Species composition and interspecific behavior affects activity pattern of free-living desert hamsters in the Alashan Desert

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Plasticity of circadian rhythm was investigated for the model species desert hamster (Phodopus roborovskii) under natural conditions in the Alashan Desert using the radiofrequency identification (RFID) technique, that is, animals were caught in the field and marked with passive transponders, and burrows were equipped with integrated microchip readers and photosensors for detection of movements into or out of the burrow. Additionally, video observations with infrared cameras were conducted at feeding sites to verify RFID data and analyze interspecific behavior. Composition of the rodent community changed during observation periods from a midday gerbil (Meriones meridianus)-dominated community to a desert hamster (P. roborovskii)-dominated community in 2009 and from a northern three-toed jerboa (Dipus sagitta)-dominated community to a hamster-dominated community in 2010. Activity pattern of hamsters was clearly affected by species composition. In the hamster-dominated community, activity started 1.7 h ± 1.0 SD after sundown and ended 7.2 ± 1.4 h after sundown. A similar activity pattern was found for the jerboa-dominated community. In contrast, hamsters shortened their activity tremendously in the gerbil-dominated community, to 2.2 ± 1.3 h (activity began at 0.8 ± 0.3 h after sundown and ended at 3.0 ± 1.5 h after sundown). An analysis of interspecific behavior at feeding sites showed clearly that gerbil behavior was characterized by aggressive attacks (60.4% attacks versus 6.1% being attacked), whereas jerboa behavior was dominated by avoidance of direct contact (67.5% avoidance versus 22.9% attack). Hamster intraspecific behavior included all 4 elements in a similar ratio (27.3% attacks, 21.8% being attacked, 22.7% fleeing without direct contact, and 22.7% causing fleeing without direct contact).

Key words: activity pattern, heterospecific competition, Phodopus roborovskii, temporal niche plasticity
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The daily temporal niche (nocturnal versus diurnal) of each species is determined by the circadian pacemaker system and the nonparametric entrainment of this endogenous pacemaker via synchronizing stimuli from the environment (Pittendrigh and Daan 1976). Although the environmental light–dark cycle is the strongest synchronizing stimulus, so-called nonphotic stimuli also are known to affect the circadian system (Favreau et al. 2009; Golombek and Rosenstein 2010; Hut et al. 2011). Furthermore, it has been shown that the temporal niche is neither constant nor identical for all individuals of one species. Instead, individuals should be able to alter their circadian rhythms over time and space to optimize their survival and reproductive fitness. Because the coexistence and interaction with other species is an omnipresent situation for nearly all species, it has been suggested that the circadian system also should be sensitive to significant interactions with other species (McPhee et al. 2010; Mistlberger and Skene 2004; Schoener 1974).

A potentially rich source of evidence for interspecific influences on circadian rhythms is the analysis of daily rhythms of mammalian behavior in natural habitats. For example, it has been demonstrated in desert habitats with limited resources that species with similar demands for food can coexist in separate temporal niches. A well-described example for such a community is that of the common spiny mouse (Acomys cahirinus) and the golden spiny mouse (Acomys russatus) in Israel (Friedman et al. 1997; Kronfeld-Schor et al. 2001). Both species are adapted to nocturnal
activity, but if they coexist within the same area, *A. russatus* behaves like a diurnal species. Without the competing *A. cahirinus, A. russatus* becomes nocturnal again (Kronfeld et al. 1996; Shkolnik 1971). But competition between species for the same habitat also may result only in moderate changes of the temporal niche, as has been shown for a community of the greater Egyptian gerbil (*Gerbillus pyramidium*) and Allenby’s gerbil (*Gerbillus allenbyi*). Both species can coexist because of the plasticity of their foraging strategies (Brown et al. 1992) and a higher variability in patch use, a behavioral strategy called temporal partitioning by Ziv et al. (1993). Similar moderate changes in activity pattern also have been reported for female golden hamsters (*Mesocricetus auratus*), which show a bimodal activity pattern under wildlife conditions in contrast to the well-known, strictly nocturnal activity pattern under laboratory conditions (Gattermann et al. 2008).

Previous research in our own laboratory on chronobiological effects of interspecific contact demonstrated that a single contact between the dominant Mongolian gerbil (*Meriones unguiculatus*) and the subordinate desert hamster (*Phodopus roborovskii*) induced pronounced phase shifts in the activity pattern of the desert hamster with phase advances at the end of the activity period, that is, circadian time 18 (Scheibler and Wollnik 2009). Furthermore, long-term contact between both species, where the animals were kept in the same cage and separated only by a wire mesh, resulted in a phase advance of activity offset and a shortening of nocturnal activity by several hours (Scheibler 2012; Scheibler and Wollnik 2009). Such a change in the activity pattern may be interpreted as a contact-avoiding strategy and indicates a behavioral flexibility of the otherwise strictly nocturnal activity pattern.

The objective of this study was, therefore, to analyze the activity pattern of desert hamsters under natural conditions, namely in the Alashan Desert, to investigate whether the coexistence with a competitive species affects the activity pattern in a similar manner as seen in the laboratory. A field study by Wu and Fu (2005) showed that in Inner Mongolia, China, the rather small desert hamster coexist with potential competitors, such as the Mongolian gerbil (*M. unguiculatus*), midday gerbil (*Meriones meridianus*), long-tailed dwarf-hamster (*Cricetulus longicaudatus*), striped dwarf hamster (*Cricetulus barabensis*), northern three-toed jerboa (*Dipus sagitta*), and Mongolian five-toed jerboa (*Allactaga sibirica*). In our study the rodent community included the midday gerbil, the northern three-toed jerboa, and as the focus species, the desert hamster. *P. roborovskii* is the smallest hamster species with a body mass of only 12–20 g and a body length of about 7 cm. The preferred habitat is that of semideserts with sparse vegetation and sandy soil. *Phodopus* lives in pairs or alone; up to 4 litters per year were recorded (Ross 1994). *M. meridianus* is a species belonging to the gerbil family. Its ecological demands are quite similar to those of *Phodopus*, but these animals are up to 4 times larger and they live socially in territorial families instead of living solitarily or in pairs (Agren et al. 1989; Scheibler et al. 2006). *D. sagitta*, as a representative of jerboas, uses a similar ecological niche, even though its exact needs compared to hamsters are still unknown. Because of their size and fast, bipedal movement, *Dipus* can maintain large home ranges compared to *Phodopus* and *Meriones*.

It is well known that species composition can change over time due to various biotic and abiotic factors such as food resources, predators, timing of reproduction, litter size, mortality, vegetation, and climate (Morin 2008). Rather fortunate for us, the composition of the rodent community indeed changed during each period of our observations, first from a *Meriones*-dominated community to a *Phodopus*-dominated community in 2009 and then from a *Dipus*-dominated to a *Phodopus*-dominated community in 2010. The aim of our study was to examine whether changes in time niche use, which have been demonstrated under laboratory conditions, also can be observed under natural conditions in free-ranging desert hamsters. Particular attention was paid to changes of the activity pattern when the hamsters cohabitated with competitive species, such as gerbils, or with noncompetitive species, such as jerboas.

**Materials and Methods**

**Field study sites.**—Field studies were performed in the Alashan Desert, near Jiaer Gale Saihan in the Autonomous Republic of Inner Mongolia, China (37°52′N, 105°20′E). The topography of the study area was characterized by shallow hills with elevations ranging from 1,360 to 1,400 m above sea level. The ground consisted of desert soil with a sand horizon up to a depth of more than 1 m. Approximately 10–15% of the ground was covered with shrubs, herbaceous plants, and only some gramineous plants. The vegetation was dominated by *Caragana tibetica, Ammopiptanthus mongolicus, Cynanchum komarovi,* and *Zygoophyllum pterocarpum* with a vegetation height reaching 75 cm. The area is agriculturally used as a grazing area for sheep and goats.

The region shows a semiarid, continental type of climate with hot summers (June–August) and cold, dry winters (November–March). Mean annual precipitation ranges from 45 to 215 mm per year. Mean annual temperature is 8.3°C, but may reach extremes of −35°C in January and 40°C in July. The study was performed in August and September 2009 and in July and August 2010. During this time of the year, mean ground temperature 2 h after sunrise was 20°C ± 1°C SD, whereas mean temperature at 50 cm depth was 23°C ± 0.3°C. These values were obtained from the official Jiaer Gale Saihan weather station, which was located 6.5 km away from the field site. Mean times for sundown (disappearance of solar disc), sunrise (solar disc completely above horizon), and length of the light period for the different observation periods are included in Table 1. The times of sunrise and sunset were found on the U.S. Naval Observatory website (U.S. Naval Observatory 2012).

**Field studies.**—Animals were captured with live traps (20 × 15 × 30 cm, single-capture trap, handmade in the workshop of the Inner Mongolia Agricultural University, Hohhot, China) set
in 5 different transects of 8 × 7 traps each. Each live trap was provided with a shelter box to prevent danger by weather impact. The construction of the trap with a robust wire mesh in combination with the shelter box protects the animals from possible attacks by predators and hyper- or hypothermia. An important prerequisite for the successful mapping of burrows is that the animals are as unaffected as possible by the trapping so that they return to their burrow unstressed. This was obviously the case, because animals repeatedly tried to walk back into the trap to get another peanut. This, however, was not possible because traps were closed during the daytime to avoid trapping of diurnal species. Additionally, examination of our data shows that nearly all animals were trapped repeatedly. Both observations indicate that the procedure did not put an unacceptable strain on the animals. Traps were placed a distance of 15 m from one another in each cardinal direction, thus each transect covered an area of 105 × 90 m. The position of transects was located using a global positioning system (Garmin Gecko; Garmin Corporation, Olathe, Kansas). Three of these transects were located in the same area (area A; Fig. 1), and the shortest distance between transects was 50 m. The other 2 transects were located 5 km away in area B. Because both areas were quite similar with respect to vegetation, altitude, and distance between transects, position of video recordings, and distribution of burrows, area B was not included in the figures. Altogether, an area of 2.8 km² (1.6 km² in area A and 1.2 km² in area B) was investigated including adjacent areas with Phodopus burrows and 5 linear transects that will be explained below.

Traps were baited with peanuts at least 1 h before sunset. All captured individuals were identified, marked, and released at their point of capture around sunrise (0530–0600 h). Individuals of 3 species were trapped: desert hamsters (P. roborovskii), midday gerbils (M. meridianus), and northern three-toed jerboas (D. sagitta). Only individuals of Phodopus or Meriones were marked with passive transponders (ISO-compliant-transponder, ISO 11784/11785, 2 × 12 mm, 0.1 g; Tierchip Dasmann, Tecklenburg, Germany). All other animals were marked with a fur cut to distinguish between new captures and recaptures and between males and females. Marking with passive transponders is a common and accepted method for lifelong individual animal tagging (Jennings et al. 1998; Mrozek et al. 1995). The transponders were placed subcutaneously in the scapular region.

Live-trap data per area were used to determine the composition of rodent communities and the species ratio on a daily basis (Supporting Information S1, DOI: 10.1644/115.S1). A species was classified as dominant when it accounted for more than 50% of all animals caught over a period of at least 3 consecutive days. In 2009, a community dominated by Meriones was observed from 11 August until 16 August.

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Phodopus-dominated community in 2009 (condition B)</th>
<th>Meriones-dominated community in 2009 (condition C)</th>
<th>Phodopus-dominated community in 2010 (condition D)</th>
<th>Dipus-dominated community in 2010 (condition E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>% occurrence of species</td>
<td>Phodopus roborovskii 66 ± 8</td>
<td>17 ± 4</td>
<td>76 ± 3</td>
<td>16 ± 4</td>
</tr>
<tr>
<td></td>
<td>Meriones meridianus 29 ± 8</td>
<td>62 ± 5</td>
<td>24 ± 3</td>
<td>13 ± 3</td>
</tr>
<tr>
<td></td>
<td>Dipus sagitta 6 ± 1</td>
<td>17 ± 3</td>
<td>0</td>
<td>68 ± 7</td>
</tr>
<tr>
<td>No. days</td>
<td>16</td>
<td>5</td>
<td>9</td>
<td>21</td>
</tr>
<tr>
<td>Photoperiod</td>
<td>Sundown 1921 ± 0006</td>
<td>1935 ± 0002</td>
<td>1939 ± 0002</td>
<td>1951 ± 0004</td>
</tr>
<tr>
<td></td>
<td>Sunrise 0614 ± 0003</td>
<td>0605 ± 0001</td>
<td>0602 ± 0001</td>
<td>0551 ± 0004</td>
</tr>
<tr>
<td>Length of photoperiod</td>
<td>13 h 18 min ± 12 min</td>
<td>13 h 45 min ± 5 min</td>
<td>13 h 36 min ± 5 min</td>
<td>14 h 1 min ± 9 min</td>
</tr>
</tbody>
</table>

FIG. 1.—Overview of study area A showing 3 of the 5 rectangular transects for live traps (8 × 7 lines with traps at a distance of 15 m, gridded square), location of the Phodopus (filled circles) and Meriones (empty circles) burrows, and 2 of the 5 linear transects with feeding sites for potential video recordings (triangles) and the actual video recording site (triangle with circle).
period will be referred to as condition C below. A community dominated by *Phodopus* was observed from 17 August until 2 September (condition B). In 2010, the rodent community was dominated by *Dipus* between 14 July and 4 August (condition E) and by *Phodopus* between 5 August and 14 August (condition D). Condition A comes from laboratory data explained below. The percentages for each species are given in Table 1. For a representative example of changes in species composition over time see Supporting Information S1.

Activity.—Trapped *Phodopus* were weighed and their sex and gonadal status (males: palpation; females: visual inspection of vaginal opening) were determined. The animals were marked with a passive transponder, as described above, and checked for recapture with a microchip reader (TC 560 ISO-Multi; Tierchip Dasmann). Mean weight (±SD) of males was 17.0 ± 3.8 g (2009: 15.7 ± 2.7 g; 2010: 18.5 ± 4.5 g), mean weight of females was 14.9 ± 3.1 g (2009: 13.9 ± 2.0 g; 2010: 16.4 ± 3.6 g). Animals were released and tracked until they went into a burrow or dug a new one. The position of the burrow was assessed via a global positioning system (Garmin Gecko; Garmin Corporation). The entrance hole was then equipped with an artificial tunnel system (length: 15 cm, diameter: 3.5 cm) containing an integrated microchip reader (radiofrequency identification [RFID]) and photosensors for the detection of movements in or out of the burrow (see Supporting Information S2. DOI: 10.1644/115.S2). The chronology of entries and exits of the individuals was used to determine the time spent outside the burrow. Outside stays of less than 1 min were not included in the calculation, because the distance between surface and light sensor was 6 cm, that is, approximately the body length of a *Phodopus*. Therefore, we could not differentiate whether the animal remained at the tunnel exit or actually left the burrow for a brief period of time. Furthermore, video recordings confirmed that animals had always left their burrow when the time gap between the 2 signals was longer than 1 min. Overall, 59 burrows (2009: 32; 2010: 27) were marked with an RFID device; data were collected at 37 burrows (2009: 16; 2010: 21). After completion of the 2009 observation period, 12 burrows were excavated using a spade to clarify if the burrow was abandoned and if there was a 2nd entrance hole. Only 2 of these 12 burrows contained nesting material; no food storage was found except for wings of bugs and other insects, confirming the use of the burrow by *Phodopus*.

Video recordings.—Video recordings were performed to verify the activity data determined by the RFID technique and to determine the activity patterns of the 2 cohabitant species, that is, *Meriones* and *Dipus*. Therefore, 5 linear transects oriented north–south, east–west, and so on were set between 500 m and 1.5 km from the live traps and RFID-marked burrows of *Phodopus*. Two of these linear transects were located in area A (Fig. 1), the other 3 were located in area B (not shown). Each linear transect was equipped with 5 feeding sites 30 m apart from each other. Three days before each recording, 20 g of peanuts per night were provided at each feeding site. After sunrise the sites were checked for tracks of the different species and the amount of peanuts taken. Finally, 1 observation site per transect was chosen that was most frequently used by both *Phodopus* and other rodent species. There, nocturnal video recordings were conducted from 1 h before sundown until 1 h after sunrise for 4 consecutive nights (20 nights total). Video observations were performed using an infrared camera (ICD-49E; Ikegami Tsushinki Co., Ltd., Tokyo, Japan) and an infrared lamp (850 nm; Videor E. Hartig GmbH, Roeddermark, Germany), both powered by a car battery. The videos were stored on a digital recorder (Abus Security Tech, Wetter-Volmarstein, Germany). Online live observations were possible via a monitor (Conrad Electronic SE, Hirschau, Germany), but most analyses of the digital recordings were performed afterward. During observation periods a large amount of peanuts (20 g) was provided only at the camera site, while the other feeding sites received a reduced amount (5 g). A total of 161.6 h of video recordings was taken. These video recordings provided information on activity onset (1st appearance at the feeding site after sunset), activity offset (last appearance at the feeding site before sunrise), and activity duration of the 2 cohabitant species, that is, *Meriones* and *Dipus*, and also were used to verify the RFID activity data for *Phodopus*. Of the video recordings, 24.2 h showed interacting animals and were thus analyzed with respect to intra- and interspecific behavior. Behavioral analyses focused on which species met at the feeding site; and what behavior the animals showed at the feeding site and toward the oncoming individual. Sociopositive behavior was recognized when the animals were contact-sitting (2 or more animals sitting side by side with close body contact), allogrooming (individuals grooming each other), or showing courtship behavior (anogenital contacts, circling, mounting, etc.). Neutral behavior was recognized when animals were feeding, autogrooming (an individual grooming itself), or sitting and resting. Aggressive behavior included chasing (one animal trying to escape with the aggressor following closely) and biting (an animal being attacked by an aggressor). Agonistic behavior without direct contact appeared as keeping distance (animals hiding away when the oncoming animal appeared).

Laboratory experiments.—Measurements under laboratory conditions were performed at Stuttgart University in Germany (48°46′N, 9°4′E) under constant temperature (22°C ± 1°C SD) and humidity (55% ± 5% SD), but with natural light conditions through glass windows with twilight and gradual changes of photoperiod. All animals used in Germany were bred from our own laboratory breeding stock, which was based on breeding pairs provided by the Institute of Zoology of Martin-Luther-University, Halle-Wittenberg, Germany, in 2006. Measurements of locomotor activity were done in September 2009 under a photoperiod (14 h 20 min) similar to that during the field studies in the Alashan Desert, that is, sundown was at 2039 h ± 0014 SD and sunrise at 0617 ± 0014 h. This period will be referred to as condition A below.

Food pellets (Altromin, Lage, Germany) and tap water were provided ad libitum; chow was complemented by apples and curds. Male and female desert hamsters were housed...
individually in Macrolone cages (type IV, Tecniplast, Hohenpeissenberg, Germany) filled with nesting material, houses, sand baths, and a running wheel (diameter 17 cm).

Running-wheel activity was measured by a magnetic reed switch on the wheel axle, and impulses were saved every minute on a personal computer. The software ClockLab (Coulbourn Intruments Inc. 2009) was used to collect activity data, plot actograms, and analyze period length (Coulbourn Intruments Inc. 2009) was used to collect activity data, plot actograms, and analyze period length (τ) and activity onsets and offsets. The software calculated the onset of activity by a template-matching algorithm that searches for 6 h of bins without activity followed by an activity level of at least 5% of all bins measured for the day. The similar, inverse algorithm was used to define activity offset, that is, 6 h of activity followed by an activity level of less than 5% of the whole-day activity were searched. Thereby, all bins exceeding a threshold of 20% of all nonzero counts were defined as activity.

All experiments were performed in concordance with the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011). Guidelines for the use of animals in research, the legal requirements of Germany and China, and any institutional guidelines also have been adhered to in this study. Experiments conducted in Germany were reported to the Regional Council of Stuttgart (AZ: 35–9185.81/0263); and experiments conducted in China were reported to the Grassland Office of Bayan Hot.

Statistics.—Statistical analysis was carried out with SPSS 17.0 (SPSS, Inc. 2008). The data were tested for normality against a standard normal distribution using the Shapiro–Wilk test. Even though single parameters showed parametric distributions, only nonparametric tests were conducted because of the majority of nonparametric data. In addition, circular statistics and plots were performed with Oriana 3.0 (Kovach Computing Services 2011). The Ralgh test was used to assess phase coherence and the Watson–Williams F-test to compare phases. Differences were considered significant at P < 0.05.

RESULTS

Field study trap data.—Altogether, 231 individuals of 3 species were trapped (2009: 11 trap nights, 115 animals; 2010: 21 trap nights, 116 animals) and 314 recaptures were documented (2009: 156 recaptures; 2010: 158 recaptures). In 2009 we caught 37 P. roborovskii (21 males and 16 females), 55 M. meridianus (33 males and 22 females), and 23 D. sagitta (7 males and 16 females). In 2010 we caught 31 P. roborovskii (18 males and 13 females), 19 M. meridianus (10 males and 9 females), and 66 D. sagitta (40 males and 26 females). None of the hamsters and gerbils captured in 2009 were recaptured in 2010. All animals were subadult or adult. Only 2 juvenile M. meridianus were trapped, but were not marked and were immediately released instead. There were no pregnant or lactating females in the traps.

Activity pattern on the basis of video recordings.—Video recordings showed 4 species at the feeding sites, namely P. roborovskii, M. meridianus, D. sagitta, and long-eared hedgehogs (Hemiechinus auritus). The latter were not included in the analyses, because their appearance was too sporadic. Altogether, data of 20 nights, that is, 5 observation sites for 4 consecutive nights each, were analyzed. In general, all 3 species were nocturnal (Supporting Information S3, DOI: 10.1644/115.S3). Phodopus was observed from 2.7 ± 0.4 h after sundown until 6.6 ± 0.5 h after sundown, whereas Meriones appeared 1.5 ± 0.5 h after sunset and disappeared 7.7 ± 0.7 h after sundown. Dipus was observed from 1.5 ± 0.4 h after sunset until 8.1 ± 0.3 h after sundown. Statistical analyses revealed no significant differences between the 3 species, neither for the time of their 1st appearance after sundown, that is, onset of activity (Kruskal–Wallis: χ² = 6.45, P = 0.162), nor for the time of their disappearance before sunrise, that is, offset of activity (Kruskal–Wallis: χ² = 48.61, P = 0.006). However, statistical analyses of activity duration revealed a significant difference (Kruskal–Wallis: χ² = 6.28, P = 0.045) between 2 species. Phodopus showed the shortest duration (4.0 ± 0.6 h) at the observation sites, in contrast to Dipus (5.9 ± 0.6 h, U = 46.00, P = 0.012). No difference was found between Phodopus and Meriones (5.5 ± 1.0 h, U = 39.50, P = 0.115), or Meriones and Dipus (U = 78.00, P = 0.938).

Video recordings also were performed to verify the activity data of Phodopus determined by the RFID technique. Offset of activity measured by RFID and time of disappearance measured by video recordings were rather similar (video: 6.6 ± 0.5 h after sundown; RFID: 7.6 ± 0.7 h after sundown; U = 43.00, P = 0.172; Supporting Information S3). In contrast, onset of activity measured by RFID was significantly earlier than the time of appearance measured by video (RFID: 1.4 ± 0.3 h; video: 2.7 ± 0.4 h; U = 36.00, P = 0.003), and the duration of activity measured by RFID was longer than the duration of activity measured by video (RFID: 6.2 ± 0.3 h; video: 4.0 ± 0.6 h; U = 21.00, P = 0.006).

Activity pattern of P. roborovskii in different rodent communities.—The RFID technique was used to analyze the activity pattern of Phodopus under natural field conditions. Measurements were performed in 2 consecutive years within the same area and under similar photoperiods. However, the composition of the rodent community changed spontaneously not only from one year to the next, but also within each observation period. For a representative example of changes in species composition over time see Supporting Information S1. As shown in Table 1, 4 conditions were defined as follows: condition B with a majority of Phodopus in 2009, condition C with a majority of Meriones in 2009, condition D with a majority of Phodopus in 2010, and condition E with a majority of Dipus in 2010. In addition, activity data of Phodopus kept under laboratory conditions but natural photoperiod in 2009 were included for comparative reasons (condition A). Because these laboratory data were obtained with a different technique,
First of all, we noted a difference in activity onset between both Phodopus and Dipus. In 2009, c) Meriones in 2009, d) Phodopus in 2010, and e) Dipus in 2010. Vertical dashed lines indicate sundown and sunrise; and horizontal lines separate laboratory conditions not included in the statistical analyses and both years of the field study. Significant differences are indicated by asterisks (*) for onsets (left side) and offsets (right side) of activity. The asterisk on the left side indicates the general difference between activity onsets in 2009 versus 2010.

Supporting Information S4 (DOI: 10.1644/115.S4) summarizes various activity parameters for each condition, both as group means and separately for males and females. Because of the small number of animals in conditions C and D, statistical analyses of possible sex-specific differences were performed only for conditions B and E. No sex-specific difference was found in these cases, neither for Phodopus living in a community dominated by themselves (condition B; onset: $U = 15.00, P = 0.464$; offset: $U = 12.00, P = 0.788$; duration of activity: $U = 12.00, P = 0.788$) nor for Phodopus living in a community dominated by Dipus (condition E; onset: $U = 26.00, P = 0.806$; offset: $U = 14.00, P = 0.604$; duration of activity: $U = 10.00, P = 0.604$).

As depicted in Fig. 2, Phodopus showed a nocturnal activity pattern both in the laboratory and in the field, however, with differences between years and between rodent communities. First of all, we noted a difference in activity onset between consecutive years not only between both Phodopus-dominated communities (B versus D: $U = 8.00, P = 0.007$) but in general (Kruskal–Wallis: $\chi^2_3 = 25.38, P < 0.001$; post hoc U-tests: B versus E: $U = 9.00, P < 0.001$; C versus D: $U = 3.00, P = 0.028$; C versus E: $U = 5.00, P = 0.014$). Therefore, statistical comparisons between rodent communities were restricted to the same year. In 2009, the activity patterns of Phodopus differed considerably between the 2 rodent communities. Although activity onset occurred at rather similar times, activity offset differed significantly ($U = 0.05, P = 0.002$) between animals living in a Phodopus-dominated community (8.5 ± 1.9 h) and animals living in a Meriones-dominated community (3.0 ± 1.5 h). As a consequence, duration of activity was significantly shorter in the Meriones-dominated community ($U = 0.00, P = 0.002$).

In 2010, no statistically significant differences were found between the rodent communities dominated by Phodopus or Dipus. Onset of activity was almost identical ($U = 31.00, P = 0.640$). Offset of activity was earlier in the Dipus-dominated community; however, this difference failed to prove significant due to the high interindividual variation and the low number of animals ($U = 28.00, P = 0.454$).

Circular statistics revealed significant mean vectors for the timing of activity onsets and offsets under all 5 conditions (Supporting Information S5, DOI: 10.1644/115.S5; A–E). Furthermore, the Watson–Williams F-test confirmed a significant difference ($F_4 = 33.34, P < 0.001$) between activity offsets in Phodopus-dominated ($Z = 8.82, P < 0.001, \mu = 129.5°, r = 0.89$) and Meriones-dominated ($Z = 4.42, P = 0.004, \mu = 44.9°, r = 0.94$) communities. Offset of activity occurred later in Phodopus-dominated communities (8 h 40 min after sunset) than in Meriones-dominated communities (3 h after sunset). In 2010, the Watson–Williams F-test failed to reveal any difference ($F_4 = 0.02, P = 0.900$) between activity offsets in Phodopus-dominated ($Z = 5.65, P < 0.001, \mu = 25.5°, r = 0.97$) and Dipus-dominated ($Z = 13.98, P < 0.001, \mu = 24.4°, r = 0.97$) communities. Here, onsets of activity were less coherent in the Dipus-dominated community, resulting in a slightly shorter vector length of $r = 0.71$ compared to $r = 0.94$ in the Phodopus-dominated community.

Intra- and interspecific behavior.—As described above, 161.6 h of video were analyzed, 24.2 h of which showed 1 or more of the species P. roborovskii, M. meridianus, D. sagitta, and H. auritus. Phodopus spent time at the feeding site when they put peanuts in their pouches and when they were feeding. Dipus was rather prominent at the feeding sites because of the high number of individuals within the community and their intense locomotion. Also, they fed directly at the feeding site, for an overall of 14.1 h, followed by Phodopus with 4.9 h, Meriones with 2.9 h, and the hedgehog H. auritus with 2.4 h. Interspecific behavior with the hedgehog could not be analyzed in detail because it lasted only 24 s in total.

Even though direct and aggressive interactions were observed between all species, there were significant differences in some pairings. A detailed summary is given in Table 2. The highest ratio of aggressive interactions was found between Meriones and Phodopus, followed by intraspecific Phodopus contact; the lowest ratio was found between Dipus and Phodopus. Furthermore, several interspecific contacts ended with one animal disappearing after no direct interaction.
Because of the limited resources in the desert, it appears unlikely that the animals were able to collect food during these short-term activity bouts. Therefore, these short-term bouts are a clear sign for activity and appetency behavior, but should not be regarded as foraging activity. In summary, RFID-based determination of activity offers a detailed and precise view of the temporal organization of activity behavior including stays inside the burrow, short-term activity above ground, and foraging walks. Obviously, this method would also allow conclusions about the concurrent use of 1 burrow by different individuals or dispersal between burrows, but this was not the focus of the current study.

The main objective of the present study was to investigate the activity pattern of desert hamsters under natural conditions in the Alashan Desert and to evaluate changes in the activity pattern due to potential competitors. There are many studies of circadian activity rhythms in *Phodopus* under laboratory conditions that demonstrate that *Phodopus* is a nocturnal species (Bilbo and Nelson 2004; Petri et al. 2010; Scribner and Wynne-Edwards 1994; Steinlechner and Heldmaier 1982; Steinlechner et al. 2002; Weinert et al. 2009; Widmaier and Campbell 1980). However, studies in the field or under seminatural conditions are rare. A recent study by Weinert et al. (2009) compared circadian rhythms in all 3 *Phodopus* species (*Phodopus sungorus*, *Phodopus campbelli*, and *P. roborovskii*) under seminatural and laboratory conditions. Although no specific values were given, activity offset seems to be comparable to the results of our study, that is, within the 1st hour after lights-off or sunset. Another study using radiotelemetry investigated free-living *P. campbelli* and *P. sungorus* and also verified that both species are nocturnal, but *P. campbelli* started its activity earlier than *P. sungorus* (Wynne-Edwards et al. 1999). To conclude, desert hamsters are nocturnal animals under controlled laboratory conditions as well as under seminatural and natural conditions, and also in different habitats.

An interesting result of the present study is the finding of subtle changes in the activity pattern of desert hamsters under natural conditions. First, activity onset occurred 40–50 min later in 2010 than in 2009. Because measurements in 2009 and 2010 were done at slightly different times of the year, one possible explanation is small differences in photoperiod (Table 1). However, activity onset also was more variable in 2010, although a similar number of animals were captured and the study site was the same. As seen in Supporting Information S5, activity onsets were strongly clustered in 2009. In 2010, the majority of animals started their activity at the same time, but some individuals delayed their activity onset by 2–5 h. We therefore assume that differences in activity onsets between 2009 and 2010 are caused not only by the rather small differences in the natural photoperiod, but also by other biotic and abiotic effects (overview in Dunlap et al. 2004; Levy et al. 2007; Ylőnen and Brown 2007) such as ambient temperature or energy demand (Bacigalupe et al. 2003; Halle 1995; Hut et al. 2011), rainfall (Muñoz-Delgado et al. 2004), moon phase

### Table 2

<table>
<thead>
<tr>
<th>Is attacked by . . .</th>
<th>Phodopus</th>
<th>Phodopus</th>
<th>Dipus</th>
<th>Meriones</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attacks . . .</td>
<td>21.8%</td>
<td>22.9%</td>
<td>60.4%</td>
<td></td>
</tr>
<tr>
<td>Disappears when . .</td>
<td>27.3%</td>
<td>9.6%</td>
<td>6.1%</td>
<td></td>
</tr>
<tr>
<td>Causes disappearance of . .</td>
<td>22.7%</td>
<td>33.9%</td>
<td>21.4%</td>
<td>12.1%</td>
</tr>
</tbody>
</table>

**DISCUSSION**

The nocturnal activity pattern of wild-living desert hamsters was affected by the species composition of the rodent community, that is, the presence or absence of potential competitors. Although activity onset occurred at rather similar times, activity offset differed significantly between animals living in a *Phodopus*-dominated community (8.5 ± 1.9 h after sundown) and animals living in a *Meriones*-dominated community (3.0 ± 1.5 h after sundown). As a consequence, duration of activity was significantly shorter in the *Meriones*-dominated community.

The RFID technique provided precise and detailed information on the activity pattern outside the burrow of free-living animals. In general, desert hamsters under natural conditions left their burrows in the 1st hour after sundown and returned before sunrise. These findings are in agreement with measurements of running-wheel activity performed in our laboratory under similar natural photoperiods. According to other authors, running-wheel activity is a good indicator of an animal’s foraging behavior outside the burrow (DeKock and Rohn 1971; Rusak 1989; Wollnik et al. 1991). The findings of the present study support this assumption.

In addition to the RFID technique, activity and interindividual behavior in the field were further determined by video observations. Direct comparison of both video observations and RFID data (Supporting Information S3B) revealed that the animals left their burrows approximately 1.3 h before they appeared at the observations sites. This time lapse can be easily explained by the distance between burrows and video observation sites and by other activities of the animals, such as exploration or foraging. Again, a time lapse of 1 h was determined between disappearance on screen and return at burrow. A closer look at the data showed a higher variance in the video data compared to the RFID data, which we explain with the unknown time for exploration and time needed for the way back.

In general, measurements using the RFID technique were more accurate than those using video recording, because this technique determines the activity of individual animals with a resolution of seconds. However, this high temporal resolution resulted in a higher variance in mean onset. For example, if an animal left its burrow for more than 1 min, this was evaluated as aboveground activity. Such short-term stays outside the shelter occurred repeatedly. Possible reasons for fast returns could be rain, predators, competitors, intruders, or strong wind.
(Kappeler and Erkert 2003), or predation (Daly et al. 2000; Fenn and MacDonald 1995; Kitchen et al. 2000).

Second and even more important, the nocturnal activity pattern of Phodopus was affected by the species composition of the rodent community, that is, the presence or absence of potential competitors. The most dramatic change in the activity pattern was observed in 2009 between a Phodopus-dominated community and a Meriones-dominated community. As verified by 2 different statistical methods (nonparametric Kruskal–Wallis analysis and circular statistics), activity offset occurred approximately 5.5 h earlier and duration of activity was correspondingly shorter in the Meriones-dominated community. In a previous study, similar changes in the activity pattern were observed under laboratory conditions in an experimental setup in which desert hamsters were housed in the same cage with the closely related species M. unguiculatus, only separated by a wire mesh contact bar to prevent serious injuries (Scheibler 2012; Scheibler and Wollnik 2009). In this previous study, we found the same shortening of the hamster’s activity duration from 8 to 3 h if the hamsters had no chance to avoid contact.

The observed changes in the activity pattern can be explained by 2 different mechanisms. The presence of the competitive species Meriones may change the activity pattern of desert hamsters either by masking the activity offset (Mrosovsky 1999) or by entrainment or synchronization (or both) of the endogenous circadian system (Pittendrigh and Daan 1976). This issue was already addressed in the previous study (Scheibler and Wollnik 2009) by establishing a phase response curve for single contacts between both species. This phase response curve was characterized by 2 regions of phase advances: 1 during subjective day, that is, circadian time 3 and circadian time 9, and 1 at the end of the subjective night at circadian time 18. Phase advances during subjective day are a well-documented feature of nonphotic zeitgebers, such as arousal or novel wheel access (Hastings et al. 1992; Mead et al. 1992). In contrast, the observed phase advances at circadian time 18 are not comparable with any known nonphotic zeitgeber stimuli, suggesting that contact with a potential competitor represents a different quality of zeitgeber stimulus. Furthermore, the observed phase advances at circadian time 18 after a single, 2-h-long contact between both species are in perfect agreement with the observed shortening of activity duration under long-term contact, because according to the nonparametric model of entrainment, repeated contact between both species should shorten activity duration of desert hamsters (Daan and Pittendrigh 1976). Therefore, we suggest that the observed shortening in the activity duration represents a change in the circadian system, that is, a different phase angle of entrainment, induced by interspecific competition.

Interspecific competition between Phodopus and Meriones is supported by the video data. Aggression toward Phodopus was observed in Meriones, but not in Dipus. Also, the foraging strategy differs between species; while Phodopus collects food in their pouches, Dipus eat it at the food source, and Meriones carry it to their burrows. Possible reasons could be the energy investment for foraging or the need to rely on a food resource for a longer period. Both Dipus and Phodopus can reduce the number of walks between food resource and home burrow because their body size allows them to eat a large amount of food, or they can collect it in their pouches, respectively. Meriones, on the other hand, needs to invest more energy because they can carry only a few pieces of food to their burrows. These rodents thus depend on a food resource to a rather high degree, especially under the restricted conditions of a desert habitat. Unpredictable food availability and limited resources pose a major challenge for all desert species, and behavioral flexibility significantly improves the chance of survival (Kronfeld and Dayan 1999; Randall 2007; Ziv et al. 1993). Unfortunately, not much is yet known about whether the animals use the same plants as a food resource, and about the possible competition for the various parts of the plant. This is one of the issues of a currently ongoing study. In fact, we do not know which biotic or abiotic factors were responsible for the changes in species composition (conditions B–E) we observed during our study. However, the video data presented here very clearly indicate that in the case of direct competition (for peanuts), the aggression levels between species are quite different.

Studies on other communities, however, found similar and diverging results. For example, the community of common spiny mouse (A. cahirinus) and golden spiny mouse (A. russatus) in Israel shows temporal resource partitioning as a strategy for coexistence under harsh desert conditions (Kronfeld-Schor et al. 2001; Shkolnik 1971). Both species are nocturnal, but if they coexist within the same area, A. russatus behaves like a diurnal species. Interestingly, a study by Pinter-Wollman et al. (2006) showed that the diurnal activity pattern of the golden spiny mouse (A. russatus) is not caused by direct, aggressive interactions with the common spiny mouse (A. cahirinus). Instead, the authors suggest that other factors such as foraging efficiency, antipredator avoidance, water conservation, or productivity may account for the shift of golden spiny mouse into diurnal activity.

In contrast, aggressive interactions are clearly the cause for temporal segregation in another example of interspecific competition, namely between cotton rats (Sigmodon hispidus) and prairie voles (Microtus ochrogaster) in old-field habitats in northeastern Kansas (Glass and Slade 1980). In this rodent community, prairie voles showed a rather variable activity pattern depending on the reproductive status of the cotton rats, which closely correlated with an increase in aggressive behavior. It remains to be determined which biotic factor caused the shortening of activity of Phodopus in the present study. Because Meriones is well known as a strong territorial species with a high level of aggression against intruders of other species (Ginsburg and Braud 1971; Reynieres 1971; Roper and Polioudakis 1976; Scheibler et al. 2004, 2005; Thiessen and Yahr 1977), we assumed that the observed behavior can be explained with aggression in combination with limited alternatives for separation.
Finally, odor and direct contact are cues that are repeatedly discussed as an explanation for changes in activity patterns (Carver et al. 2011; Glass and Slade 1980; Johnston 2008; McPhee et al. 2010). Although odor is a strong signal from predator to prey and has the power to influence activity patterns, especially in rodents (Apfelbach et al. 2005; McPhee et al. 2010), it is still unclear if it can affect the activity pattern if the consequences of interspecific contact are not as dire as between predator and prey. This should be the subject of future studies.

In summary, our observations indicate that activity rhythms in desert hamsters are much more flexible and sensitive to biotic environmental factors than expected. Because changes of species composition are common in desert populations, temporal niche plasticity is a biologically relevant strategy in coping with these variations.

**Supporting Information**

 SUPPORTING INFORMATION S1.—Daily Capture Data. Found at DOI: 10.1644/12-MAMM-A-115.1.S1


 SUPPORTING INFORMATION S3.—Activity Onset and Offset Determined by Video Recording. Found at DOI: 10.1644/12-MAMM-A-115.1.S3

 SUPPORTING INFORMATION S4.—Activity Onset, Offset and Duration of Activity. Found at DOI: 10.1644/12-MAMM-A-115.1.S4


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**Literature Cited**


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