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Circadian Rhythms of Locomotor Activity in Solitary and Social Species of African Mole-Rats (Family: Bathyergidae)

Maria K. Oosthuizen,^{*,1} Howard M. Cooper,[†] and Nigel C. Bennett^{*}

^{*}Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa, [†]INSERM U371, 18 Avenue du Doyen Lépine, Bron. France

Abstract Mole-rats are strictly subterranean and hardly, if ever, come into contact with external light. As a result, their classical visual system is severely regressed and the circadian system proportionally expanded. The family Bathyergidae presents a unique opportunity to study the circadian system in the absence of the classical visual system in a range of species. Daily patterns of activity were studied in the laboratory under constant temperature but variable lighting regimes in individually housed animals from 3 species of mole-rat exhibiting markedly different degrees of sociality. All 3 species possessed individuals that exhibited endogenous circadian rhythms under constant darkness that entrained to a light-dark cycle. In the solitary species, *Georychus capensis*, 9 animals exhibited greater activity during the dark phase of the light cycle, while 2 individuals expressed more activity in the light phase of the light cycle. In the social, *Cryptomys hottentotus pretoriae*, 5 animals displayed the majority of their activity during the dark phase of the light cycle and the remaining 2 exhibited more activity during the light phase of the light cycle. Finally in the eusocial *Cryptomys damarensis*, 6 animals displayed more activity during the light phase of the light cycle, and the other 2 animals displayed more activity during the dark phase of the light cycle. Since all three mole-rat species are able to entrain their locomotor activity to an external light source, light must reach the SCN, suggesting a functional circadian clock. In comparison to the solitary species, the 2 social species display a markedly poorer response to light in all aspects. Thus, in parallel with the sociality continuum, there exists a continuum of sensitivity of the circadian clock to light.

Key words circadian, rhythm, locomotor, activity, entrainment, mole-rat, Bathyergidae

Circadian rhythms are present in all mammals, and a wide variety of biological processes undergo rhythmic daily changes (Reuss, 1996). Although an endogenous circadian timing system generates circadian rhythms, the rhythms are influenced by environmental cues. These periodic changes act as synchronizing agents to which organisms react (Roenneberg and Foster, 1997). Circadian rhythms are consequently

proposed to have developed as a selective adaptation allowing animals to anticipate predictable changes in the environment associated with the day-night cycle. Animals are thus able to alter their activity over time and space to optimize their survival.

The different temporal niches that animals utilize influence the amount of light that they are subsequently exposed to. African mole-rats are an extreme

1. To whom all correspondence should be addressed: Maria Oosthuizen, Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa; e-mail: moosthuizen@zoology.up.ac.za.

example of animals that are seldom, if ever, exposed to external light, as they are subterranean and rarely emerge above ground (Bennett and Faulkes, 2000).

Mole-rats show a number of morphological and physiological adaptations to underground life, including a severely regressed visual system. The eye and all the brain structures associated with vision are severely degenerated (Cooper et al., 1993).

However, the bilateral projection to the circadian system seems to be fully conserved, and retinofugal fibers to the suprachiasmatic nucleus and the lateral geniculate nucleus can clearly be demonstrated using anatomical tracing techniques (Bronchti et al., 1989a, 1989b). Over the course of evolution, the visual system of mole-rats has undergone both degenerative and progressive adaptations (Cooper et al., 1993).

Although the circadian systems of other rodents have been extensively studied, the knowledge on mole-rats is less extensive. Early investigators reported that these animals were insensitive to light (Eloff, 1958; Haim et al., 1983). However, more recently, a number of mole-rat species have been investigated, all of which have revealed evidence of light entrainment and/or rhythmicity to varying degrees (Bennett, 1992; Lovegrove et al., 1993; Lovegrove and Papenfus, 1995; Goldman et al., 1997; Tobler et al., 1998; Riccio and Goldman, 2000). Most of these studies have investigated locomotor activity rhythms and found evidence of entrainment to light cycles, although the degree of entrainment varies according to the species.

The family Bathyergidae exhibits a continuum of sociality ranging from strictly solitary (e.g., *Georchus capensis*) to eusocial (e.g., *Cryptomys damarensis*). Three mole-rat species with different life history characteristics and varying degrees of sociality (from strictly solitary to eusocial) were investigated enabling a comparison of differences that may occur across this sociality continuum. The subjects of this investigation were the solitary Cape mole-rat, *Georchus capensis*, the social highveld mole-rat, *Cryptomys hottentotus pretoriae*, and the eusocial Damaraland mole-rat, *Cryptomys damarensis*. The Cape mole-rat occurs in mesic areas along the southern coasts of the western Cape province. This species is a seasonal breeder producing offspring in spring (August-September) at the end of the rainy season and is highly aggressive toward conspecifics outside the breeding season (Bennett and Jarvis, 1988a). The highveld mole-rat occurs in the highlands of South Africa, characterized by hot, moist summers and cold, dry winters and have colony sizes

ranging from 2 to 11 animals. Reproduction is confined to a single breeding pair within a colony; this species reproduces in summer, during the rainy season (Janse van Rensburg et al., 2002). The Damaraland mole-rat is widely distributed in arid areas of northern South Africa, central and northern Namibia, and Botswana and Zimbabwe. This species is one of two known eusocial mole-rat species, with up to 41 individuals in a colony (Jarvis and Bennett, 1993). Each colony composes a reproductive female with one or two male consorts, and colonies exhibit a work-related secondary division of labor. It breeds throughout the year and has the potential to produce four litters per annum (Bennett and Jarvis, 1988b).

MATERIAL AND METHODS

Animal Maintenance

Experimental animals were wild caught, and individuals from *C. h. pretoriae* and *C. damarensis* were obtained from various colonies. Animals were all adult, and age was unknown since they were wild captured. Animals were housed singly in cages (60 × 30 × 30 cm), which were provisioned with wood shavings. The cages were fitted with Perspex divisions to create topside-open tunnels and included a 15 × 15 cm closed nest box. Cages were cleaned once every 2 weeks during light cycles and once a month during DD cycles. Animals were fed ad libitum on chopped sweet potatoes, carrots, gem squash, and apples once a day at random times. The general health of the animals was monitored during feeding and cleaning times. Animals were maintained in temperature- and light-controlled chambers at 26 °C.

Activity Recording

Three cages were placed on energized receivers covering the whole surface of the cage, to receive signals from implanted emitters within the mole-rats. Four cages were fitted with running wheels and magnetic switches. Four cages were equipped with infrared detectors placed over the middle of the cage such that the range covered the whole width of the cage and the animal had to pass underneath to reach either the food or nesting chamber. Activity was recorded by a Minimitter recording system. Once a minute, the collective activity during that period was recorded on a computer installed outside the climate room.

Experimental Protocol

Animals were maintained on a 12L:12D light cycle for approximately 8 weeks prior to the commencement of experiments. Temperature was maintained at 26 °C during all the experimental phases. Emitters were implanted 12 weeks prior to recordings.

Seven female *Georychus capensis* (3 emitters, 4 infrared (IR) captors) were maintained on a 12L:12D cycle (0800-2000 L: 2000-0800 D) for approximately 10 days, until daily patterns of activity were observed. The 1st phase investigated whether this species was able to entrain to a light cycle. Once the animals were entrained to the light cycle, the light regime was changed to constant darkness (DD). Total darkness was maintained for approximately 14 days to detect the presence of endogenous rhythms. The 3rd phase of the experiment involved re-entraining the animals to the previous 12L:12D light cycle for 14 days. One mole-rat died at the end of this phase and was replaced. During this stage, 4 extra mole-rats (4 females) were coupled to the system, with running wheels. These animals were subjected to all the other experimental conditions. The light cycle was then shifted 6 h forward (0200-1400 L:1400-0200 D), while still maintaining 12 h light and 12 h darkness. Animals were kept on this cycle for approximately a month to observe any shifts to the new light cycle. The next step was a backward shift of 9 h in the light cycle, simultaneously shortening the night part of the cycle from 12 to 8 h (0500-2100 L:2100-0500 D). After 1 month, the cycle was inverted to produce an 8-h light and a 16-h dark phase (2100-0500 L:0500-2100 D).

Seven *Cryptomys hottentotus pretoriae* (1 emitter, 2 wheels, 4 IR captors) were recorded on a 12L:12D cycle (0700-1900 L:1900-0700 D) for a month to allow entrainment of activity rhythms. When the mole-rats were entrained to the 12L:12D cycle, the light cycle was changed to total darkness (DD). The animals were kept on this cycle for 1 month to allow expression of the endogenous rhythm.

After DD, animals were re-entrained to the previous LD cycle for a month, thereafter followed by an inverse of the LD cycle (1900-0700 L:0700-1900 D). This cycle was maintained for approximately 1 month. The last part of the experiment involved animals being maintained in constant light (LL) for 1 month.

Eight *Cryptomys damarensis* (2 emitter, 2 wheels, 4 IR captors) were recorded on a 12L:12D (0700-1900 L:1900-0700 D) cycle for a month until clear rhythms could be seen. When the mole-rats were entrained to

the 12L:12D cycle, the light cycle was changed to total darkness (DD). The animals were then kept in this cycle for 1 month.

After DD, animals were re-entrained to the previous LD cycle for a month, whereafter the light cycle was inverted (1900-0700 L:0700-1900 D). This cycle was maintained for approximately 1 month. The last part of the experiment involved animals being maintained in constant light (LL) for 1 month.

Analysis

Recordings from the activity captors were fed directly into the computer, and data were processed to a suitable format for use in other programs. Actiwatch and Clocklab software were employed to analyze behavioral patterns and generate actograms. Actograms were double-plotted with consecutive days in a downward sequence. The period of the endogenous rhythm was obtained where possible (mean \pm SD), using both the Clocklab program and a *tau* cursor line by means of the eye-fit method. The percentage activity during a certain phase of the light cycle was calculated for 12L:12D, 16L:8D, and 8L:16D where applicable. Microsoft Excel macro programs were used for this purpose.

RESULTS

Georychus capensis

Six of the 11 mole-rats (1 emitters, 2 IR captors, 3 wheels) showed clear entrainment to a specific phase from the 1st cycle that was recorded for the specific animal (Fig. 1A). The other 5 animals (2 emitters, 2 IR captors, 1 wheel) displayed weak or no noticeable entrainment to light cycles (Fig. 1B).

Of the 7 animals subjected to the first LD cycle, 3 animals displayed the majority of their activity during the light phase of the cycle (3 IR captors), while 4 animals showed more activity during the dark phase of the cycle (3 emitters, 1 IR captor).

When placed in DD, 4 animals showed some degree of free-running rhythms (1 emitter, 3 IR captors). The period of the rhythms was generally around 24 h ($\tau = 24.1 \pm 0.48$, $n = 4$). One animal showed clear drift (emitter) with a τ slightly shorter than 24 h ($\tau = 23.43$), but the rhythms in the other animals were close to or slightly longer than 24 h long.

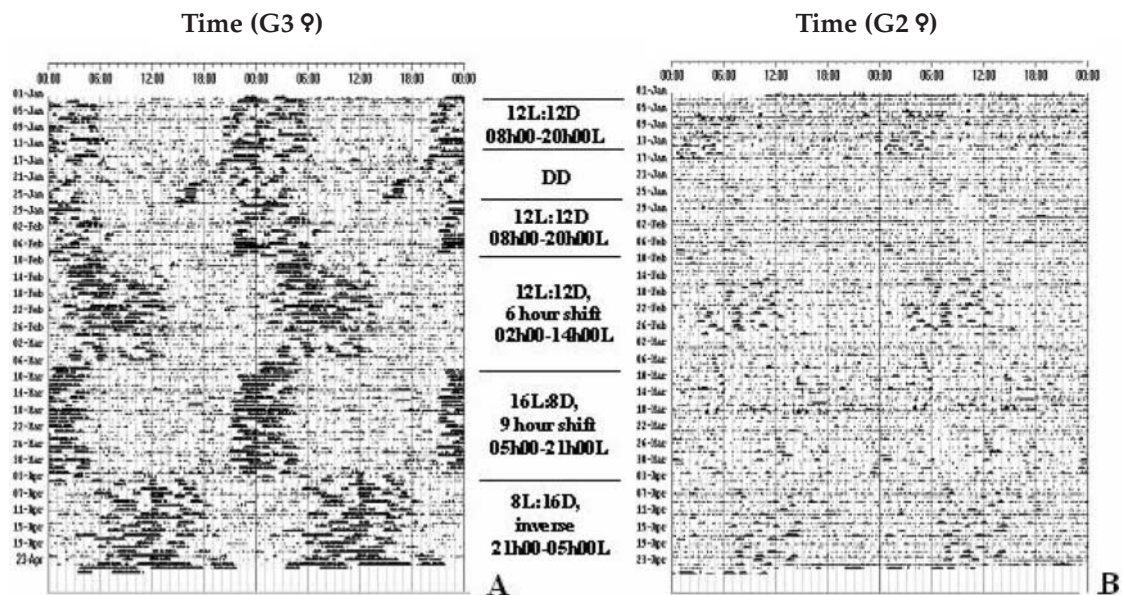


Figure 1. *Georychus capensis*: A illustrates an actogram of a Cape mole-rat with clear entrainment (emitter) while entrainment was not obvious in B (infrared captor).

There was no relation between amount of activity displayed during a certain phase of the 24-h cycle during the previous cycle, as 2 animals had more activity during the day and 2 during the night during the previous cycle. The remainder of the animals displayed arrhythmic behavior (2 emitters, 1 IR captor).

During the re-entrainment LD cycle, the mole-rats exhibited the same preference for the phase of activity as during the 1st light cycle.

Following a 6-h forward shift in the light cycle, 1 animal altered its activity to the dark phase, while the rest of the animals changed the majority of their activity according to the shift. Of the 4 running-wheel animals, 2 did not use the running wheel immediately, and of the remaining 2, 1 was active during the dark portion of the LD cycle and the other during the light phase.

A 9-h backward shift in the light cycle, simultaneously lengthening the light phase to 16L:8D, resulted in adjustments of the length of active time according to the change. Animals with a preference for nocturnal activity shortened their active time according to the length of the dark phase, and vice versa in the animals that were active during the day. Two mole-rats continued to display more diurnal activity (1 IR captor, 1 wheel), while all the rest of the animals were more active during the dark phase of the cycle.

A similar pattern was observed when the 16L:8D cycle was inverted. One of the animals that displayed

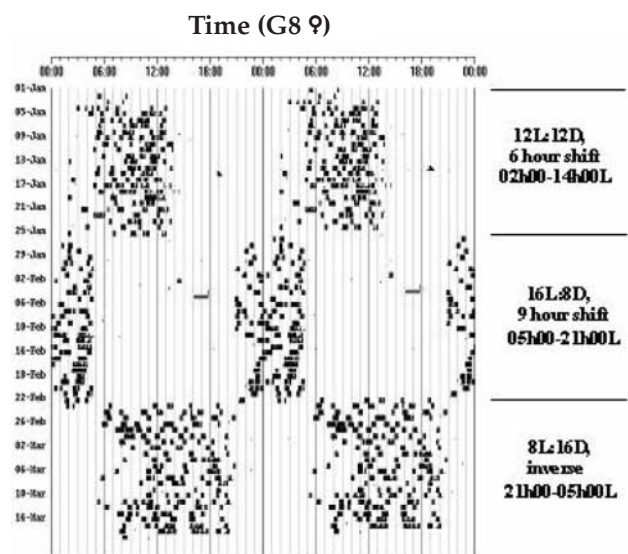


Figure 2. *Georychus capensis*: This actogram represents an animal that shifted its activity according to shifts in the light cycle, as well as adjusting the duration of activity to light cycles of different durations (wheel recording).

activity during the day (wheel) modified its activity to exhibit the greater part of the activity during the dark phase (Fig. 2).

Large variations were noted in the proportion of activity exhibited during the light and dark part of light cycles and the amount of time it took for animals to re-entrain to a new light cycle, but the majority of

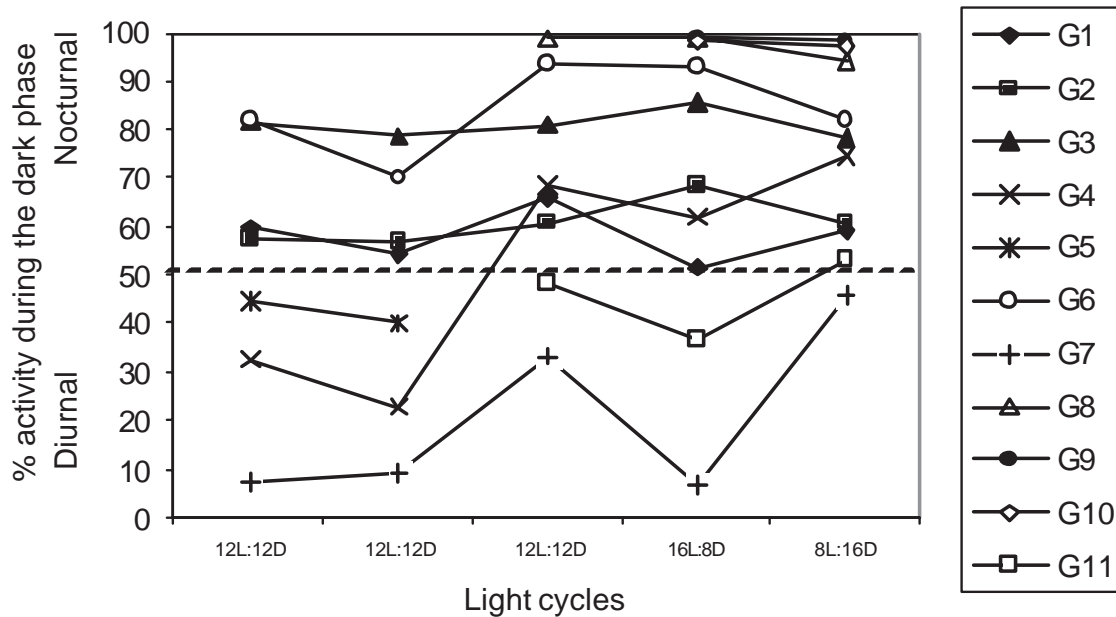


Figure 3. *Georychus capensis*: This graph illustrates the percentage of activity that each animal exhibited during the day or night phase of each of the LD schedules. G1-3 = emitters, G4-7 = infrared captors, G8-11 = wheels.

the Cape mole-rats appear to have a preference for activity during the dark phase of the light cycle (see Fig. 3).

Cryptomys hottentotus pretoriae

Three of the 7 mole-rats (2 IR captors, 1 wheel) displayed clear entrainment according to a specific phase during the 1st recording period (Fig. 4). The remainder of the animals exhibited weak or no apparent entrainment (1 emitter, 2 IR captors, 1 wheel).

During the 1st 12L:12D cycle, 5 of the 7 highveld mole-rats exhibited more activity during the dark phase of the light cycle (4 IR captors, 1 wheel), while 2 animals displayed the majority of their activity during the day (1 emitter, 1 wheel). The 2 mole-rats that exhibited more activity during the light phase had values close to 50% activity in either phase of the cycle. One animal displayed 2 bouts of activity (IR captor), one toward the end of the light phase and another toward the end of the dark phase of the LD cycles. The diurnal activity bout seemed to disappear under constant darkness conditions, leaving only the subjective night bout during this period, but the diurnal bout reappeared as soon as the animals were placed under an LD cycle again.

Following the LD cycle, animals were subjected to DD, where 5 animals displayed noticeable endoge-

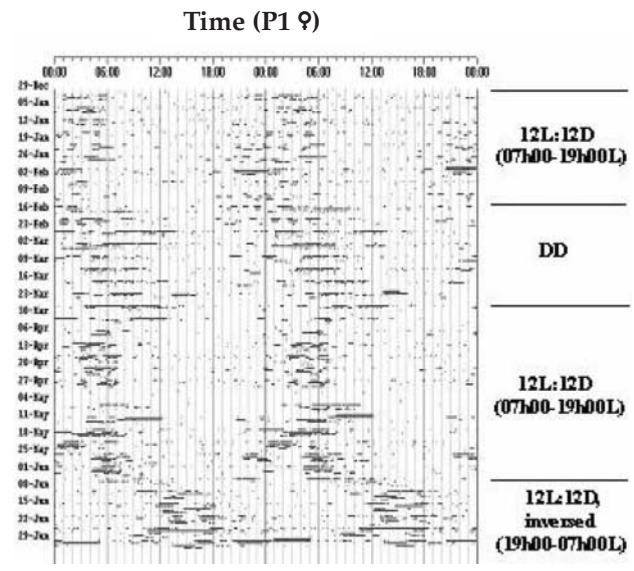


Figure 4. *Cryptomys hottentotus pretoriae*: An example of a highveld mole-rat that entrained to the different light cycles (infrared captor).

nous rhythms (1 emitter, 3 IR captors, 1 wheel). Four of the 5 animals had more activity in the dark phase during the previous cycle (3 IR captors, 1 wheel), and 1 was more active during the day (emitter). The lengths of the endogenous rhythms were close to 24 h ($\tau = 24.1 \pm 0.103$, $n = 5$). The other 2 animals did not exhibit any rhythmic behavior during DD (1 IR captor, 1 wheel).

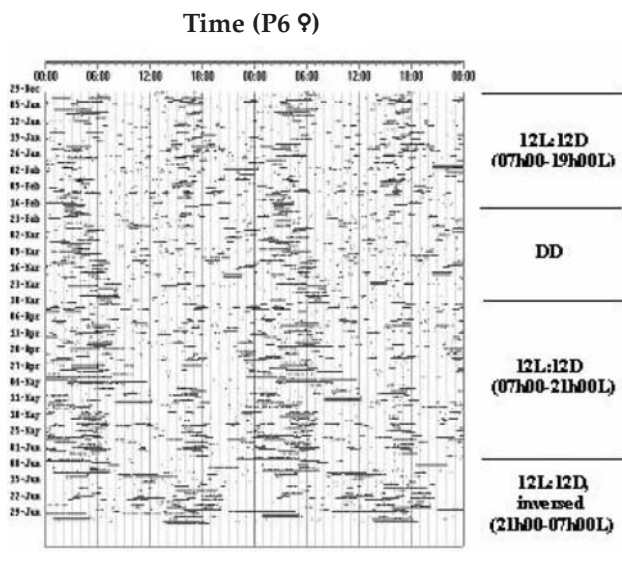


Figure 5. *Cryptomys hottentotus pretoriae*: An example of a highveld mole-rat that shows ultradian bouts of activity (infrared captor).

One mole-rat appeared to be arrhythmic (IR captor) but did display an endogenous rhythm after some time under constant conditions. All the animals retained their activity preference for a certain phase of the day during the re-entrainment phase, except 1 that changed from exhibiting more activity during the dark part of the light cycle to more activity during the light. Only 1 individual changed its activity from mainly during the day to mostly during the night (emitter). One animal appeared to display bimodal activity after about a month and a half in 12L:12D, both bouts of activity manifested during the dark phase (Fig. 5).

After inverting the light cycle, all the animals were more active during the dark part of the light cycle. Only 1 animal shifted its activity immediately (emitter); clear entrainment of the other mole-rats took place over a few days (Fig. 6).

During LL, 2 mole-rats displayed visible rhythms (2 IR captors) and the other animals became arrhythmic. The 2 endogenous rhythms were both longer than 24 h ($\tau = 24.96 \pm 0.898$, $n = 2$). Six of the 7 highveld mole-rats appeared to have a preference for activity in the dark phase of the light cycle (Fig. 7).

Cryptomys damarensis

Four of the 8 Damaraland mole-rats (1 emitter, 2 IR captors, 1 wheel) displayed obvious entrainment

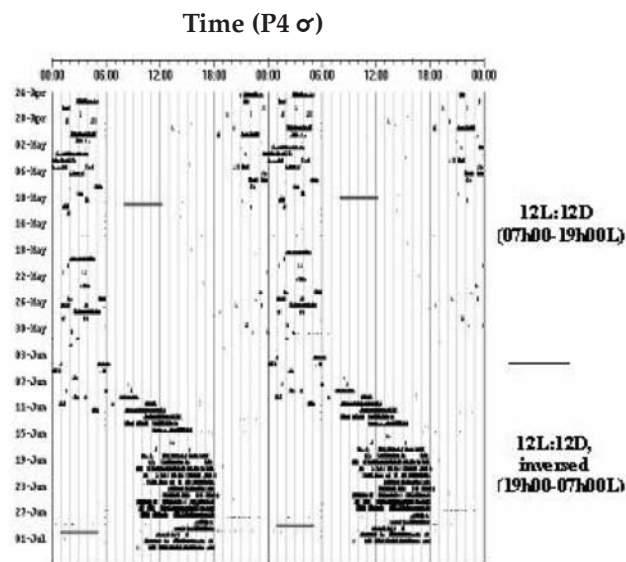


Figure 6. *Cryptomys hottentotus pretoriae*: An actogram of a wheel-running mole-rat that shifts its activity according to a new light cycle over the course of a few days.

according to a specific phase of the LD cycle during the 1st recording (Fig. 8), while the rest of the animals showed weak or no entrainment (1 emitter, 2 IR captors, 1 wheel).

Six of the 8 mole-rats (3 emitters, 2 IR captors, 2 wheels) exhibited more activity during the light phase of the 1st LD cycle, while 2 animals were more active during the night (2 IR captors). The 6 animals active during the day displayed endogenous rhythms in DD ($\tau = 24.01 \pm 0.17$, $n = 6$). Neither of the 2 animals that were active during the night exhibited endogenous rhythms. During the re-entrainment LD cycle, all 8 mole-rats were more active during the light phase. One animal that showed a good free-running rhythm under DD (IR captor) maintained its free-running rhythm in LD, then appeared to lose rhythmicity as the activity onset reached the dark phase and resumed when the activity onset reached the light phase. The animal re-entrained to the LD cycle just before it was inverted. Three animals shifted their activity according to the inversion of the light cycle to display more activity during the light phase (3 IR captors), 2 animals were initially more active during the dark phase but subsequently became arrhythmic (1 IR captor, 1 wheel). Three mole-rats (2 IR captors, 1 wheel) displayed some degree of rhythmicity during LL ($\tau = 24.07 \pm 0.18$, $n = 3$). Rhythms of the other animals disintegrated rapidly and completely.

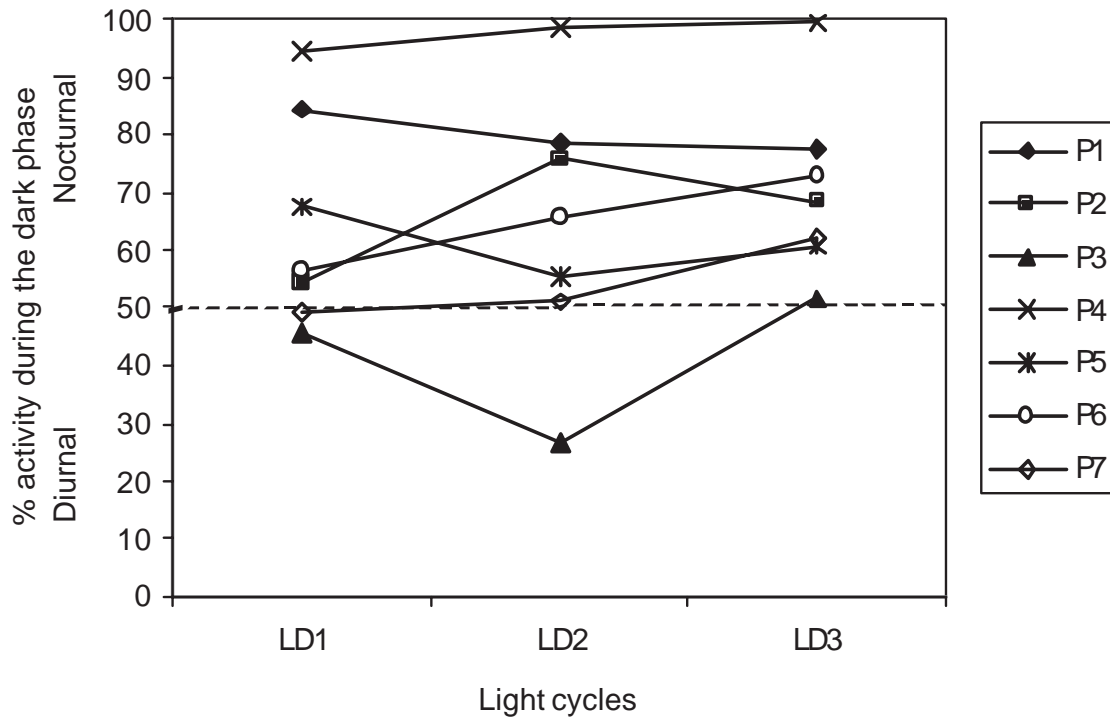


Figure 7. *Cryptomys hottentotus pretoriae*: This graph illustrates the percentage of activity that each animal exhibited during the light or dark phase of each of the light schedules.

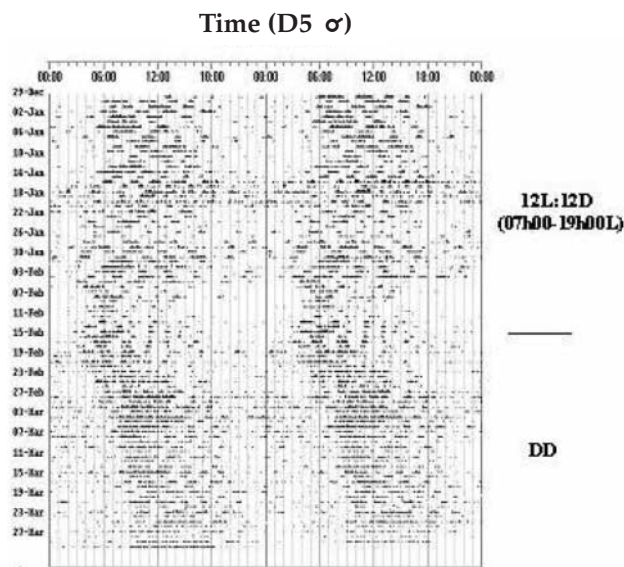


Figure 8. *Cryptomys damarensis*: An example of a Damaraland mole-rat that displays entrainment to the 1st light cycle and free-runs in constant darkness.

Entrainment of the Damaraland mole-rat appears less stable than the solitary species; 4 of the 8 mole-rats changed their time of activity from mainly during the light phase to the dark phase or visa versa (2 IR cap-

tors, 2 wheels). Activity was also not as restricted to a specific phase of the light cycle, and animals did not re-entrain to new light cycles as readily as the solitary species. In contrast to the other 2 species investigated, the Damaraland mole-rat had a preference for activity during the light phase of the light cycle (Fig. 9).

DISCUSSION

Temporal Activity Distribution

Mole-rats are able to perceive the difference between light and dark, since most individual animals of all species preferentially display locomotor activity during either the nocturnal or diurnal phase of the light-dark cycle. In the solitary Cape mole-rat, the majority of the animals clearly show the main largest part of their activity during the dark phase of the light cycles.

This study confirms the findings of Lovegrove and Papefus (1995), who found all of their experimental *Georychus* mole-rats to be nocturnally active. These animals were from the Natal population, whereas the mole-rats in the present study came from the Cape Town area.

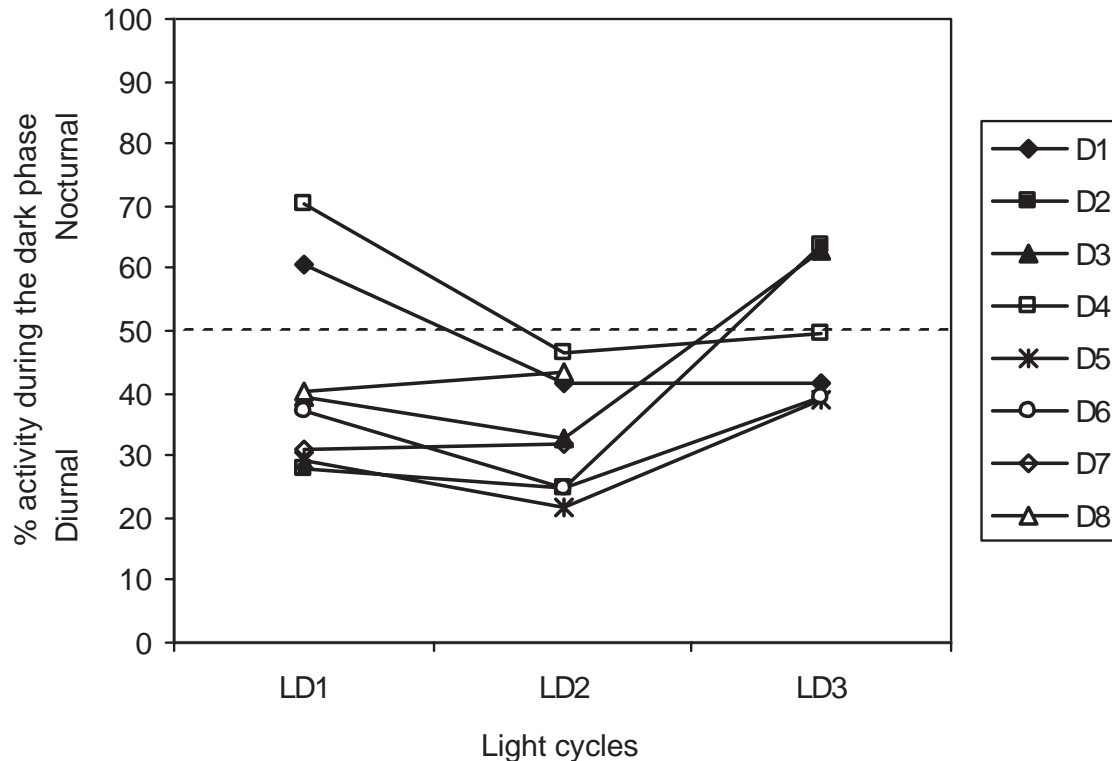


Figure 9. *Cryptomys damarensis*: This graph illustrates the percentage of activity that each animal exhibited during the day or night of each of the light schedules.

It appears that the more extensively studied subterranean mammal, *Spalax ehrenbergi*, also a solitary species, exhibits somewhat less clear-cut patterns in daily activity. Goldman et al. (1997) indicated that all of their animals displayed diurnal activity, whereas Tobler et al. (1998) stated that the majority of their experimental subjects were nocturnal. Nevertheless, long-term observations revealed that most of these nocturnal animals altered their activity to become diurnal.

In contrast with the solitary species, the activity of social species appears to be less restricted to a specific phase of the light-dark cycle. Activity is more uniformly distributed over the 24-h day, although the animals still displayed more activity during either the dark or light phase.

In the present study, all the entraining highveld mole-rats expressed nocturnal activity, contrasting earlier studies that found a lack of distinct activity rhythms (Hickman, 1980; Bennett, 1992). The majority of the entraining Damaraland mole-rats exhibited diurnal activity, a pattern also noted in the study by Lovegrove et al. (1993) using colonies, instead of sin-

gle animals. As in the highveld mole-rat, the activity in this species was more uniformly distributed over the 24-h period. From these results, it can be inferred that social species are less capable of displaying distinct nocturnal or diurnal activity rhythms when compared to solitary species, and this could be interpreted as a weaker link between the pacemaker and its output rhythms. However, a study on the naked mole-rat, *H. glaber*, has revealed that most of the animals exhibited robust nocturnal activity rhythms (Riccio and Goldman, 2000), but this may be as a result of prescreening the animals and only using animals that exhibited good wheel running.

The reason why some mole-rat species are more active during the light phase of a light cycle and others during the dark phase remains unknown. It may simply reflect the fact that light is an unusual situation for a subterranean mole-rat. It may be that some unknown evolutionary pressure in the past is the foundation of the selective temporal distribution of activity in mole-rats, but it still does not account for diurnal and nocturnal activity of animals within the same species.

Entrainment of Activity Cycles

The present study suggests that most individual Cape mole-rats display entrainment and circadian rhythmicity of locomotor activity, since 80% of the animals entrain to the light cycles and exhibit distinct rhythms. This percentage is comparable to that of *S. ehrenbergi*, a solitary mole-rat species from North Africa and the Middle East (Goldman et al., 1997), which also displays a relatively high percentage of entrainment among experimental animals.

Social species are also able to perceive changes in light conditions and synchronize their activity to a light cycle. However, in comparison with the solitary Cape mole-rat, a larger proportion of individual animals of the social species were unable to entrain to LD cycles. In social species, only half of the animals exhibited entrainment. The low percentage of entrainment could be indicative of a weaker link from the clock to its output, or alternatively a relatively high threshold for response to light.

In contrast to animals housed singly, colonies of Damaraland mole-rats have been found to show good entrainment to LD cycles (Lovegrove et al., 1993). This can be ascribed to either an individual animal behaving unnaturally when separated from its colony or that there is a component of social entrainment. In this study, the role of social entrainment is difficult to evaluate but could provide a possible explanation for the difference in results.

In all the mole rat species studied to date, relatively large intraindividual variability is observed, some animals entrain very well to the light regimes, some show weak entrainment, whereas others do not entrain their activity at all. The phase angle of activity also differed considerably between animals. Some animals became active immediately after the change of lights and remained active until the lights changed again, while others became active only later and concentrated their activity at the end of the 12-h period. This large variation in the phase angle, as well as the number of arrhythmic or weakly entrained animals, indicates that the circadian clock is not very strongly coupled to the photic input in this species. About 50% of *S. ehrenbergi* entrained to temperature rhythms (Goldman et al., 1997), suggesting that nonphotic cues may play an important supporting role in entrainment of subterranean species.

In the solitary Cape mole-rat, activity was shifted according to changes in the light cycles almost immediately in the majority of the individuals. Activity was

adjusted to light regimes of different durations, implying that light is effectively perceived and integrated by the circadian pacemaker. Both social species also altered their activity according to an inversion in the light cycle; however, in contrast to the solitary species, this change took place over the course of several days.

Constant Conditions

Cape mole-rats that entrained to the 1st light cycle displayed endogenous rhythmicity, and the rhythm started to drift from the same phase angle that the animal was entrained to. This indicates that these animals were entrained to the light cycle and that the behavioral response to the light cycles was not merely due to masking. Clear endogenous rhythms were, however, not obtained from all the animals, thus it is still possible that some animals may have displayed masked responses. The period of constant darkness was too short to make conclusive statements other than that some of the individuals did display an endogenous rhythm.

Both social species also exhibited endogenous rhythms; the number of individuals displaying endogenous rhythms was equal to the percentage of entraining animals within each species. The existence of endogenous rhythms on DD of these species suggests a functional circadian clock. Some of the animals did not show any entrainment to LD cycles but did exhibit endogenous rhythms under constant conditions, suggesting weak integration of photic information by the circadian clock. Generally rhythms disappear rapidly under constant light conditions. Very few animals show traces of rhythmic behavior under this cycle.

In comparison to other rodents, mole-rats have a relatively high threshold response to light. Under normal circumstances, these animals spend nearly all of their time underground and are not exposed to light for extended periods. It has also been suggested that the abnormal 12-h or longer light periods of laboratory experiments may cause retinal damage and result in reduced photosensitivity (Ricchio and Goldman, 2000).

Seasonal breeding may provide an explanation for the gradient in light sensitivity encountered in this family. Solitary species are highly xenophobic toward other animals outside the breeding season. As external cues have to provide an indication of the start of the breeding season in order for individuals to search

for breeding partners, it is essential for this species to be able to perceive at least seasonal changes in the environment. The Cape mole-rat is sighted above ground more regularly than the 2 social species (NC Bennett, personal communication, 2001).

Likewise, the highveld mole-rat is a seasonal breeder, but unlike the Cape mole-rat, it does not need to look for breeding partners as they occur within the same colony. Thus, being able to perceive seasonal changes still has a functional role in this species. In contrast with the other species, the Damaraland mole-rat breeds aseasonally, and this species would therefore be expected to show less response to cyclic environmental factors such as light than species that breed seasonally.

In conclusion, all 3 species of mole-rat show daily entrainment of locomotor activity to external light stimulation, confirming that light information is transmitted to and integrated by the SCN. The ability of these species to adapt their activity according to shifts in the LD cycle demonstrates that these species do entrain to light and not other cues. Finally, under conditions of constant darkness, endogenous rhythms are present in all 3 species, providing evidence for a functional circadian clock.

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REFERENCES

- Bennett NC (1992) The locomotor activity patterns of a functionally complete colony of *Cryptomys hottentotus hottentotus* (Rodentia: Bathyergidae). *J Zool Lond* 228:435-443.
- Bennett NC and Faulkes CG (2000) *African Mole-Rats: Ecology and Eusociality*. Cambridge University Press, New York.
- Bennett NC and Jarvis JUM (1988a) The reproductive biology of the Cape mole-rat, *Georchus capensis* (Rodentia: Bathyergidae). *J Zool Lond* 214:95-106.
- Bennett NC and Jarvis JUM (1988b) The social structure and reproductive biology of colonies of the mole-rat *Cryptomys damarensis* (Rodentia: Bathyergidae). *J Mammal* 69:293-302.
- Bronchti G, Heil P, Scheich H, and Wolberg Z (1989a) Auditory pathway and auditory activation of primary visual targets in the blind mole rat (*Spalax ehrenbergi*): I. A 2-deoxyglucose study of subcortical centers. *J Comp Biol* 284:253-274.
- Bronchti G, Heil P, Scheich H, and Wolberg Z (1989b) Auditory activation of cortical visual fields in the blind mole-rat. In J Erber, R Menzel, H-J Pflugger, and D Todt, eds, *Neural mechanisms of behavior, Proceedings of the 2nd International Congress of Neuroethology*, Thieme, Stuttgart.
- Cooper HM, Herbin M, and Nevo E (1993) Ocular regression conceals adaptive progression of the visual system in the blind subterranean mammal. *Nature* 361(6408):156-159.
- Eloff G (1958) The functional and structural degeneration of the South African rodent moles, *Cryptomys bigalkei* and *Bathyergus maritimus*. *S Afr J Sci* 54:293-302.
- Goldman BD, Goldman SL, Riccio AP, and Terkel J (1997) Circadian patterns of locomotor activity and body temperature in blind mole-rats, *Spalax ehrenbergi*. *J Biol Rhythms* 14(4):348-361.
- Haim A, Heth G, Pratt H, and Nevo E (1983) Photoperiodic effects on thermoregulation in a 'blind' subterranean mammal. *J Exp Biol* 107(4):59-64.
- Hickman, GC (1980) Locomotor activity of captive *Cryptomys hottentotus* (Mammalia: Bathyergidae), a fossorial rodent. *J.Zool.Lond.* 192:225-235.
- Janse van Rensburg L, Bennett NC, Van der Merwe M, and Schoeman AS (2002) Seasonal reproduction in the highveld mole-rat, *Cryptomys hottentotus pretoriae* (Rodentia; Bathyergidae). *Can J Zool* 80:1-11.
- Jarvis JUM and Bennett NC (1993) Eusociality has evolved independently in two genera of bathyergid mole-rats—but occurs in no other subterranean mammal. *Behav Ecol Sociobiol* 33:253-260.
- Lovegrove BG, Heldmaier G, and Ruf T (1993) Circadian activity rhythms in colonies of 'blind' mole-rats, *Cryptomys damarensis* (Bathyergidae). *S Afr Tydskr Dierk* 28(1):46-55.
- Lovegrove BG and Papenfus ME (1995) Circadian activity rhythms of the solitary Cape mole-rat *Georchus capensis* (Bathyergidae). *Physiol Behav* 58(4):679-685.
- Reuss S (1996) Components and connections of the circadian timing system in mammals. *Cell Tissue Res* 285:353-378.
- Riccio AP and Goldman BD (2000) Circadian rhythms of locomotor activity in naked mole-rats (*Heterocephalus glaber*). *Physiol Behav* 71:1-13.
- Roenneberg T and Foster RG (1997) Twilight times: light and the circadian system. *Photochem Photobiol* 66(5):549-561.
- Tobler IJ, Herrmann M, Cooper HM, Negroni J, Nevo E, and Achermann P (1998) Rest-activity rhythm of the blind mole-rat, *Spalax ehrenbergi*, under different lighting conditions. *Behav Brain Res* 96:173-183.