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Wheel-Running Activity Patterns of Five Species of Desert Rodents

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Abstract

In contrast to the extensive laboratory data on activity patterns in rodent species inhabiting temperate zones, much less is known about the activity patterns of desert rodents. In order to address this issue, we measured wheel-running activity patterns in males and females of five species of wild-trapped desert rodents (*Dipodillus dasyurus*, *Gerbillus andersoni*, *Gerbillus pyramidum*, *Meriones shawi*, and *Acomys cahirinus*) in long 'summer-like' and short, 'winter-like' day lengths. The specific goals of the present study were to characterize activity patterns in several desert rodent species in the laboratory and to determine if activity patterns are expressed in a seasonal or sexually dimorphic manner. Specifically, wheel-running was measured for 11 weeks in long days followed by 11 weeks in short days to test for photoperiodic entrainment as well as responsiveness to changes in the light-dark cycle. All animals exhibited rhythmic patterns of wheel-running with consistent onsets and offsets that had well-defined relations with the light-dark cycle. All individuals of *G. andersoni* showed nocturnal activity patterns. Most individuals of *G. pyramidum* had nocturnal activity patterns, but some individuals showed a short bout of activity at the beginning of the light period. Most individuals of *D. dasyurus* and *M. shawi* showed bimodal (i.e., nocturnal and diurnal) activity patterns, although some showed markedly nocturnal activity patterns. There was no sexual dimorphism in wheel running activity rhythms in any of the species examined. As expected, decreases in day length resulted in an overall increase in the duration of activity in all species. Collectively, these data provide an initial characterization of activity patterns within desert rodents in a controlled laboratory setting.

Keywords: nycthemeral rhythms, photoperiod, spiny mice, gerbils, jirds.

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Introduction

Individuals of most mammalian species have evolved discrete patterns of activity and inactivity to coordinate their behavior with optimal times of the day and year in order to maximize survival. For example, most animals demonstrate reliable patterns of daily activity, (i.e., circadian rhythms) that continue even in the absence of any environmental cues. Under natural conditions, these rhythms are entrained by environmental stimuli that act as cues to determine the time of day (Pittendrigh & Daan, 1976; Rusak & Zucker, 1979). In addition to these daily rhythms, animals also display distinct seasonal patterns of behavior in response to changes in environmental conditions (e.g., day length, ambient temperature, social cues) (Bronson & Heideman, 1994). Despite a wide variety of cues that vary seasonally, photoperiod (day length) appears to be the primary cue used by mammals to determine the time of year. With just two pieces of information, the absolute duration of daylight and the direction of change, animals can determine the precise time of year (Bronson & Heideman, 1994).

Despite the ubiquity of daily and seasonal activity rhythms across a wide range of species, the daily pattern of locomotor activity has been studied extensively in the laboratory in only a few mammalian species, primarily laboratory-reared rodent species (e.g., rats (*Rattus norvegicus*), house mice (*Mus domesticus*), Syrian hamsters (*Mesocricetus auratus*)). Typically, the goal of such studies is to provide a controlled, systematic analysis of the activity patterns displayed by these animals and to examine the physiological mechanisms underlying their activity rhythms. Because laboratory-reared strains of mice and rats are typically used in these studies, however, it is difficult to make any generalizations from the results of these studies to behavior seen in the natural environment. In addition, most of the laboratory research examining activity rhythms in wild-trapped mammals has been conducted using temporate or boreal zone rodent species. Very little is known about the daily activity (nycthemeral) rhythms of many other species of mammals, especially desert-dwelling rodents.

The activity patterns of at least one wild-trapped desert rodent species, Mongolian gerbils (*Meriones unguiculatus*), have been studied extensively within a controlled laboratory setting. It remains unclear, however, whether individuals of this species display nocturnal, diurnal, or crepuscular locomotor activity patterns (for review see Bartness & Albers, 2000). For example, Mongolian gerbils kept under a light-dark cycle of LD 12:12 h in the laboratory display either nocturnal (Roper, 1976) or both nocturnal and diurnal (Hallonquist et al., 1996) activity rhythms when tested using running wheels. Gerbils, in contrast, exhibit crepuscular (i.e., dawn/dusk) locomotor activity rhythms under the same photoperiod when activity is measured by the spontaneous tilt-box method (Stutz, 1972). Similar results have been reported when gerbils are studied under natural lighting conditions with activity measured by observing animals' movements and activity for 15-seconds interval every 10 minutes across several hours (Pietrewicz et al., 1982).

The existence of a sexual dimorphism in gerbil locomotor activity also is a matter of controversy. For example, sex differences in wheel-running during the light phase of the light-dark cycle seem to exist (with males, but not females, exhibiting wheel running activity during the light period (Roper, 1976)). Other studies, however, have reported a lack of a sex difference in locomotor activity patterns by gerbils, regardless of the mode of measurement of the activity rhythms (Hallonquist et al., 1996). Thus, our current knowledge of the locomotor activity rhythms of desert-dwelling Mongolian gerbils appears confusing at best.

Considerably more information is known about the locomotor activity of another desert-dwelling rodent, Syrian hamsters. Unfortunately, the extensive documentation about the highly regular and nocturnal rhythms of Syrian hamsters (for review see Morin, 1985) is offset by the lack of genetic diversity due an extreme genetic bottleneck experienced by the founder colony (Murphy, 1985). Because of this bottleneck, it is difficult to speculate on the functional, adaptive significance of activity rhythms by Syrian hamsters. In addition, the rhythms of these animals in the laboratory cannot be easily compared to locomotor behavior displayed in the field because Syrian hamsters have been virtually eradicated in their native habitats (Murphy, 1985). Thus, surprisingly little is known about the locomotor activity patterns of most extant desert rodent species within the laboratory.

Activity patterns have been examined in the field in ecologically similar species of *Acomys* inhabiting hot rocky deserts in southern Israel. Interestingly, common spiny mice (*A. cahirinus*) appear to be nocturnal, while golden spiny mice (*A. russatus*) display diurnal activity patterns with a midday peak in winter and a bimodal pattern (with peaks in morning and afternoon) during summer (Shkolnik, 1971; Kronfeld et al., 1996). Because of their common evolutionary history and geographical coexistence, the precise reason for the differences in activity patterns between the two species are not known. It has been speculated, however, that the less typical diurnal pattern demonstrated by *A. russatus* is due to competitive displacement (Kronfeld et al., 1996). Furthermore, little is known regarding activity patterns in *Acomys* in more controlled laboratory settings.

Wheel-running activity rhythms also have been examined in Nile grass rats (*Arvicanthis niloticus*), a group-living murid rodent inhabiting subSaharan Africa (Katona & Smale, 1997; McElhinny et al., 1997). Field studies on *A. niloticus* suggest that individuals of this species display primarily diurnal activity rhythms (Packer, 1982). When tested in the laboratory, *A. niloticus* display predominantly diurnal wheel-running activity rhythms, with peaks in activity occurring at dawn and dusk (Katona & Smale, 1997). Additionally, these rhythms appear stable and responsive to shifts in the light-dark cycle (Katona & Smale, 1997; McElhinny et al., 1997). Some individuals within *A. niloticus*, however, display nocturnal activity patterns, and the offspring of two nocturnal parents are more likely to be nocturnal than offspring of animals with predominantly diurnal activity patterns, suggesting that these rhythms are influenced by parentage (Blanchong et al., 1999). Primarily diurnal locomotor activity has been reported for another rodent species, *Octodon degus*, a hystricomorph rodent occupying the Chilean Andes of South America (Kas & Edgar, 1998). Both field studies (Fulk, 1976; Iriarte et al., 1989) and laboratory experiments (Goel & Lee, 1996; Kas & Edgar, 1998) have demonstrated predominantly diurnal locomotor activity with bouts of activity at dawn and dusk for this species. It is interesting to note, however, that when these animals are provided unrestricted access to a running wheel, the overt wheel running rhythms switch from diurnal to nocturnal (Kas &

Edgar, 1999). Furthermore, the nocturnal pattern of wheel running is sustained when animals are maintained in constant darkness, but revert to diurnal rhythms when the wheels are removed (Kas & Edgar, 1999). These findings stress the importance of environmental factors on activity patterns in rodents, and likely other mammalian species.

The goals of the present study were to examine the locomotor activity patterns of five species of wild-trapped desert rodents, including gerbils, jirds and spiny mice in a controlled laboratory setting and to evaluate the evidence for sex differences or seasonal changes in locomotor activity patterns. The five species examined in the present experiment were: Wagner's dipodils (*Dipodillus dasyurus*), Anderson's gerbils (*Gerbillus andersoni*), Greater gerbils, (*G. pyramidum*), Shaw's Jirds (*Meriones shawi*) and Egyptian spiny mice (*Acomys cahirinus*). These species were selected because they provide a representative sampling from a broad range of desert climates from the coastal regions of Southern India to the inland regions of Northern Africa, including Syria, Iraq, Israel, Egypt and the Arabian Peninsula (Nowak, 1991). The present study provides the first systematic study of gender and photoperiodic differences in activity patterns in several desert rodent species and these data, in conjunction with other laboratory and field studies, provide some much needed data on the activity patterns of desert rodents.

Materials and Methods

Animals

Adult wild-trapped males and females of five rodent species, *D. dasyurus* (n = 11 males, 11 females), *A. cahirinus* (n = 11 males, 10 females), *G. andersoni* (n = 9 males, 6 females), *G. pyramidum* (n = 10 males, 9 females), and *M. shawi* (n = 8 males, 11 females) were obtained from a commercial supplier (El-Hakim Company, Egypt) in August 1996. Upon arrival in the laboratory, the animals within each species were divided on the basis of gender and group-housed (7–10 per cage) within each gender. They were maintained for six weeks in long days (14 h light, 10 h dark; lights on at 03:00) at a constant temperature (22 ± 2°C) and humidity (50 ± 5%) before the start of the experiment. The light intensity of the rooms was approximately 75–100 lux at cage-top level. The parameters of the LD cycle were chosen because they represent approximately the longest day length at the latitude in which the animals were trapped (~30°N). Food (Purina Rodent chow #5001) and water were available *ad libitum*. All procedures were approved by the Georgia State University Institutional Animal Care and Use Committee and are in accordance with the Center for Disease Control and Prevention (CDC) guidelines for housing and handling wild animals (Biosafety Level 2).

Experimental procedures

All animals were weighed and housed individually in polypropylene cages (45.6 × 23.4 × 20.0 cm) equipped with a running wheel (52.4 cm circumference). Wheel revolutions were recorded automatically when a magnetic bar attached to each wheel passed by a sensor that was mounted on the wheel-housing. Wheel running data were collected for 11 weeks and stored in 10-min bins using Dataquest III® (Data Sciences) by a computer located in a different room. Subsequently, the animals were transferred to short days (10 h light, 14 h dark; lights on at 05:00 h) for 11 weeks. The length of the short-day photoperiod was chosen based on the shortest naturally occurring day length at the latitude where the animals were trapped (~30°N).

Data analysis

In addition to the Dataquest III® system, the Tau® program (Mini-Mitter Co., Inc.) also was used to analyze the activity data. Activity bouts that occurred due to cage maintenance were excluded from the analysis. Activity onset was operationally defined as the start time of the first block of activity that lasted at least for three consecutive 10 minute bins and was not separated from the next block of activity by more than 30 minutes. Activity offset was operationally defined as the end of last block of activity that was followed by at least 1 hour of inactivity. The duration of daily activity (α) was assessed by calculating the difference between daily activity offset and onset times. Re-entrainment rates were determined for activity onsets after the light/dark cycle change. The day of re-entrainment was defined as the day after which the activity onset did not advance further.

Differences in wheel-running activity were assessed using a 2 (gender) × 2 (photoperiod) × 5 (species) two-tailed, mixed-model analysis of variance (ANOVA, SYSTAT version 6.01). Differences in pair-wise means were determined using *post hoc* comparisons (Tukey's HSD test) only when significant simple effects were present to control for unnecessary inflation of Type I error due to multiple test comparisons. Group differences were considered statistically significant if $p < 0.05$. Test values and exact probabilities are not presented for purposes of clarity and simplicity of data presentation.

Results

Wheel-running in long days

Animals from all five species examined exhibited significant rhythmic (i.e., nycthemeral) patterns of wheel-running activity with precise and stable onsets and offsets entrained to the LD cycle (Fig. 1). There was, however, considerable within-species as well as between-species variability in the wheel running patterns. Nocturnal patterns were evident in all individuals of *G. andersoni* (Fig. 1A). Individuals of *G. pyramidum* also were nocturnal, but 26.3% of these animals showed an additional short bout of activity at the beginning of the light phase (Fig. 1B). Seventy-eight percent of *D. dasyurus* and *M. shawi* had bimodal activity patterns that appeared to reflect a crepuscular-like rhythm, in that they had pronounced peaks of activity around the time of lights-off (i.e., dusk) and at the time of lights-on (i.e., dawn) with little activity during the middle of the dark phase (Figs. 1D & 1E). The remaining 22% of *D.*

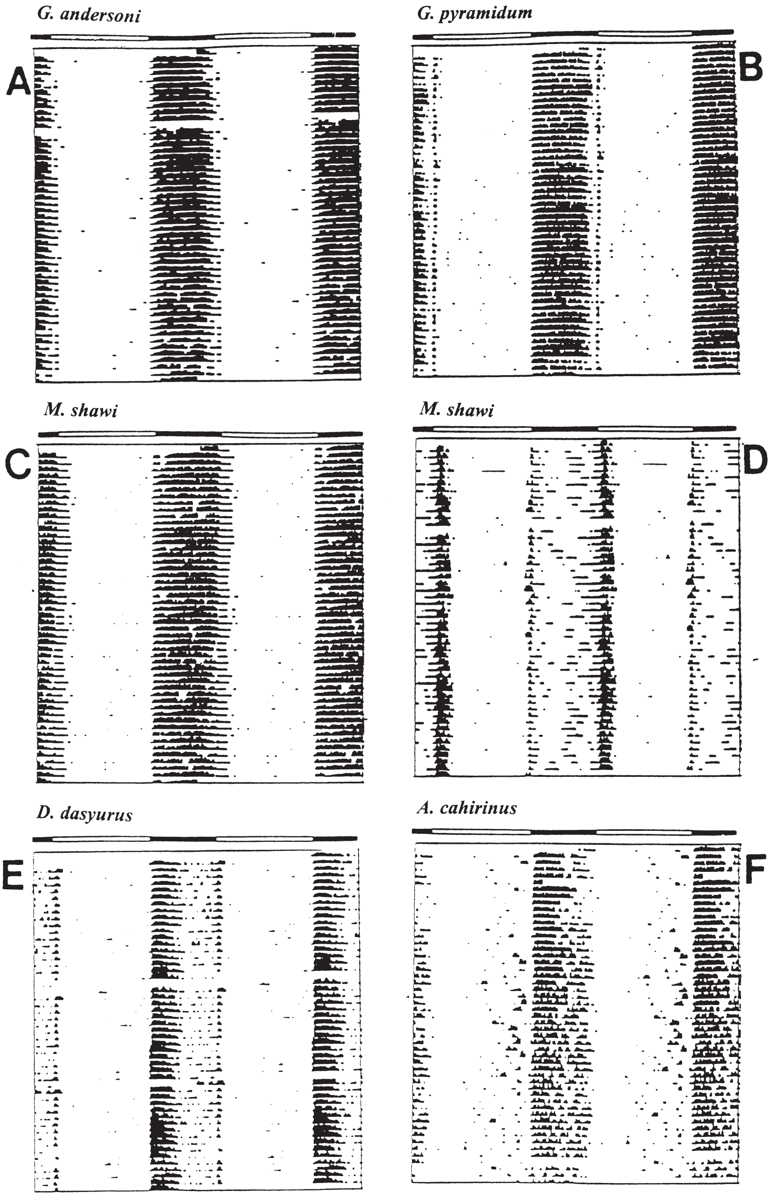

Figure 1. Representative double-plotted actograms illustrating wheel running records of 6 male animals, representative of each species studied. (A) *Gerbillus andersoni*; (B) *Gerbillus pyramidum*; (C, D) *Meriones shawi*; (E) *Dipodillus dasyurus*; (F) *Acomys cahirinus*. Actograms represent a period of 50 days under long photoperiod (LD 14:10) exposure. The blank lines indicate days with missing data due to system errors. The open and closed bars at the top of the actograms illustrate the LD cycle (open = light). Each line represents one 48-h period, and successive days are shown from top to bottom.

dasyurus and *M. shawi*, however, displayed nocturnal, activity patterns (Fig. 1C). The majority of activity of *A. cahirinus* occurred during the dark phase, although all individuals exhibited pronounced bouts (i.e., ≥1 h) of activity during the light phase (Fig. 1F).

The average times of activity onsets and offsets, as well as the duration of daily activity are shown for each species in Table 1. In the four species that belong to the family Cricetidae (*G. andersoni*, *G. pyramidum*, *D. dasyrus*, and *M. shawi*) (Osborn & Helmy, 1980), the onset of activity was precise, occurring shortly after lights-off (*G. andersoni*, *G. pyramidum*, *D. dasyrus*, and female *M. shawi*) or just before lights-off (male *M. shawi*). In 76.2% of individuals, wheel-running began about 3 h before lights-off, continued sporadically during the rest the of light phase, and terminated shortly before the beginning of the dark phase with another major activity bout starting just after lights-off (Figs. 1F, 4E). The remaining 23.8% of *A. cahirinus* initiated wheel-running activity shortly after lights-on and continued to run during the light and dark periods, with the majority of their running occurring during the dark period. These individuals only stopped running for a very short period right before lights-on (Fig. 2). In all species, a few animals (16.3% of all animals) had brief, stable bouts of activity during the light period that were consistent from day-to-day and preceded their major bout of activity (Fig. 3).

The phase difference between lights-off and the beginning of activity was longest in *G. pyramidum* ($p < 0.05$) compared with *A. cahirinus*, *D. dasyrus*, and *M. shawi*. There were no significant differences in timing of activity onset between *G. pyramidum* and *G. andersoni*. *A. cahirinus*, *D. dasyurus*, and *M. shawi* also did not differ significantly from each other in their activity start times. The activity offset showed more pronounced intra-specific and inter-specific variability than activity onset. In *G. andersoni*, *D. dasyurus*, and *M. shawi*, most animals (78% of all animals) stopped running after lights-on. In *G. pyramidum* and *A. cahirinus*, the locomotor activity terminated before lights-on. The duration of activity was significantly longest in *M. shawi* followed by *D. dasyurus* compared with *G. pyramidum*, *G. andersoni* and *A. cahirinus* ($p < 0.05$). Alpha was not significantly different among *G. pyramidum*, *G. andersoni* and *A. cahirinus* ($p > 0.05$). In the present study, males and females of all species did not differ significantly from each other in any aspect of wheel-running activity rhythm in long-day conditions (Table 1).

Wheel-running activity in short days

Decreased day length resulted in changes in the wheel-running activity pattern of all species. Furthermore, in 97% of animals that exhibited crepuscular-like activity rhythms in long days, the peak of activity around lights-on disappeared after short-day exposure (Figs. 4C, 4D). Alpha increased under short days for all species (Table 1).

The phase difference between lights-off and the onset of activity was significantly longer in *G. pyramidum* and *G. andersoni* than in the other three species (*A. cahirinus*, *D. dasyurus* and *M. shawi*) in short days ($p < 0.05$). These latter three species did not differ significantly from each other in their activity onsets. Only *G. pyramidum*

Table 1. Measurements of wheel-running activity of five species of desert rodents.

	Acomys Cahirinus		*Gerbillus adersoni*		*Gerbillus pyramidum*		*Dipodillus dasyurus*		*Meriones shawi*	
	M	F	M	F	M	F	M	F	M	F
Onset (LD)	17:15 ± 0.04	17:11 ± 0.03	17:27 ± 0.03	17:21 ± 0.04	17:34 ± 0.03	17:30 ± 0.03	17:09 ± 0.04	17:11 ± 0.03	16:57 ± 0.04	17:10 ± 0.04
Offset (LD)	1:41 ± 0.06	1:54 ± 0.07	3:14 ± 0.06	3:04 ± 0.06	2:32 ± 0.08	2:22 ± 0.04	3:07 ± 0.06	3:38 ± 0.07	3:58 ± 0.1	4:28 ± 0.07
α (LD)	8.41 ± 0.31	8.72 ± 0.32	9.78 ± 0.31	9.57 ± 0.36	8.85 ± 0.44	8.86 ± 0.22	9.98 ± 0.33	10.42 ± 0.34	11.02 ± 0.10	11.29 ± 0.33
Onset (SD)	15:18* ± 0.1	15:12* ± 0.05	15:53 ± 0.06	16:01 ± 0.04	15:58 ± 0.05	15:54 ± 0.05	15:2* ± 0.04	15:2* ± 0.07	15:2* ± 0.09	15:1* ± 0.4
Offset (SD)	2:01* ± 0.11	3:01* ± 0.09	4:20* ± 0.14	4:11* ± 0.12	2:25* ± 0.16	2:01* ± 0.09	4:23* ± 0.09	4:23* ± 0.17	3:45* ± 0.11	4:00* ± 0.26
α (SD)	10.72 ± 0.44	12.07 ± 0.42	12.45 ± 0.59	12.17 ± 0.53	10.43* ± 0.77	10.02 ± 0.46	12.99 ± 0.41	12.91 ± 0.95	12.42* ± 0.09	12.69 *± 0.6
Reentrain Rate	5.25 ± 0.75	4.8 ± 0.86	11 ± 0.95	10.75 ± 0.91	11.67 ± 1.12	11 ± 0.63	6.2 ± 0.79	5.67 ± 1.42	3.67 ± 1.02	2.5 ± 0.84

Data represent mean ± SEM. LD, long days; SD, short days; M, males; F, females; α, alpha; Re-entrain Rate, re-entrainment rate. Means for onset and offset are times of the day. Standard errors and alpha are in hours. Re-entrainment rates are in days. (*) short days versus long days $p < 0.05$.

A. cahirinus

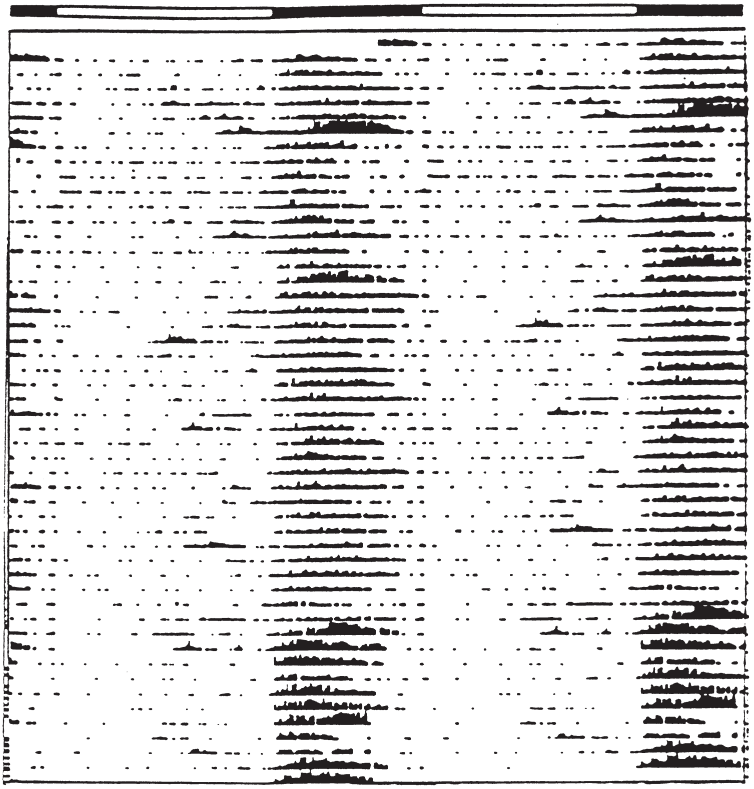

Figure 2. Representative double-plotted activity record for one male individual of *Acomys cahirinus* housed in a 14:10 LD cycle depicting a 40-day period of wheel running. This animal was active during both light and dark periods. Note the onset and offset of activity (see text for details). The black and white bar above the actogram illustrates the LD cycles. Each line represents one 48-h period, and successive days are shown from top to bottom.

and *G. andersoni* significantly increased the phase difference between lights-off and the beginning of activity compared with this measure under the long-day conditions ($p < 0.05$). The activity offsets were much more variable than onsets between and within species in short days. The majority of animals in all species (86.3%), however, stopped running before lights-on. The activity offset relative to lights on was not significantly different in short- versus long-day housed animals. The duration of daily activity increased in short days in all species and was significantly longer than in long days ($p < 0.05$), except for male and female *M. shawi* and *male G. pyramidum*. Differences between species in the duration of activity were less pronounced in short- compared to long-day housed animals. *G. pyramidum* had a significantly shorter α compared with *G. andersoni, D. dasyurus and M. shawi.* Some individuals (8.5%) of

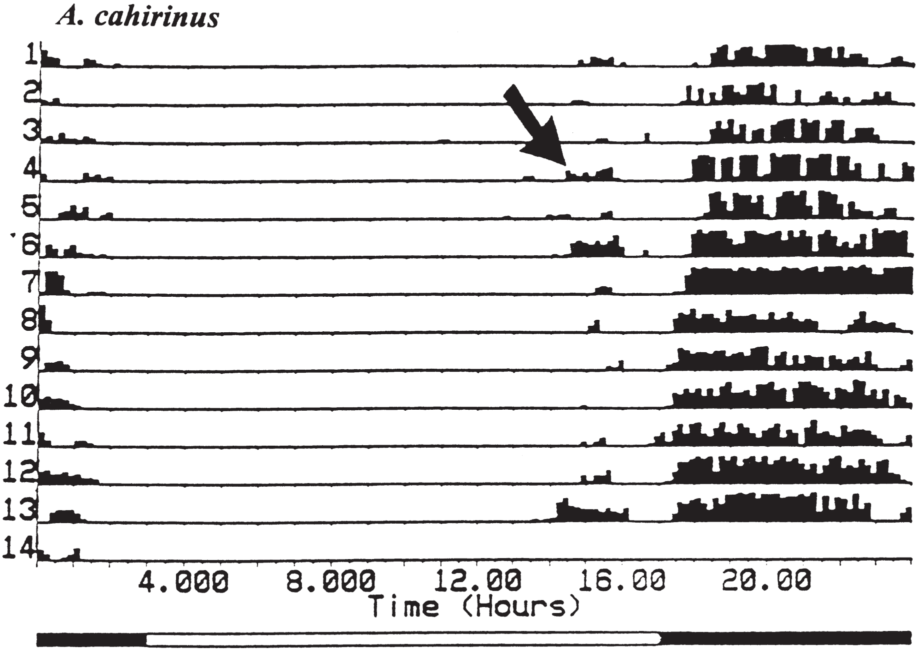

Figure 3. Representative single plotted actrogram of a male *Acomys cahirinus* housed in a 14:10 LD cycle depicting a 10-day period of wheel running. Note the brief bouts of activity (arrow; see text for details). The black and white bar below the actogram represents the LD cycle.

all species exhibited brief bouts of dawn (Fig. 4A) or dusk (Fig. 5) activity that were separated from the main nocturnal activity bout. There were no significant differences between males and females with respect to the patterns of activity or to α in short days (Table 1).

Transfer from long to short days

The transfer of animals from long days to short days accomplished by advancing lights-on and delaying lights-off symmetrically, was followed by a rapid, well-defined re-entrainment to the time of lights-off in all species. The activity onsets of most individuals gradually advanced towards lights-off until they reached a steady state at different species-specific rates (Table 1). Although all animals showed some wheel running activity at lights-off from the first day of the photoperiod shift to the day of complete re-entrainment, these bouts of activity were very short and not prominent in most animals (84.9%, Fig. 4). A few individuals (15.1%), however, showed pronounced abrupt advances of their activity onsets on the first day of the shift (Fig. 4). The re-entrainment patterns of the activity offsets were not as consistent as activity onsets. In general, re-entrainment of activity offsets to short days occurred slowly; in

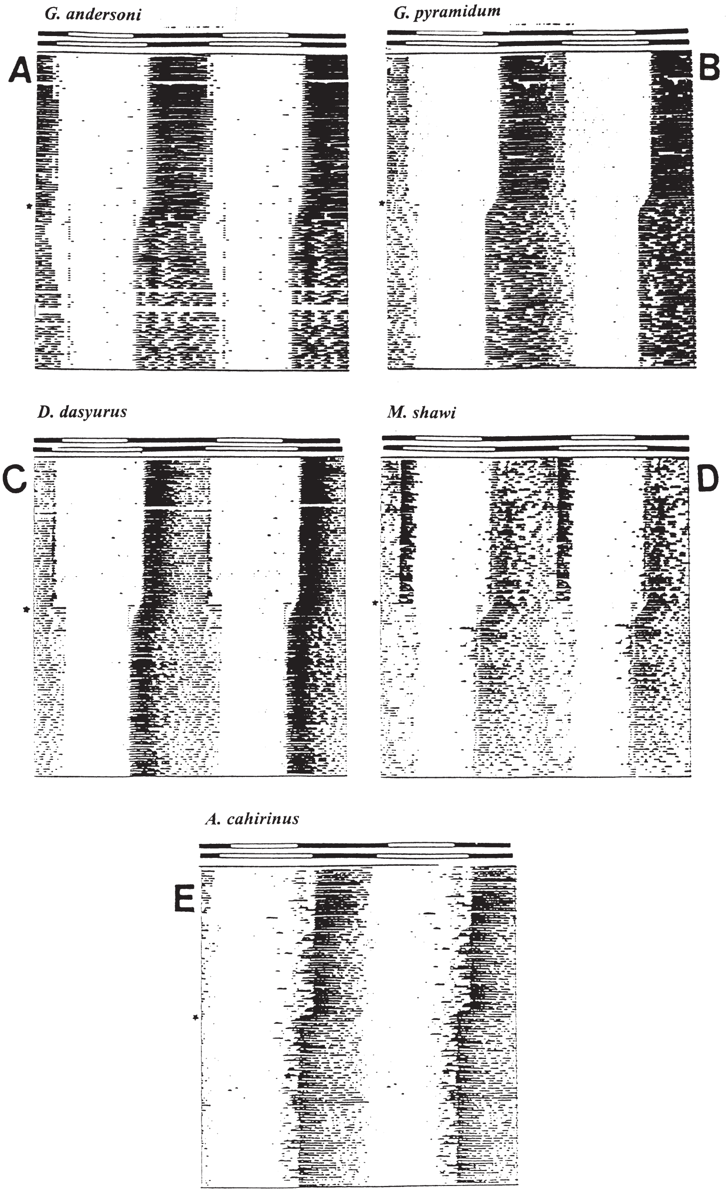

Figure 4. Representative double-plotted activity records for one typical male animal of each species exposed to a shift from LD 14:10 to LD 10:14. The shift was accomplished by deleting the first and last two hours of the light phase. Record shows the last 50 days of the 14:10 LD cycle followed by 70 days of the 10:14 LD cycle. The starting day of the latter is indicated by an asterisk. The blank lines indicate days with missing data. Bars above the figures represent the hours of light and dark exposure. The top bar represents short days while the bottom bar represents long days. (A) *Gerbillus andersoni*; (B) *Gerbillus pyramidum*; (C) *Dipodillus dasyurus*; (D) *Meriones shawi*; (E) *Acomys cahirinus*. Each line represents one 48-h period, and successive days are shown from top to bottom.

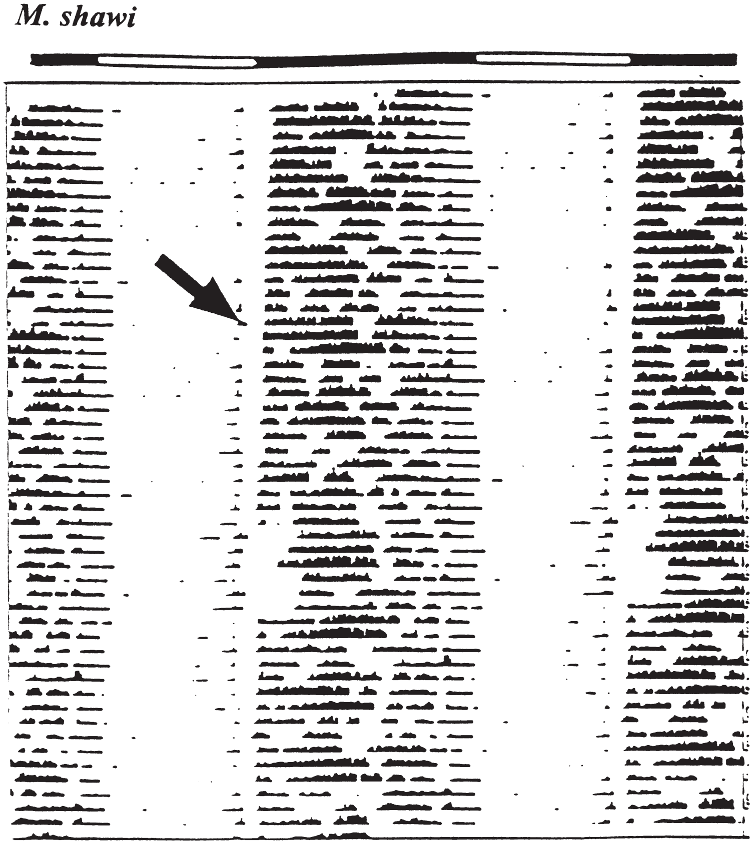

Figure 5. Representative double-plotted activity record for one male individual of *Meriones shawi* exposed to a 10:14 LD cycle. Note the brief bouts of activity (arrow; see text for details). Bar above the figure represents the hours of light and dark exposure. Each line represents one 48-h period, and successive days are shown from top to bottom.

some individuals (7%) it seemed to be still in progress at the last day of the experiment. The re-entrainment rate did not differ significantly among *G. andersoni*, *G. pyramidum* and *D. dasyurus*. There was, however, a significant difference in the re-entrainment rate between these three species and the other two species (*A. cahirinus* and *M. shawi*) in that the re-entrainment rate was faster in *A. cahirinus* and *M. shawi* than in *G. andersoni*, *G. pyramidum* and *D. dasyurus*.

Discussion

All five desert rodent species examined in the present study displayed rhythmic wheel-running activity patterns (i.e., nycthemeral rhythms) in the laboratory. Three of the five species examined (i.e., *G. andersoni*, *G. pyramidum*, and *A. cahirinus*) exhibited patterns of wheel-running that are best characterized as nocturnal, whereas the remaining two species (i.e., *M. shawi* and *D. dasyurus*) displayed primarily nocturnal activity with some bouts of activity present during lights-on, similar to the activity patterns seen in mice. The predominance of nocturnal activity in these species appears logical, given the harsh daytime temperatures experienced by these animals in their desert environments. Given the predominance of nocturnal locomotor activity among most rodent species, however, these results likely reflect a common evolutionary history for rodents rather than a behavioral pattern unique to desert species. For example, restricting activity to the night may have evolved in individuals of many rodent species as an adaptation to avoid predators; nocturnality may be 'enhanced' in desert rodents given the added constraints of harsh daytime temperatures in desert environments, although this idea remains to be tested. Taken together, the results of the present study provide further evidence of primarily nocturnal locomotor activity rhythms by desert rodent species. Specifically, they demonstrate rhythmic patterns of wheel running activity with high activity levels and consistent onsets and offsets that had defined relations with the light-dark cycle.

It is important to note that two of the species studied appeared to display a bimodal pattern of wheel-running activity immediately before their major bouts of nocturnal activity. From an adaptive functional perspective, is possible that the bouts of daytime activity in individuals within *D. dasyurus* and *M. shawi* evolved because of the presence of more favorable climates for daytime foraging behavior in their natural environment compared to the other desert rodent species. Although this idea is speculative, some evidence for it exists. For example, the desert regions that *D. dasyurus* and *M. shawi* inhabit (i.e., Syria, Morocco, Arabian Peninsula) typically experience lower daytime ambient temperatures than the habitats of the other three desert rodent species examined (i.e., Tunisia, Tanzania, North Africa) (Prakash & Ghosh, 1975). Because *D. dasyurus* and *M. shawi* experience less severe fluctuations in ambient temperature, selective pressure could favor some diurnal activity in individuals of *D. dasyurus* and *M. shawi.* Although this idea is intriguing, further studies are required to test it.

In the present study, shortening the photoperiod from a 14:10 to a 10:14 light/dark cycle affected the wheel running patterns of all species. Short-day housed animals also showed species-related differences in the rate of re-entrainment of the activity rhythm to the light-dark cycle. These differences may reflect the variability in the abilities of different circadian clocks to be phase shifted following a shift in the synchronizing light-dark cycle. From an ecological perspective, increasing the duration of nighttime activity in short days can be considered adaptive in that allows for increased foraging during times of the year when environmental conditions in the desert are more conducive to increased activity (i.e., winter). For example, animals that increase their foraging activity during optimal times of the year increase their chances for survival and thus, increase their reproductive fitness.

The diurnal bout of activity in animals displaying bimodal activity patterns mostly disappeared under short days. These results do not support the previous findings in which lengthening of the dark period results in an increase in the temporal relation between the two major activity bouts of bimodal activity patterns (Aschoff, 1966). These data also are in contrast to the bimodal activity pattern of rats (Siebert & Wollnik, 1993), where lengthening of the photoperiod does not affect the temporal relationship of the two major activity bouts. The reason for this discrepancy is unknown. This difference could be due to the direct masking effect of light (i.e., light influences the behavior itself, rather than the circadian pacemaker that is driving it). Alternatively, the difference also may be due to the ability of desert rodents to alter their locomotor activity rhythms across the seasons (Ghosh, 1975). For example, some desert species that show crepuscular activity rhythms during the summer exhibit a more diurnal rhythm in the winter (Ghosh, 1975; Prakash, 1962). In the present study, the species that had bimodal, crepuscular-like rhythms in long days had nocturnal patterns of wheel-running in short days.

There were no differences between males and females in their rhythmic locomotor activity patterns in any of the species examined, although there is some evidence of sex differences in rhythmic behavior patterns in other species. For example, male, but not female, gerbils display wheel-running activity during the light period of 12:12 light-dark cycle. Female gerbils, however, run more than males (Roper, 1976). Female Syrian hamsters also are more active than males (Davis et al., 1983). Under LD (14:10), females begin their activity earlier and show greater variability in the timing of activity than do males (Davis et al., 1983). Although the precise reasons for the lack of a sex difference in wheel-running activity in the present study remain unknown, these results likely reflect species differences in activity patterns.

G. andersoni and *G. pyramidum* were similar in most parameters of wheel running, including the duration of activity in long days, the activity onsets and offsets in both long and short days, as well as the phase difference between lights-off and the activity onset in both day lengths. As expected, these results suggest the presence of common selective pressures on the evolution of activity patterns in species within the same genus.

In summary, the present study provides a much needed characterization of wheel running activity patterns in five species of desert rodents. These patterns of activity allow individuals within these species to time their behavior to optimal times of the day and season in order to maximize their survival. In addition, changes in the photoperiod from long days to short days increased the duration of activity in all five species. Increases in the duration of activity when animals are switched from long to short days likely reflects the fact that environmental conditions in short ‘winter-like’ days are more conducive to extended locomotor activity. Collectively, the results of the present study suggest that activity patterns may have evolved in individuals of these species to cope with fluctations in environmental conditions (i.e., ambient temperature; predation pressures). The present study did not address the origin of the rhythmic wheel running in these species. Whether these activity patterns are circadian-based (i.e, independent of environmental regulation) or simply behavioral responses to fluctuating environmental conditions requires future experiments with animals housed under constant environmental conditions.

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