Activity measurement

An artificial tunnel system (length of 15 cm and diameter of 3.5 cm) was used for the measurements. The combination of an integrated microchip reader (RFID) and photosensors for the detection of movements into or out of the burrow made it possible to determine the point of time when an animal left its burrow and came back. Based on the chronology of ins and outs during the night (and day), activity behavior of hamsters was measured. If an animal spent less than 1 min outside, this was not evaluated as an outside stay, because pretrials had shown that animals stay in front of the tunnel and perform vigilance behavior. All activity parameters were calculated in hours after sundown. Overall, data were collected at 59 burrows (2009, 16; 2010, 21; and 2012, 22). A former study focusing on intra- and interspecific competition revealed the

ability to shorten activity if desert hamsters had to coexist with the numerically overrepresented midday gerbil (Scheibler et al. 2013), that is why periods with a majority of midday gerbils were not included in the analysis in order to avoid possible influence on data.

#### Moon

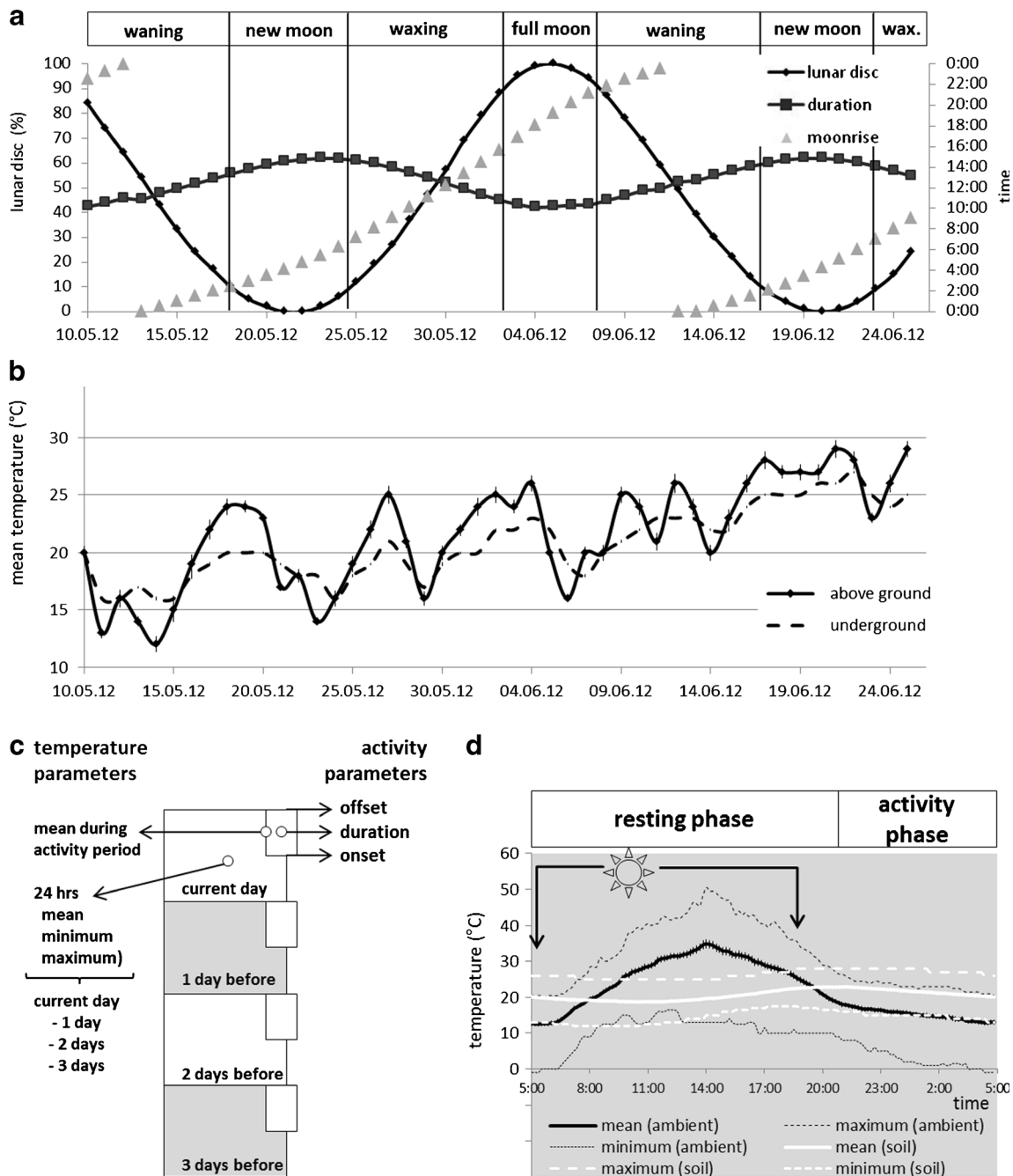
Mean times for moonset (disappearance of lunar disk), moonrise (lunar disk completely above horizon), and size of lunar disk were obtained by the Astronomical Applications Department of the US Naval Observatory ([www.aa.usno.navy.mil/](http://www.aa.usno.navy.mil/)). Lunar illumination would have been influenced by cloud cover, but this was not the case here, because few clouds developed and those disappeared very quickly due to omnipresent winds. A closed cloud cover was observed only in rainy nights; here, no animal data were collected, as animals did not leave their burrows in rain. Moon phases were classified as follows: new moon, lunar disk size 0 to 10 % and full moon, lunar disk size 90 to 100 % (Fig. 1a).

#### Temperature

Detailed measurements of temperature were performed for a period of 60 days in 2012. Two iButton viewers (Thermochron, DS1922L-F5#, Fuchs Elektronik, Weingarten, Germany) were placed in an *Ammopithantus mongolicus* shrub in order to prevent misrepresentation of the data by direct sunlight and to provide a shelter during sandstorms. One iButton viewer was fixed 15 cm above the ground; the second one was dug 10 cm in sand. Data were read with 1-wire-network cable (DS1402D-DB8, Fuchs Elektronik, Weingarten, Germany) and software 1-Wire Viewer, version 0.3.15.50 (free download). The following parameters were calculated for further analysis: mean temperature of the day, mean temperature of the activity phase (period from sundown until sunrise), and minimum and maximum temperature of the day. Additionally, these values were determined for 1 to 3 days before the night of activity data point.

#### Statistics

Statistical analysis was carried out with SPSS 17.0. The data were tested for normality against a standard normal distribution using the Shapiro–Wilk test ( $n < 50$ ) and the Kolmogorov–Smirnov test ( $n > 50$ ). Where possible, parametric tests were performed; if at least one subgroup was not normally distributed, corresponding nonparametric tests were conducted. In all statistical tests, an alpha level of  $p < 0.05$  was used to set significance.



**Fig. 1** **a** Example of lunar characteristics during May and June 2012. Distribution of moon phases are indicated (new moon 0–10 %, waxing 11–89 %, full moon 90–100 %, and waning 89–11 %), lunar disk size in percent (black circle), time that the moon is visible above the horizon in hours (black squares), and time of moonrise in the course of the day (gray triangle). **b** Mean ( $\pm$ SEM) daily ambient temperature measured in an

*Ammopiptanthus mongolicus* shrub 15 cm above the ground and 10 cm underground. **c** Overview of periods of time in which ambient temperature was determined and activity parameters analyzed. **d** Ambient mean temperature ( $\pm$ SEM), maximum and minimum temperature measured in an *Ammopiptanthus mongolicus* shrub 15 cm above the ground, and 10 cm underground in the course of the day during May and June 2013

**Results**

**Lunar effects**

First, a statistical analysis was performed with calculation of correlations, and the moon disk size was used as the component. Here, we found a negative relationship between the onset

of activity and the moon disk size (Spearman  $\rho = -0.161$ ;  $p = 0.048$ ) demonstrating an earlier onset of activity with increasing moon disk size. Although the offset remained unaffected (Spearman not significant (n.s.)), duration of activity was positively correlated with the moon disk size (Spearman  $\rho = 0.237$ ;  $p = 0.025$  and Pearson  $r = 0.210$ ;  $p = 0.041$ ; Fig. 2a). Furthermore, we found a prolongation of aboveground stays



with increasing moon disk size (Pearson  $r=0.037$ ;  $p=0.037$ ). Duration of single stays in the subterranean burrow in the course of the activity phase remained unaffected (Pearson n.s.).

Second, activity data of moon phases were compared, but here, only slight variation was observed. Neither for the onset of activity, for the offset nor for the duration of activity were differences found (Kruskal–Wallis n.s.). Animals left their burrow within 2 h after sundown (new moon  $1:57\pm 0:04$  h ( $n=28$ ), waxing moon  $1:49\pm 0:03$  h ( $n=31$ ), full moon  $1:39\pm 0:05$  h ( $n=9$ ), and waning moon  $1:57\pm 0:03$  h ( $n=40$ )). Activity above ground ended more than 9 h after sundown (new moon  $9:15\pm 0:16$  h ( $n=16$ ), waxing moon  $9:02\pm 0:20$  h ( $n=19$ ), full moon  $9:01\pm 0:33$  h ( $n=8$ ), and waning moon  $9:34\pm 0:13$  h ( $n=17$ )). These on- and offsets of activity resulted in a duration of  $7:12\pm 0:15$  h ( $n=16$ ) during new moon,  $7:40\pm 0:18$  h ( $n=15$ ) during waxing moon,  $7:27\pm 0:14$  h ( $n=17$ ) during waning, and  $8:02\pm 0:17$  h ( $n=4$ ) during full moon nights. Differences in the number of values are caused by the disappearance of animals and changes of burrows. It has to be mentioned here that irrespective of the nonexisting significance, the full moon phase was prominent regarding onset of activity associated with the duration—and the number—of observed animals above the ground. During a full moon, less than the half of the animals became active, and in these cases, 20 min earlier than in a new moon. Because the offset was very similar between moon phases, duration of activity was slightly prolonged (approximately 30 min). This circumstance was again observed in the analysis of the duration of foraging walks above the ground. Again, the Kruskal–Wallis test failed, although aboveground stays during full moon nights lasted  $2:25\pm 0:48$  h ( $n=7$ ) in contrast to  $1:08\pm 0:12$  h ( $n=24$ ) in new moon phases,  $1:50\pm 0:23$  h ( $n=21$ ) in waxing moons, or  $1:34\pm 0:21$  h ( $n=25$ ) in waning moons. A similar observation was made for the durations of inside stays in the course of the nocturnal activity phase. Again, animals spent slightly longer periods during full moon phases ( $1:27\pm 0:29$  h,  $n=6$ ) in their burrow. Results were similar in the other moon phases (new moon  $0:55\pm 0:09$  h

( $n=21$ ), waxing moon  $0:42\pm 0:08$  h ( $n=17$ ), and waning moon  $1:06\pm 0:16$  h ( $n=16$ ); Kruskal–Wallis n.s.).

#### Temperature effects

Mean temperatures of different periods of time were tested with regards to a possible influence on activity (overview shown in Fig. 1c) with special focus on ambient and soil temperature of the activity phase, the whole day, and the minimum and maximum temperature for the time periods current day and 1, 2, and 3 days before data point of activity. Regarding aboveground ambient temperature, Spearman correlations showed no interaction between any temperature parameter and the onset of activity ( $p>0.05$ ), duration of inside stays ( $p>0.05$ ), and foraging walks ( $p>0.05$ ).

In contrast, comprehensive results were found indicating a shortening of activity with increasing temperatures due to earlier offsets of activity, i.e., animals finished their nocturnal aboveground activity much earlier (Table 1). This was verified for the days before activity was determined, but it was not true for temperatures of the current day.

Additionally, multiple regression analyses were performed in order to clarify the most influential parameter. A regression analysis was performed including moon disk size, maximum ambient temperature 3 days before, and mean soil temperature of the activity phase 1 day before activity determination. Here, only the mean soil temperature of the activity phase 1 day before was entered ( $R=0.532$ ;  $R^2=0.283$ ;  $F=8.666$ ;  $p=0.008$ ); duration of activity =  $0.612 - 0.016 * \text{mean soil temperature of activity phase 1 day before}$ .

Further stepwise regression analyses were performed for ambient and soil temperatures separately with a put-in-criterion of  $p<0.05$ ; put-out-criterion was  $p>0.10$ . Only one model was determined including one single element—the “maximum ambient temperature 3 days before activity determination” (duration of activity  $R=0.499$ ;  $R^2=0.249$ ;  $F=7.281$ ;  $p=0.013$ ). The resulting regression equation can be formulated as follows:

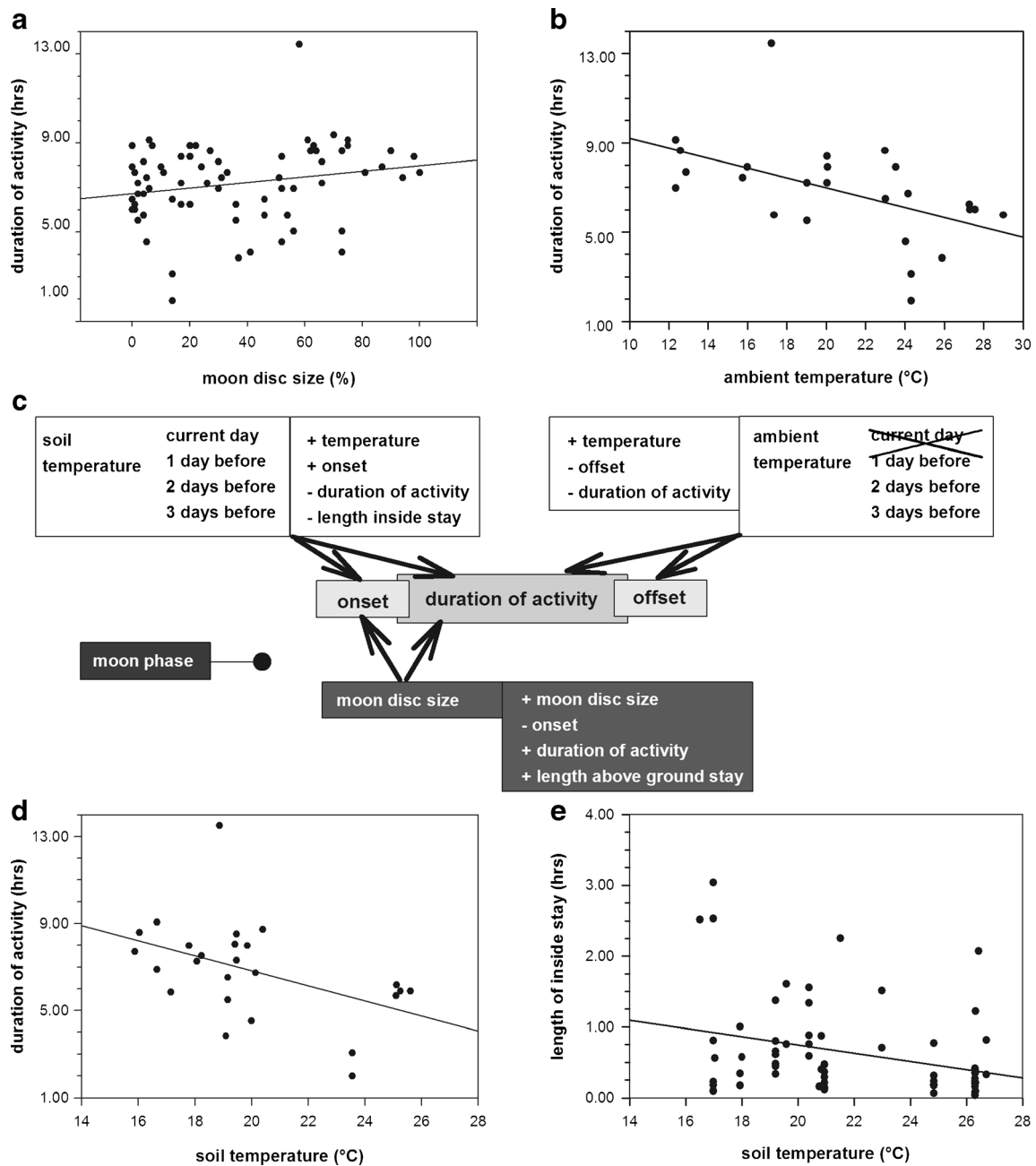
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$$\text{duration of activity} = 0.489 - 0.006 * \text{maximum ambient temperature 3 days before}$$


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The analysis soil temperature resulted in a comparable data set. Increasing underground temperatures were associated with a shortening of activity that was again explained by an advance of offsets which lead to a shortened aboveground activity. Nevertheless, the length of aboveground foraging walks remained unaffected, but durations of nocturnal inside stays were shorter in conditions of elevated underground temperatures. This was true for all periods of time (detailed data summarized in Table 1). Again, a stepwise regression

analysis was conducted with the same criterions as written above. This time “mean soil temperature of the activity phase 1 day before data point measured” was most decisive ( $R=0.644$ ;  $R^2=0.283$ ;  $F=7.458$ ;  $p=0.004$ ); duration of activity =  $0.554 - 0.058 * \text{mean soil temperature of activity phase 1 day before}$ . A detailed analysis of temperature in general showed that temperatures did not differ within 3 days. Comparisons of temperatures of the current day until 3 days before activity measurements showed only slight variation



**Fig. 2** Effects on duration of aboveground activity by **a** moon disc size (Spearman  $\rho=0.237$ ;  $p=0.025$ ) and **b** ambient maximum temperature 3 days before activity (Spearman  $\rho=-0.478$ ;  $p=0.018$ ), **c** schematic summary of activity-influencing factors including lunar aspects, **d** effects

on duration of aboveground activity by mean soil temperature of the activity phase 1 day before activity (Spearman  $\rho=-0.613$ ;  $p=0.001$ ), and **e** effects on duration of nocturnal inside stays by mean soil temperature of the activity phase (Spearman  $\rho=-0.453$ ;  $p<0.001$ )

between  $0.10 \pm 1.34$  °C for the maximum and  $0.81 \pm 1.08$  °C for the minimum temperatures (Friedmann n.s.); mean temperature of the day varied in the range of  $0.37 \pm 1.00$  °C and the mean of the activity phase of  $1.03 \pm 1.01$  °C (Friedmann n.s.), respectively.

As presented in Fig. 1d and because of the cloudless nights in the desert, there is a strong relationship between the

disappearance of the sun and cooling in the course of the night (Pearson night effect for mean temperature of the day  $r=-0.617$ ;  $p=0.002$  and day effect  $r=0.621$ ;  $p=0.002$ ). However, a test as to whether duration of activity was influenced by the length of the night showed a positive relationship. Animals remained active for longer times in longer nights (Pearson  $r=0.432$ ;  $p=0.001$ ).

**Table 1** Summary of Spearman correlation results for activity and temperature data

	Interval of temperature measurements	Current day ( <i>n</i> =25)	One day before ( <i>n</i> =25)	Two days before ( <i>n</i> =25)	Three days before ( <i>n</i> =24)	
Ambient temperature	Offset of nocturnal aboveground activity					
	Mean of the day	$\rho=-0.172$ <i>p</i> =0.456	$\rho=-0.561$ <i>p</i> =0.008	$\rho=-0.397$ <i>p</i> =0.075	$\rho=-0.499$ <i>p</i> =0.025	
	Activity phase	$\rho=-0.201$ <i>p</i> =0.383	$\rho=-0.578$ <i>p</i> =0.006	$\rho=-0.490$ <i>p</i> =0.024	$\rho=-0.367$ <i>p</i> =0.112	
	Maximum of the day	$\rho=-0.166$ <i>p</i> =0.473	$\rho=-0.519$ <i>p</i> =0.016	$\rho=-0.335$ <i>p</i> =0.137	$\rho=-0.633$ <i>p</i> =0.003	
	Minimum of the day	$\rho=-0.353$ <i>p</i> =0.117	$\rho=-0.500$ <i>p</i> =0.021	$\rho=-0.478$ <i>p</i> =0.028	$\rho=-0.431$ <i>p</i> =0.058	
	Duration of nocturnal aboveground activity					
	Mean of the day	$\rho=-0.192$ <i>p</i> =0.357	$\rho=-0.618$ <i>p</i> =0.001	$\rho=-0.464$ <i>p</i> =0.02	$\rho=-0.439$ <i>p</i> =0.032	
	Activity phase	$\rho=-0.221$ <i>p</i> =0.289	$\rho=-0.576$ <i>p</i> =0.003	$\rho=-0.492$ <i>p</i> =0.012	$\rho=-0.216$ <i>p</i> =0.311	
	Maximum of the day	$\rho=-0.13$ <i>p</i> =0.536	$\rho=-0.615$ <i>p</i> =0.001	$\rho=-0.426$ <i>p</i> =0.034	$\rho=-0.478$ <i>p</i> =0.018	
	Minimum of the day	$\rho=-0.322$ <i>p</i> =0.117	$\rho=-0.547$ <i>p</i> =0.005	$\rho=-0.454$ <i>p</i> =0.023	$\rho=-0.284$ <i>p</i> =0.178	
	Soil temperature	Offset of nocturnal aboveground activity				
		Mean of the day	$\rho=-0.416$ <i>p</i> =0.061	$\rho=-0.477$ <i>p</i> =0.029	$\rho=-0.414$ <i>p</i> =0.062	$\rho=-0.524$ <i>p</i> =0.018
		Activity phase	$\rho=-0.103$ <i>p</i> =0.656	$\rho=-0.507$ <i>p</i> =0.019	$\rho=-0.446$ <i>p</i> =0.043	$\rho=-0.444$ <i>p</i> =0.050
		Maximum of the day	$\rho=-0.238$ <i>p</i> =0.299	$\rho=-0.496$ <i>p</i> =0.022	$\rho=-0.365$ <i>p</i> =0.104	$\rho=-0.554$ <i>p</i> =0.011
		Minimum of the day	$\rho=-0.576$ <i>p</i> =0.006	$\rho=-0.434$ <i>p</i> =0.049	$\rho=-0.447$ <i>p</i> =0.042	$\rho=-0.420$ <i>p</i> =0.065
		Duration of nocturnal aboveground activity				
Mean of the day		$\rho=-0.455$ <i>p</i> =0.022	$\rho=-0.649$ <i>p</i> =0.001	$\rho=-0.487$ <i>p</i> =0.014	$\rho=-0.436$ <i>p</i> =0.033	
Activity phase		$\rho=-0.116$ <i>p</i> =0.581	$\rho=-0.613$ <i>p</i> =0.001	$\rho=-0.624$ <i>p</i> =0.001	$\rho=-0.447$ <i>p</i> =0.028	
Maximum of the day		$\rho=-0.268$ <i>p</i> =0.196	$\rho=-0.517$ <i>p</i> =0.008	$\rho=-0.393$ <i>p</i> =0.052	$\rho=-0.476$ <i>p</i> =0.019	
Minimum of the day		$\rho=-0.546$ <i>p</i> =0.005	$\rho=-0.586$ <i>p</i> =0.002	$\rho=-0.439$ <i>p</i> =0.028	$\rho=-0.345$ <i>p</i> =0.098	
Duration of nocturnal inside stay						
Mean of the day		$\rho=-0.415$ <i>p</i> <0.001	$\rho=-0.448$ <i>p</i> <0.001	$\rho=-0.440$ <i>p</i> <0.001	$\rho=-0.306$ <i>p</i> =0.008	
Activity phase		$\rho=-0.453$ <i>p</i> <0.001	$\rho=-0.394$ <i>p</i> <0.001	$\rho=-0.470$ <i>p</i> <0.001	$\rho=-0.356$ <i>p</i> =0.002	
Maximum of the day		$\rho=-0.398$ <i>p</i> <0.001	$\rho=-0.334$ <i>p</i> =0.004	$\rho=-0.413$ <i>p</i> <0.001	$\rho=-0.361$ <i>p</i> =0.002	
Minimum of the day		$\rho=-0.441$ <i>p</i> <0.001	$\rho=-0.470$ <i>p</i> <0.001	$\rho=-0.336$ <i>p</i> =0.003	$\rho=-0.283$ <i>p</i> =0.014	

Significant results are marked by gray shadows

## Discussion

Our results indicate a slight prolongation of aboveground activity with increasing moon disk size, in contrast, a more pronounced shortening of activity was determined with an increasing ambient and soil temperature. This study here was a further approach to understand time niche plasticity in a desert rodent species—the desert hamster, *P. roborovskii*.

A prolongation of activity under bright moonlight conditions seems to be contradictory, since moonlight avoidance is known as the most common vigilance strategy implying reduced presence during bright moonlight (Brown et al. 1988; Clarke 1983; Kaufman and Kaufman 1982; Kotler et al. 1991; Zollner and Lima 1999) and even in current reviews (Kronfeld-Schor et al. 2013), this mechanism is still accepted as common and widely distributed in herbivore or rodent species. Nevertheless, our observations coincide with apparently contradictory studies even though the antipredator effect is not neglected (Griffin et al. 2005; Kotler et al. 2010; Upham and Hafner 2013). What does this mean?—the elevated lunar illumination especially in desert conditions with less shelter affects behavior, but antipredator strategies differ. If an animal spends less time outside the burrow, the risk of becoming prey should be reduced. For example, such a strategy was described in oldfield mice (*Peromyscus polionotus*) (Wolfe and Summerlin 1989), Merriam's kangaroo rats (*Dipodomys merriami*) (Daly et al. 1992), or Allenby's gerbils (*Gerbillus allenbyi*) (Kotler et al. 2010). Penteriani et al. (2013) described, in a detailed analysis, behavioral adaptations of rabbits (*Oryctolagus cuniculus*) with shortenings of foraging walks and smaller home ranges in full moon nights. During new moon nights, rabbits changed their exploratory behavior again and moved further.

In contrast, we found prolongation of aboveground activity and of foraging walks. This may be explained by the repeatedly freezing behavior in case of danger which we saw in another experiment (unpublished data). Hamster then preferred hiding places in vegetation (*Bassia dasyphylla*) or unused foreign burrows for long periods—and these periods with vigilance and freezing were prolonged and occurred more frequently during bright nights. In an extensive study in the Great Basin Desert, Upham and Hafner (2013) analyzed spatial behavior of several rodent species in different habitats and in the course of changing nocturnal illumination. Their final conclusion was that moonlight avoidance with a measurable shortening of activity is only observable for bipedal, jumping species. In contrast, quadrupedal moving species did not avoid moonlit nights because of their comparably low speed, elevated use of shelter burrows, and raised level of vigilance behavior during bright nights. That is why we assume the reason for lengthened activity by an elevated level of vigilance behavior; we do not suggest a change in home range size. Beyond that, we want to make clear that there is, in

effect, only a 1-h difference between the new and full moon activity. However, duration of single foraging walks differed strongly with the factor “two” between the new and full moons. As for soil and ambient temperature effects, a negative correlation was shown indicating shortening of activity with increasing temperatures, and this effect was more notorious than lunar illumination: a 10 °C increase of ambient temperature led to a shortening of the activity phase by about 3 h. This is of particular importance, because ambient temperatures measured in this study here varied between 12 and 30 °C and the thermoneutral zone (TNZ) of the desert hamster ranges between 25 and 33 °C (Zhan and Wang 2004). We could show that desert hamsters were only active within or beneath the TNZ, but never beyond that. Moreover, a shortening of activity in low temperature conditions was not observed by us—desert hamsters prolonged their activity in longer nights, although temperature decreases continuously in the course of a night until the next sunrise. A hypothesis was discussed by Banta (2003), who determined under laboratory conditions a preference of temperatures lower than the TNZ in Merriam's kangaroo rats (*D. merriami*) and explained this with a trade-off in favor of a water conservation strategy instead of an energy-saving one. It is conceivable that a comparable trade-off could be realized for our focus species in the Gobi desert. In this study, desert hamsters were only active within their TNZ or underneath, but never beyond it. As mentioned above, desert hamsters are well adapted toward arid environments displaying ability to reduce water loss through skin and lungs if air humidity is low, despite their excretion of highly concentrated urine (Sokolov and Meschersky 1989)—but these processes mean elevated energy demand, which is in contrast to the poor food availability in a desert. In a laboratory study, mainly diurnal common degus (*Octodon degus*) were kept in ambient temperature cycles with  $31.3 \pm 1.5$  °C during daytime and  $24.2 \pm 1.6$  °C during nighttime. Those animals developed pure nocturnality, i.e., a preference of lower ambient temperatures but still within their TNZ (Vivanco et al. 2010), which is in concordance with our observations. In the subterranean coruro (*Spalacopus cyanus*), Rezende et al. (2003) reported a switch between a bimodal activity pattern with activity during dusk and dawn during warm periods or summer, respectively, and diurnal activity during cold periods in winter. Finally, based on these comparable observations in diverse species with distinct ways of life, we conclude a general reduction of aboveground activity in warmer periods due to an energy-saving strategy, and this energy saving includes water and thermal balance.

Moreover, we found that animals shortened their nocturnal stay underground in their burrow with increasing soil temperature. These underground stays are of importance as it allows semifossorial desert animals to cool down (Chappel and Bartholomew 1981; Hogan et al. 2011). Indeed, temperatures measured in soil in 10-cm depth coincide with air temperature



in 70-cm depth in a natural or artificial burrow (Kay and Whitford 1978). Even though these data were estimated for Banner-tailed kangaroo rat (*Dipodomys spectabilis*) burrows, we assume comparability as burrows of desert hamsters are dug up the same depth and as the simple burrow structure allows similar ventilation (Flint 2006).

A possible explanation for the change of nocturnal burrow use could be the more effective cooling above the ground due to omnipresent wind. Conditions in the burrow or tunnel respectively could be characterized by a continuous elevation of humidity because of the animal's presence after foraging and because of the soil warming which would lead to an evaporation of soil moisture. The so-called humidex or heat index considers the felt increase of temperature due to elevated air humidity. Finally, the surrounding condition for animals could be more suitable at the burrow entrance or in vegetation shelters. When we dug out burrows, we found moist nesting material supporting our hypothesis.

Besides this approach from the animal's point, we found another possible explanation for shortenings of aboveground activity: the elevated food availability. Desert hamsters or hamsters in common collect seed and insects in their pouches in order to store or to feed it in their burrow. We examined about ten burrows with the focus on burrow construction and contents. All diggings were conducted in summer, and all burrows were actively used, but we did not find food storage in any of the burrows. We only found parts of insects and nesting material. Furthermore, animals changed their burrows repeatedly, and usually they used a burrow for 4 to 10 days during the summer time (Scheibler et al. 2013). Because of this seasonal-specific burrow use, animals only have to collect food for short times, allowing them to reduce foraging activity during summer months. We found that the maximum ambient temperature 3 days before activity was measured was most decisive. The time gap between the temperature data point and final activity suggests an influence of plant and seed availability, because not only germination is favored by temperature, the opening mechanism of seed coats depends on temperature and water loss which is finally due to solar irradiation (Baskin and Baskin 2001; Partzsch et al. 2011). As shown in Fig. 1b, several heat waves occurred and could have led to batch-wise release of seeds. This short-term plethora may reduce inter- and intraspecific competition (Jones et al. 2001; Kotler et al. 2002; Meyer and Valone 1999; Ziv and Kotler 2003) and makes animals more successful. With faster filled pouches, animals return faster to their burrows and return again to the earlier used food patch.

To sum up, both moon and temperature influenced the activity of desert hamsters but in diverging severity. Although lunar illumination affects predator–prey relationship, animals may cope with elevation of vigilance behavior and an adapted ranging strategy, which lead to a prolongation of aboveground activity. A preference of new moon phases or

night periods without lunar illumination was not observed. Overall, the impact power of the moon on time management is lower than that of temperature. The shortening of activity with increasing temperatures in combination with shorter nocturnal burrow stays can be explained by a strategy against overheating due to ambient temperatures and worse possibilities to cool down. Moreover, plausible arguments were found which support the preference of a water conservation strategy in contrast to an energy-saving one, and finally, a batch-wise increased food availability may result in shortened aboveground activity in days of or after heat waves.

**Acknowledgments** We want to thank Elisabeth Hummel, Shuai Yuan, Fu-Shun Zhang, and Xiao-Dong Zhang for their great help in the field, beyond that, Prof. Franziska Wollnik, Prof. Heping Fu, and Prof. Xiaodong Wu for their advice and support, and all Chinese colleagues worked in the College of Ecology and Environmental Science, Inner Mongolia Agricultural University, Hohhot, China. The authors thank Hong Jun Gan and Guohai Sang of the Grassland Office in Jiaer Gale Saihan for their great support. We also thank Jeremy Woods for revising the English language. Valuable hints and information about germination of plants in steppes and arid environments was provided by Dr Monika Partzsch from Martin Luther University of Halle-Wittenberg. We thank the Federal State of Baden-Württemberg and the European Social Fund for approving the grant for Elke Scheibler by the Margarete von Wrangell program and by the program to realize research stays in China in the field of applied biology provided by the Ministry of Science, Research and Art of the Federal State of Baden-Wuerttemberg, Germany.

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