

Notes and Comments

On the Use of the Time Axis for Ecological Separation: Diel Rhythms as an Evolutionary Constraint

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Temporal partitioning as a mechanism of coexistence among competitors has seldom been explored and is considered uncommon (Schoener 1986). Understanding ecological and evolutionary plasticity in use of the temporal niche axis is significant for assessing the potential for temporal partitioning and may be key to understanding the relative rarity of this phenomenon.

Daily rhythms in mammalian physiology, hormone concentrations, biochemistry, and behavior are driven by an internal circadian clock that is entrained to the predictable 24-h change in light intensity (Heldmaier et al. 1989; Refinetti et al. 1992; Smith et al. 1998). Entrainment to this overriding cue ("zeitgeber") allows mammals to choose the right time for a given response or activity without being easily misled by minor environmental disturbances (Aronson et al. 1993). Thus, a degree of rigidity to environmental nonphotic stimuli is built into the circadian system. However, under laboratory conditions, small mammals can be forced to shift their locomotor activity patterns by nonphotic stimuli (Mistlberger 1991; Cambras et al. 1993; Challet et al. 1997; Brinkhof et al. 1998), indicating that activity is not tightly controlled by the circadian clock

(Mrosovsky 1999). As locomotor activity in mammals increases their body temperatures in proportion to the severity of activity (Minors et al. 1996), forced shifts of activity patterns also affect overt temperature rhythms. Whether a real shift in endogenous rhythmicity of activity and body temperatures is achieved with nonphotic stimulation, or whether the perceived shift is merely a masking effect, is still subject to debate (Edgar and Dement 1991; Edgar et al. 1991; Mrosovsky 1995; Meerlo and Daan 1998). Masking is defined as "any process that distorts the original output from the internal clock whether this originates from inside or outside the body" (Minors and Waterhouse 1989, p. 30). As soon as the masking effect is removed, the underlying circadian rhythm is revealed (Waterhouse et al. 1996).

Two ecologically similar spiny mouse species coexisting in rocky deserts of the Middle East (Shkolnik 1971; Kronfeld et al. 1996) allow an excellent test of the effect of competitively induced temporal partitioning on diel rhythms at the evolutionary scale and may provide insight into ecological aspects as well. The nocturnal common spiny mouse (*Acomys cahirinus*; mean body mass = 34 g) and the diurnal golden spiny mouse (*Acomys russatus*; mean body mass = 43 g) overlap in their biology (Shargal et al. 2000), diet (Kronfeld-Schor and Dayan 1999), and foraging microhabitat use (Jones et al. 2001). A key study demonstrated that when *A. cahirinus* is removed from a shared habitat, *A. russatus* shifts its activity time and becomes nocturnal, implying that the two species compete (Shkolnik 1971).

Generations of selection for diurnal activity in *A. russatus* have actually resulted in some adaptations, such as dark skin pigmentation and a high concentration of ascorbic acid in its eyes (Koskelo et al. 1989). On the other hand, *A. russatus* retains the rod-based retina typical of nocturnal mammals (Kronfeld-Schor et al. 2001a), and the potential for nonshivering thermogenesis is similar in both species and appears evolutionarily constrained, although *A. cahirinus* is exposed to much colder temperatures in winter (Kronfeld-Schor et al. 2000) and spends

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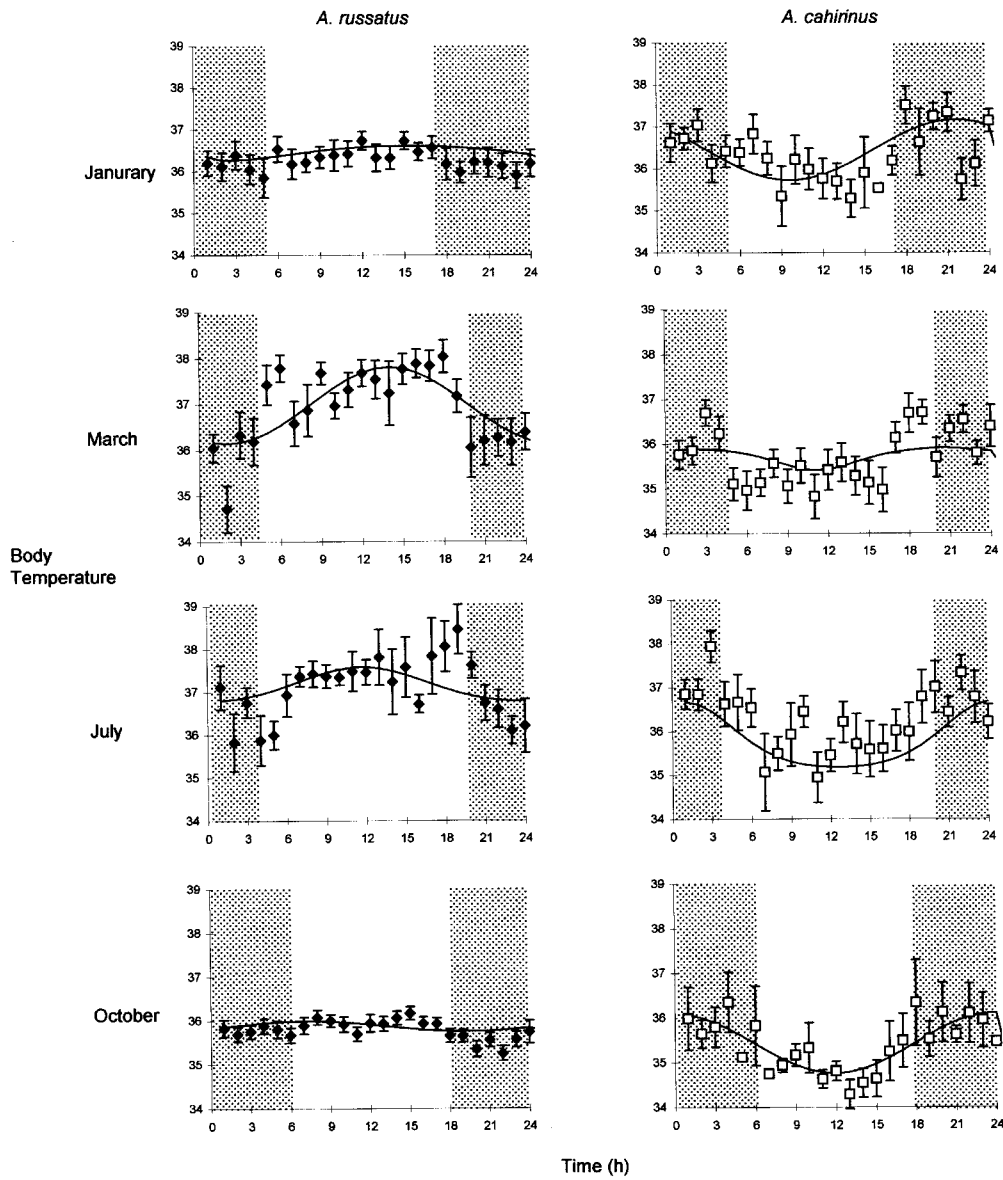


Figure 1: Seasonal body temperature ($^{\circ}\text{C}$) rhythms of *Acomys cahirinus* and *Acomys russatus* at Ein Gedi. Data points are average \pm SE. The Fourier line depicts the 24-h cosine function found using the Fourier analysis. Dark blocks represent the dark hours.

significantly more energy than its congener, probably on thermoregulation (Kronfeld-Schor et al. 2001b). Clearly, some traits are more constrained than others.

We asked whether the adaptations of *A. russatus* to a diurnal pattern of life include full entrainment of the underlying circadian rhythms. We studied the daily activity and body temperature rhythms of *A. cahirinus* and *A. russatus* in the field during all seasons and those of field-captured individuals under controlled laboratory conditions. If a full entrainment to diurnality of the

underlying circadian rhythms of *A. russatus* occurs in the free-living population, when field-captured individuals are transferred to controlled laboratory conditions in the absence of *A. cahirinus*, there will be a gradual phase shift of body temperature and activity rhythms into nocturnality. Otherwise, an abrupt change of body temperature and activity rhythms into nocturnality will support the hypothesis that the perceived diurnal activity and body temperatures in the field merely result from a masking effect.

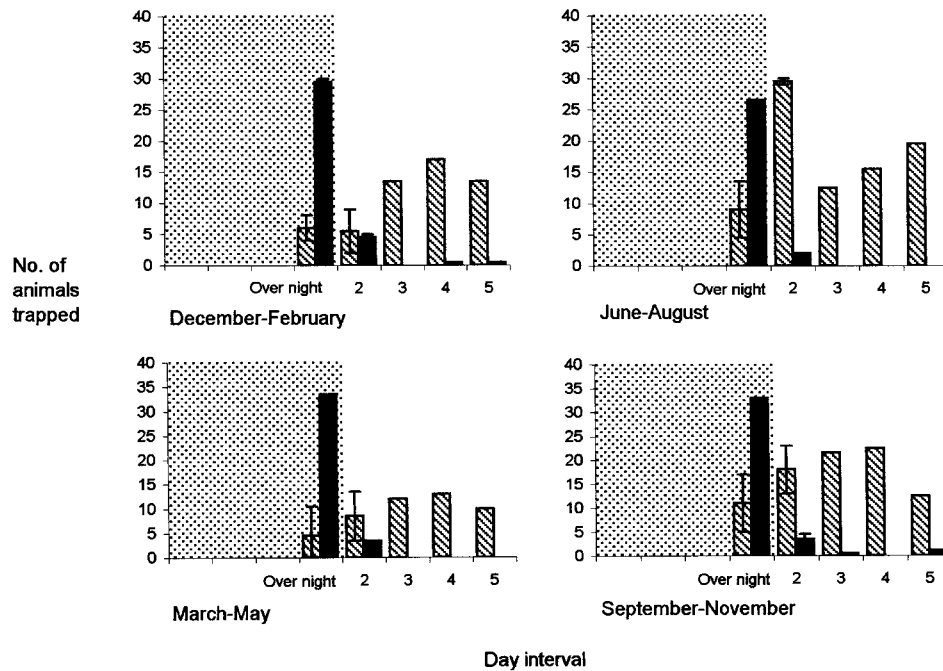


Figure 2: The number of individuals captured at each quarter of the day and overnight during each period of three consecutive months, demonstrating seasonal trapping patterns of *Acomys cahirinus* (black columns) and *Acomys russatus* (hatched columns) at Ein Gedi. Traps were checked at four equal intervals of daylight (length of the interval is determined by the length of photoperiod). Values are averages for 2 yr \pm SE. Dark blocks represent the dark hours.

Methods

We carried out field research in two areas about 2 km apart at Ein Gedi, near the Dead Sea. Spiny mice were trapped in a 5,000-sq-m grid. We set 200 Sherman box traps in the first year and 100 in the second (December 1993–November 1995). Traps were set every month for three consecutive days and nights and were checked at four equal intervals between sunrise and sunset.

Body temperatures were recorded seasonally (1995) with FM transmitters (Oekokart, Munich) that were implanted into the abdominal cavities of the mice (Elvert et al. 1999). We carried out a Fourier analysis (single-series spectrum analysis; Statistica [Statsoft 1984–1996]) of the body temperature data (published but not analyzed by Elvert et al. 1999). Numbers of implanted *Acomys cahirinus* and *Acomys russatus* individuals were March: 2, 2; July: 2, 2; October: 5, 1; and January: 2, 2; respectively. The transmitters also recorded the activity rhythm of *A. russatus* during October ($n = 5$), and we analyzed these data as well. The significance of the 24-h period was determined according to Horne and Baliunas (1986).

We trapped 24 *A. cahirinus* and 24 *A. russatus*, six of each species every 3 mo (for 1 yr) near our study sites and removed them immediately to a controlled room at

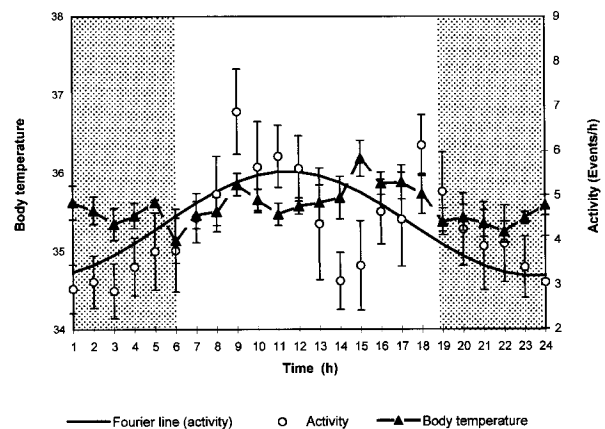


Figure 3: Body temperature ($^{\circ}$ C) and activity rhythms of *Acomys russatus* at Ein Gedi (October). Data points are average \pm SE. The Fourier line depicts the 24-h cosine function found for the activity data using the Fourier analysis (no significant 24-h rhythm of body temperature was found). Dark blocks represent the dark hours.

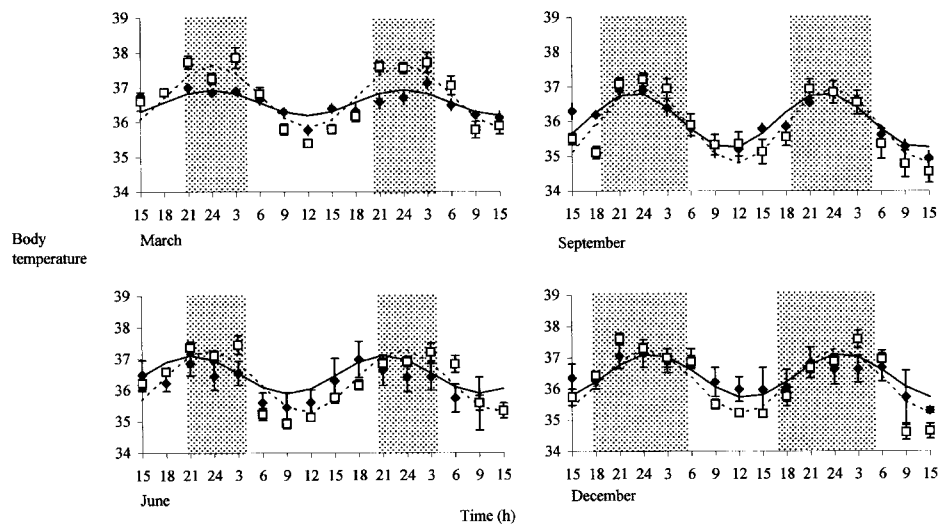


Figure 4: Seasonal body temperature ($^{\circ}\text{C}$) rhythms of *Acomys cahirinus* (open squares) and *Acomys russatus* (black diamonds) directly upon removal from the field, under controlled laboratory conditions. The lines depict the 24-h cosine function found using the Fourier analysis. Dark blocks represent the dark hours.

28°C with natural photoperiod. During the following 2 d and nights, we took their rectal temperatures at 3-h intervals with a Wescor digital TC thermometer, a method widely used in chronobiological studies (Minors et al. 1996).

The activity patterns of five individuals of *A. russatus* in June 1995 were monitored for 7 d and nights, directly after having trapped and removed them from the field (as in Friedman et al. 1997). Activity was measured by an infrared ray directed at a running wheel in each cage, in a position crossed by running mice. Every beam break was recorded for 5 min. The result was a series of numbers representing the total level of activity of each mouse per hour around the clock. We performed a Fourier (single-series spectrum) analysis on the results (Statistica [Statsoft 1984–1996]). The significance of the 24-h period was determined according to Horne and Baliunas (1986). The activity during the light versus the dark periods was tested using a Student *t*-test.

Results

Fourier analyses of body temperature data in free-living individuals of *Acomys cahirinus* in the field revealed a significant ($P < .001$) 24-h rhythm in all seasons, with acrophases (peaks) during the nighttime (fig. 1). These results accord with the observed nocturnal activity pattern of this species (ca. 90% of *A. cahirinus* individuals were trapped during nighttime; fig. 2). In contrast, *Acomys russatus* were active during daytime (ca. 90% of *A. russatus*

individuals were trapped during daytime; fig. 2), and a Fourier analysis revealed a significant 24-h body temperature rhythm, with an acrophase during daytime in January, March, and July. No significant rhythm in body temperature was observed during October ($P > .05$; fig. 1). Counterpart measurements of activity rhythms of these same thermally arrhythmic individuals in October revealed a significant ($P < .001$) diurnal 24-h activity rhythm, which was compatible with the trapping data (fig. 3).

In contrast to the diurnal activity in the field, body temperatures of *A. russatus* individuals exhibited a typical nocturnal ($P < .001$) 24-h rhythm immediately after capture in all seasons, as did those of *A. cahirinus* (fig. 4), indicating abrupt reversal into nocturnality. When the activity patterns of five *A. russatus* individuals trapped in June were assessed immediately after trapping (fig. 5), it was found that three of the five displayed a significant ($P < .001$) 24-h activity rhythm with an acrophase during the dark hours, while the other two were active both during the light and the dark periods. A *t*-test comparing total activity level during the dark and light periods revealed that two of the five *A. russatus* were significantly more active during the dark hours ($P < .001$) and that the other three were active throughout the day. None of the animals showed a diurnal pattern.

Discussion

Understanding ecological and evolutionary-level plasticity of endogenous rhythmicity is crucial for gaining insight

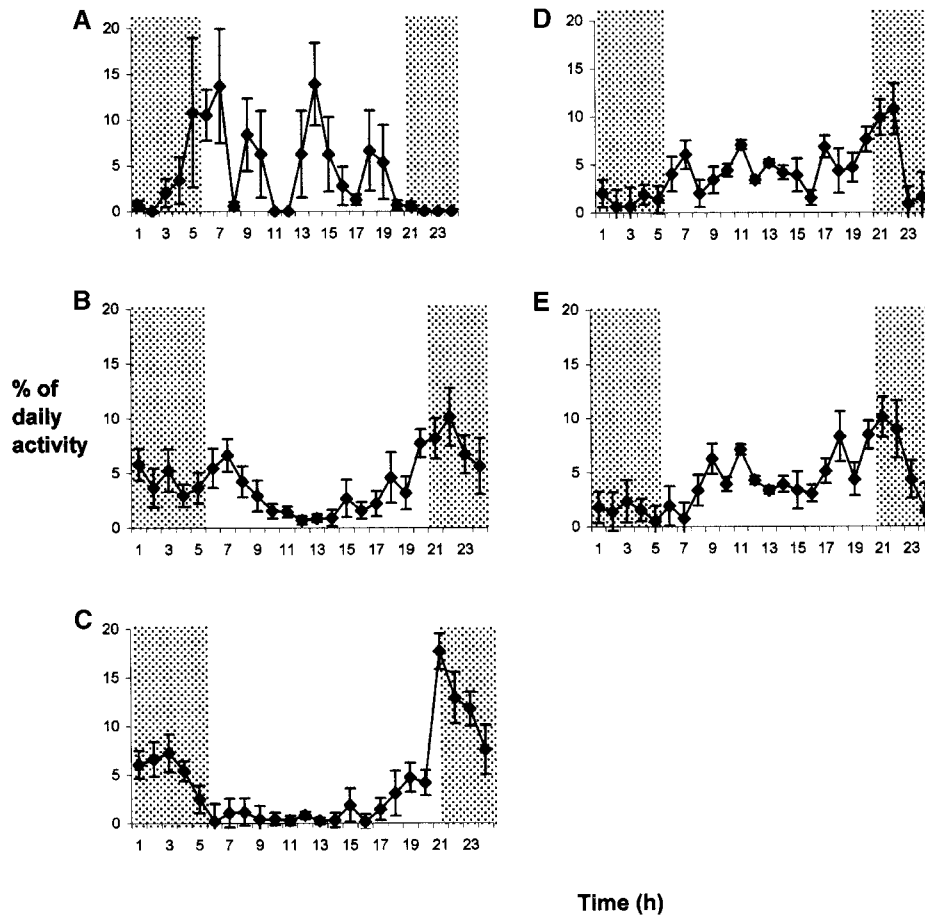


Figure 5: Activity patterns of five *Acomys russatus* individuals directly after trapping (the average rhythm for the 7 d). Data points are average \pm SE. Dark blocks represent the dark hours.

into the significance of the time niche axis for interspecific interactions. We studied this plasticity in an ecological system in which one species forces its congener into a diametrically opposite activity pattern. This “natural experiment” points to the evolutionary rigidity of internal rhythmicity in the face of environmental cues. *Acomys russatus* have been diurnally active at least since the early 1960s (Shkolnik 1971), but in light of the biogeographic history of Israel (e.g., Tchernov 1988), the time scale of their coexistence with *Acomys cahirinus* is probably millennia. In the field, *A. cahirinus* are indeed nocturnally active, while *A. russatus* are diurnally active, and their temperature rhythms are generally compatible with these activity patterns. However, immediately upon removal to the laboratory, individuals of both species exhibited typical nocturnal temperature rhythms, and *A. russatus* individuals displayed nocturnal activity rhythms, or were active both during the light and dark periods, but did not show

a diurnal activity pattern. Immediate inversion of the phase preference, without evidence of a phase shift that would be expected in the case of true entrainment (Deacon and Arendt 1996), indicates that the diurnal activity of *A. russatus* in the field, coupled with the overt temperature rhythms, are merely a masking effect. Thus, numerous generations of selection for diurnal activity in golden spiny mice have not caused a shift in their underlying rhythmicity. The diel rhythms that normally enable mammals to respond to environmental stimuli in an appropriate manner (e.g., Rusak 1981; Ticher et al. 1995) appear to lack the plasticity required to enable *A. russatus* to adapt to community-level interactions, even at this evolutionary scale.

The role of time as a niche axis has not been frequently addressed and remains controversial (e.g., Jaksic 1982; Schoener 1986). There are few published examples of mammals that invert their activity patterns as a result of

interspecific interactions (including the effect of humans) into the opposite activity phase (Wiens et al. 1986; Fenn and MacDonald 1995). Moreover, congeneric and even confamilial species are generally active during the same part of the diel cycle (Daan 1981). Most previous studies that suggest competitively induced temporal segregation deal with temporal shifts within the normal nocturnal or diurnal activity time (e.g., Kenagy 1973; Ziv et al. 1993). We suggest that, although the time axis may well be significant for ecological separation among competitors and between predators and their prey, the evolution of temporal partitioning may be severely constrained. Research at the interface between biological rhythms, animal physiology, and ecological-evolutionary selective forces (see also Marques and Waterhouse 1994) may provide valuable insight into the evolution of activity patterns and of temporal partitioning.

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