The locomotory activity rhythm of the spiny mouse, *Acomys spinosissimus* from southern Africa: light entrainment and endogenous circadian rhythms

Hoole, C[1*]., Oosthuizen, M.K[1]., Chimimba, C.T[1,2]. & Bennett, N.C[1].

[1]Mammal Research Institute (MRI), Department of Zoology and Entomology
University of Pretoria, Private Bag X20, Hatfield, 0028 South Africa
[2]DST-NRF Center of Excellence for Invasion Biology (CIB), Department of Zoology and Entomology,
University of Pretoria, Private Bag X20, Hatfield, 0028 South Africa
*Corresponding author: choole@zoology.up.ac.za

Abstract

The circadian rhythm of locomotor activity in the spiny mouse, *Acomys spinosissimus* from South Africa was investigated under controlled laboratory conditions. Nine individuals were subjected to six successive light cycles of approximately two weeks each as follows: 1) a standard light/dark (12:12LD) cycle, 2) a period of constant darkness (DD), 3) a second standard light/dark (12L:12D) cycle, 4) an inverse of the LD (12:12DL) cycle, 5) a short day cycle (8:16LD) and 6) a long day cycle (16:8LD). All the animals exhibited entrainment of their activity to the LD and DL lighting regimes. Locomotor activity of *A. spinosissimus* occurred predominantly during the dark phases of the LD, DL, long day and short day cycles. Under LD, the mean percentage of activity was 88.7% ± 0.07% during the dark phase. When subjected to constant darkness all animals expressed free-running rhythms of locomotor activity (Mean ± 1SD = 23.81h ± 0.33h; range = 23.2 h – 24.1 h). On the reverse LD cycle, the mean percentage of activity was 81.4% ± 0.09% during the dark phase of the cycle. Mice exhibited significantly more daytime activity during the long day cycle (20.3% ± 5.8%;) and no significant change in dark phase activity during the short day cycle (90.1% ± 4.01%;). The spiny mouse possesses a circadian rhythm of locomotor activity that entrains strongly to light. Locomotory activity occurs predominantly during the dark phase and can therefore be considered a nocturnal mammal.

Keywords: *Acomys spinosissimus*, circadian rhythms, entrainment, light, southern Africa.

Introduction

All eukaryotic organisms studied to date display biological rhythms which may be generated either exogenously or endogenously (Aschoff, 1960; Reuss, 1996). Endogenous rhythms are by far the more common and are characterised by a free-run period or *tau* (τ) under constant conditions and when these rhythms have a periodicity of close to 24 hrs, they are referred to as circadian (derived from the *Latin circa* = about and *diem* = day; www.freedict.com/onldict/lat.html; Haus *et al.*, 1998). Circadian rhythms are genetically regulated oscillations thought to have evolved in order to allow organisms to predict and prepare for environmental changes that occur on a daily basis (Brady, 1979; Goldman, 1999; Albrecht, 2002). Furthermore, the free-running period or *tau* (τ), reflects inter-individual variation within a species and generally ranges between 22 h and 26 h under constant darkness between species (Aschoff, 1981). Rhythmic phenomena that display daily oscillations in mammals include locomotor activity patterns, body temperature patterns and the cyclical secretion of hormones, such as melatonin (Reiter, 1988; Jacob, Vuillese & Pévet, 1997). This may also be expanded to show seasonal differences in activity as the photoperiod changes (Turek & Campbell, 1979).

The most frequently used cue to which mammals entrain their circadian rhythms is the environmental light-dark cycle (Pittendrigh & Minis, 1964; Goldman, 1999; Benstaali *et al*., 2001). In most mammals where light acts as a *zeitgeber*, the light-dark cycle entrains locomotor activity to a certain phase or phases of each day (day/night/twilight), which can be used to categorize species into being either diurnal, nocturnal or crepuscular organisms. Depending on these categories, light has different effects on animals - light generally induces locomotor activity in diurnal animals but suppresses locomotor activity in nocturnal animals (Daan & Aschoff, 1975). There are examples where these signals are more complex and either the presence or absence of moonlight may promote or restrict activity in nocturnal animals respectively (e.g. Smit *et al*., 2011).

The suprachiasmatic nucleus (SCN) is the site of the circadian pacemaker or clock in mammals (Laakso *et al.,* 1995; Benstaali *et al.,* 2001). In mammals, light

enters through the eye and is transmitted to the SCN via the retinohypothalamic tract (RHT) (Jacob *et al*., 1997). This signal translates into a physiological response which may vary with the amount/duration/intensity of stimulation resulting in both seasonal and daily activity patterns (Bearden, Fuquay & Willard, 2004).

Small mammals provide ideal models to investigate the phenomenon of circadian biology. Animals such as mice and several species of hamsters are routinely used for circadian investigations (Rusak, 1977; Yellon *et al*., 1982; Pévet, 1988; Hastings *et al*., 1992; Lin *et al*., 2002; Kakihana, 2004), and most of these studies include mammalian species from the northern hemisphere. Unlike the animals from the northern temperate zone, tropical and sub-tropical animals are not subjected to major changes in either photoperiod or temperature. However tropical and sub-tropical animals do breed seasonally or exhibit changes in activity with photoperiodic changes but may also be under the influence of variations in rainfall which often affects food availability (Bronston, 1985).

The spiny mouse is an ideal model to increase our knowledge on the chronobiology of poorly studied rodents, such as those from Africa in general and in particular southern Africa. To date it is unknown when the predominant activity period of this southern hemisphere rodent is or whether it possesses an endogenous rhythm of locomotory activity or, although anecdotal reports imply that they are mainly nocturnal (Skinner & Chimimba, 2005).

This study was conducted to: 1) describe how activity is distributed in the spiny mouse; 2) assess whether the spiny mouse possesses an endogenous rhythm of locomotory activity and, if so, whether the mouse entrains its locomotory activity rhythm to a light-dark cycle; 3) to determine the (τ) of each animal; 4) to quantitatively describe how activity within the species is distributed over the 24 h day; and 5) to investigate possible seasonal differences in activity with regard to photoperiod.

We predicted that *A. spinosissimus* would exhibit a preference for the dark phase and that the free-running period will be less than 24 h (Aschoff, 1981).

Materials and methods

Animal maintenance

Nine adult spiny mice (*A. spinosissimus*) (3 males, 6 females) were collected in and around the rocky outcrops of the Goro Game reserve in the Soutpansberg district of the Limpopo Province, South Africa (22°58.450'S, 29°24.939'E; 22°58.50'S, 29°25.032'E). Study animals were trapped using Sherman live-traps (H.B. Sherman Traps Inc. Florida, U.S.A.) baited with a mixture of peanut butter and oats. Animals were housed individually in crates (50cm x 60cm x 35cm), given a plastic mouse house (15 cm x 21 cm x 10 cm) and provided with wood shavings and tissue paper as bedding/nesting material. Fresh food was supplied at random times; this consisted of mouse pellets, carrots, apples and seeds, with water provided *ad libitum.* This was considered a balanced diet based on previous studies and the body weight varied less than five percent (See Medger *et al*., 2010; Medger *et al*., 2011). The minimum interval between supplying fresh food was 18 hrs and the maximum interval, 36 hrs and was determined using a random numbers generator.

The experimental room was temperature controlled at 25 ±1° C and the light intensity was approximately 500 lux during the light phase, and approximately 0.025 lux during the dark phase. All cages of *A. spinosissimus* were fitted with infrared motion captors (Medusa passive infrared detection, Texecom Ltd, USA) mounted in metal brackets and angled to cover the entire floor area of the cage. Animals were acclimated for two weeks on a 12L:12D light cycle prior to the commencement of experiments. Each experimental condition (lighting regime) lasted two weeks. Spiny mice were firstly subjected to a 12L:12D (light from 06h00 to 18h00) to determine whether they entrain their activity to a light cycle. Subsequently, the light cycle was changed to constant darkness (DD) to investigate whether spiny mice exhibit an endogenous circadian rhythm of locomotor activity and to assess the free-run period. Thereafter, animals were exposed to a 12L:12D light cycle similar to the first cycle to ensure that all animals were re-entrained to the light cycle once more before the light cycle was inversed (12D:12L; light from 18h00 to 06h00) to observe whether and how fast animals can shift their locomotor activity to a new lighting regime. This was followed by a short day cycle (8L:16D) and lastly a long day cycle (16L:8D) to investigate whether activity is affected by differences in the length of photoperiod

presented. Activity was recorded continuously, and total counts per minute were captured with an automated recording system using the program VitalView (VitalView ® Data Acquisition System Version 4.2 © 1999-2006 Mini Mitter Repironics Company, Inc. USA).

Activity profiles

Double-plotted actograms were derived using the program Clocklab (ClockLab TM, Actimetrics, Evanston, Il. U.S.A.) in order to render a graphic depiction of activity rhythms. The phase angle of activity was calculated for each animal. Activity onsets were defined after 10 consecutive minutes of activity, and offsets after 20 minutes of inactivity (Schumann *et al*., 2005). Activity profiles were created to provide the peak activity time, and the percentage of activity during light and dark phases was determined using Microsoft excel (Microsoft ® Office Excel ® 2007). This was achieved by looking at the ratios of total activity counts (TAC's) during the light and dark phases of the light cycles or the TAC's during the subjective days and subjective nights while under constant dark conditions. The period of the endogenous rhythm was calculated for the DD cycle by determining the amount of drift per 24 hr period i.e. the average difference in onset times from one day to the next for the period of constant darkness using ClockLab.

Data Analysis

The derived percentile data were first tested for normality and found to be not normally distributed. Consequently, an arcsine square root transformation was performed on all percentile data (Sokal & Rohlf, 1981) before re-testing the data for normality. Despite such a transformation all data were found to be not normally distributed and the non-parametric Wilcoxon's matched pairs test was conducted to analyse differences between the dark phase activity percentages of the LD1 cycle and the subjective night time activity of the DD cycle as well as the dark phase activity of the second LD and the DL cycle. A similar procedure was followed for the long and short day cycles. The percentage activity during the subjective night and day were calculated according to the period of the endogenous rhythm of each individual animal and the phase angle calculated during the light cycle. All statistical

analyses were performed using algorithms in the Statistica computer programme (Statistica 9.0 © StatSoft, Inc. 1984-2009).

Results

12L:12D

All spiny mice entrained their locomotory activity rhythms to the light cycle. They showed a preference for locomotory activity during the dark phase of the light cycle, and the majority of the activity occurred during the first part of the night. Activity profiles show an activity peak approximately 45 minutes after the lights were switched off (Fig. 1). Activity patterns showed clear onsets while the offsets were less precise, although one mouse showed slightly more defined offsets (Fig. 2). The phase angle was calculated between the time the lights went off and the beginning of activity time. The mean phase angle (± SD) was 5.03º ± 2.88º for LD1, which translates to the commencement of activity at 20.14 ± 11.51 minutes after the lights went off. During the first LD cycle the animals displayed a mean (± SD) percentage of 88.7% ± 0.07% activity during the dark phase of the light cycle, (Fig. 3). The mean (± SD) TAC for this two week period was 3522.89 ± 1466.08; no correlation was found between percentage activity and TAC's ($r = 0.50$, $n = 9$, $df = 1$)

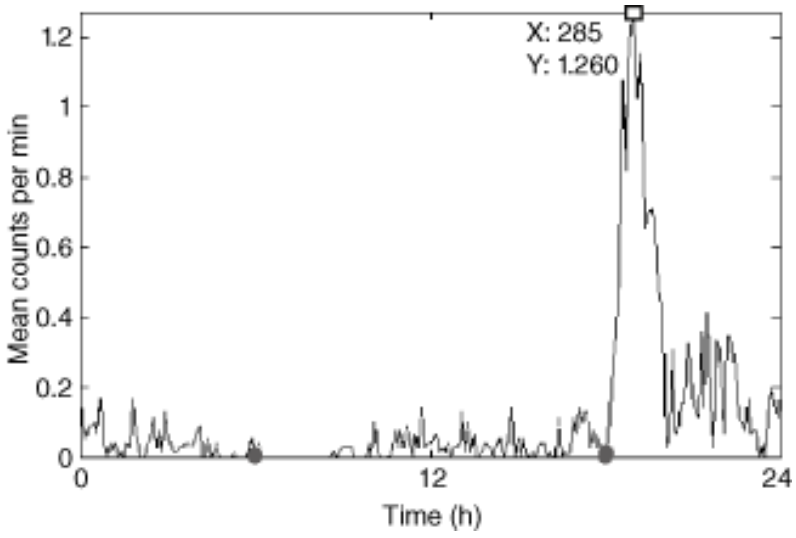

Figure 1.

Activity profile for the spiny mouse, *Acomys spinossismus* from southern Africa showing activity peak at 1 h after the start of the dark phase. The red dot indicates the beginning of the light cycle at 06:00 h, the green dot is the beginning of the dark cycle at 18:00 h.

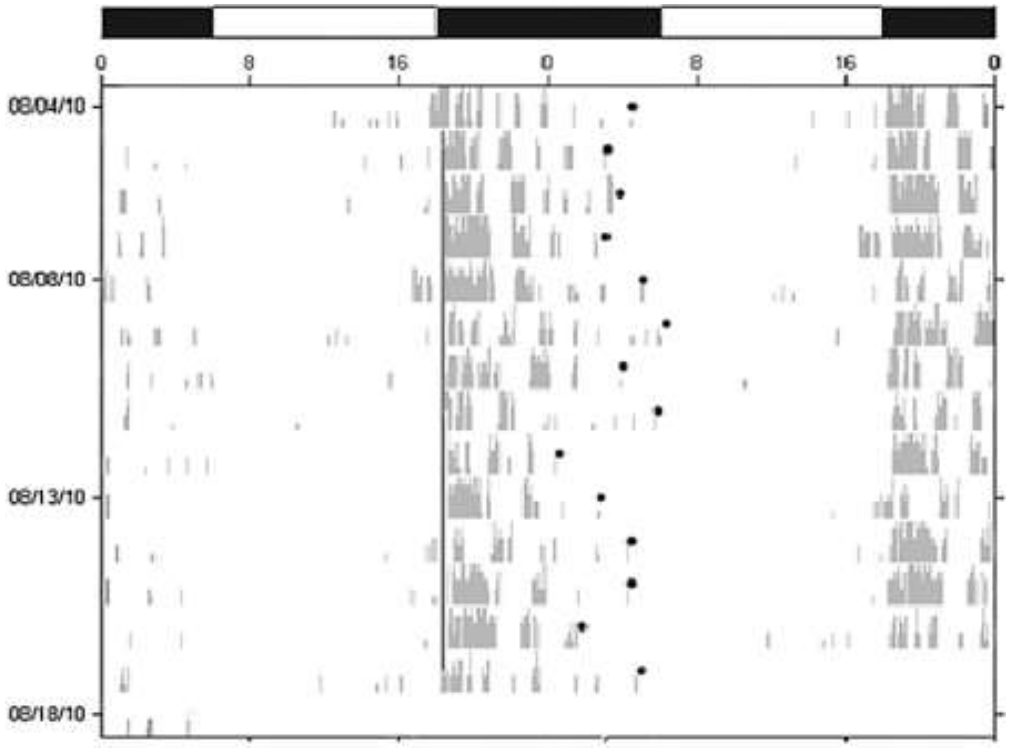

Figure 2.

Actogram of locomotor activity for the spiny mouse, *Acomys spinossismus* from southern Africa during the first light–dark (LD1) cycle illustrating precise onsets (solid line) and irregular offsets (black dots) of activity.

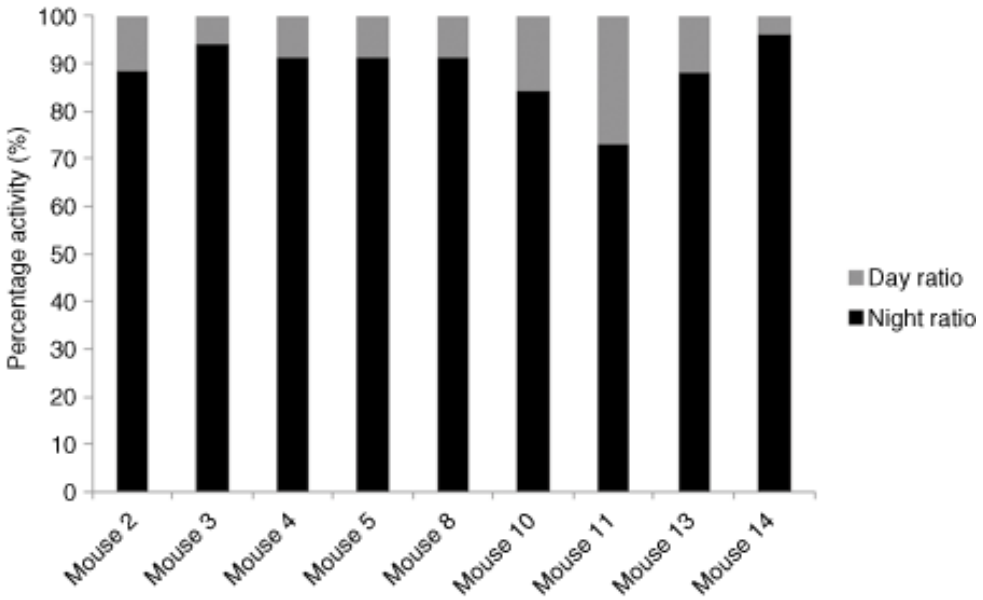

Figure 3.

Bar graph showing the percentage of locomotor activity for the spiny mouse, *Acomys spinossismus* from southern Africa during the dark and light phases of the first light–dark cycle (LD1).

DD

Under constant dark conditions, all the animals maintained rhythmic activity patterns. One mouse maintained a 24h cycle, three mice had endogenous cycles with a period of 24.1 hours (e.g., Fig. 4a), while the remaining five mice displayed endogenous rhythms with periods ranging from 0.1 to 0.8 hours less than 24 hours (e.g., Fig. 4b). The mean (± SD) period was 23.81 h ± 0.33 h. The mean (± SD) percentage activity during the subjective night was 81.4% ± 0.094 (Fig. 5). A significantly higher percentage of activity was displayed during the dark phase of the entrained rhythm than during the subjective night of the endogenous rhythm (Z = 2.67; T = 0; n = 9; P < 0.01). However the mean (± SD) TAC increased significantly to 4956.89 ± 1981.90 (p < 0.000; df = 1; n = 9). Again no correlation was found between TAC's and the percentile activity data (r = 0.19; n = 9; df = 1). There was also no correlation between TAC's and the endogenous period (r = 0.16; n = 9; df = 1). None of the animals showed distinct offsets. One mouse died after this part of the experiment and all following experiments were conducted with only eight mice.

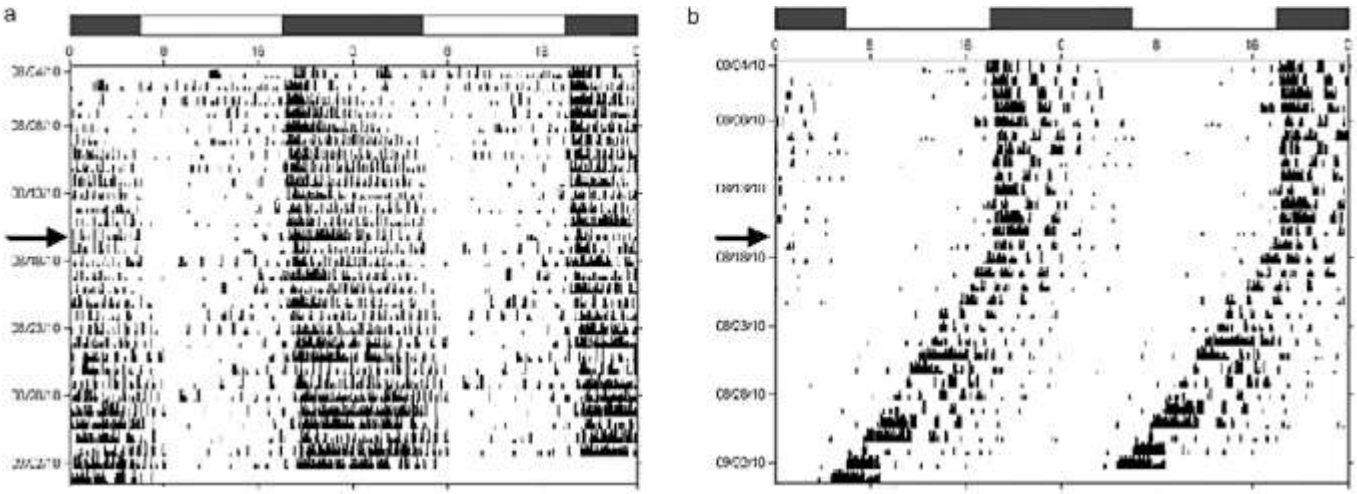

Figure 4.

Actograms for the spiny mouse, *Acomys spinossismus* from southern Africa showing the first light–dark cycle (LD1) followed by the period of constant darkness (DD). Arrows indicate change from LD to DD. (a) shows a rhythm with a tau close to 24 h, (b) shows a rhythm with a tau shorter than 24 h.

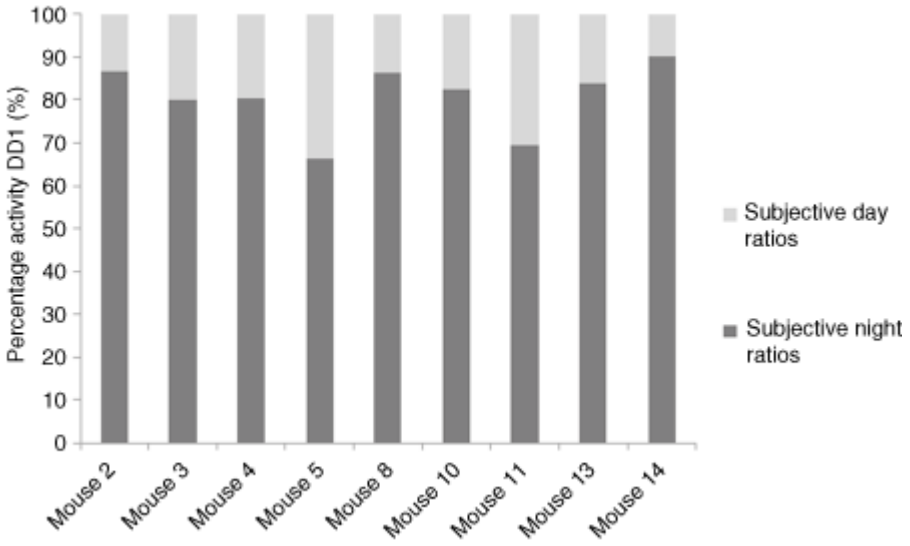

Figure 5.

Bar graph showing the percentage of locomotor activity for the spiny mouse, *Acomys spinossismus* from southern Africa during the subjective day and night of constant dark–light cycle (DD).

LD and inversed LD

When the light cycle was inverted, all eight animals showed a distinct increase in activity 21.75 ± 9.22 minutes after the new 'lights off' (Fig. 6). The offset of activity reset slowly with the total time of nightly activity increasing until the offset coincided with the lights being switched on after approximately nine days when re-entrainment was complete (Fig. 6). Using a data cursor, the x-value of this line was determined for two consecutive days and the mean (± SD) activity increase calculated. The mean increase in activity for all the mice until the offsets were fully entrained to the new lighting regime was 1h14mins ± 0.17mins per day. Although the initial percentage activity during the dark phase of the cycle was reduced, the proportion of activity during light and dark phases did not change from that of the previous LD cycle. The mean (± SD) percentage activity during the dark phases of the LD2 and DL1 cycles were 86.2% ± 0.05% and 87.3% ± 0.03%, respectively (Fig. 7). The onsets were similar to the LD1 onsets (21.75 ± 9.22 minutes after the lights went off compared to 20.14 ± 11.51 minutes during LD1). Three animals showed more distinct offsets during LD2 and five once re-entrainment was complete. There was no significant difference between the amount of activity during the dark phases of the LD2 and DL1 light cycles ($Z = 0.84$; $T = 12$; $n = 8$; $P = 0.40$).

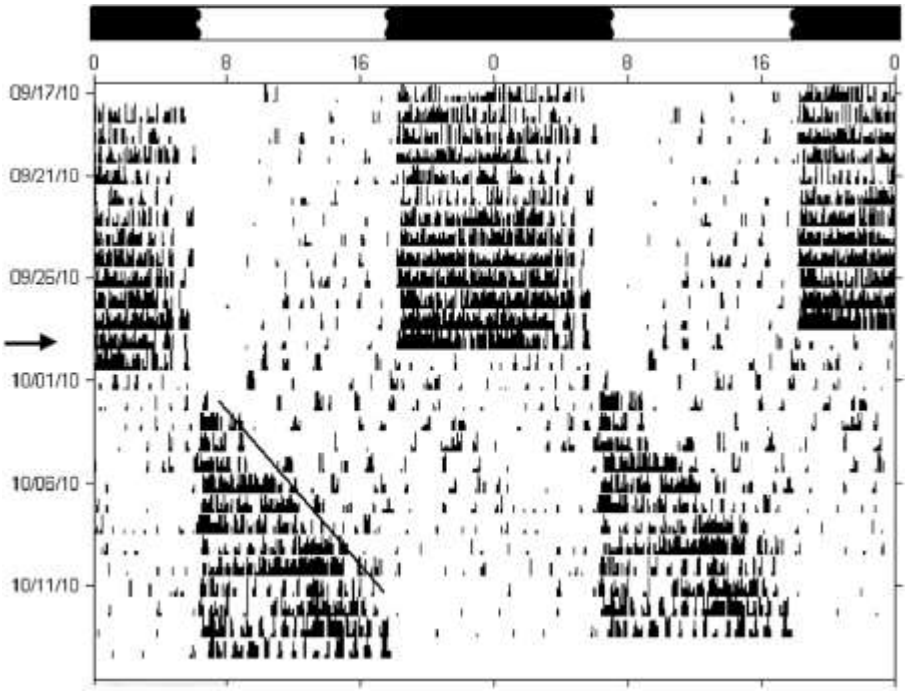

Figure 6.

Actogram for the spiny mouse, *Acomys spinossismus* from southern Africa illustrating the transition from the second light–dark cycle (LD2) to the inverted light–dark cycle (DL1).

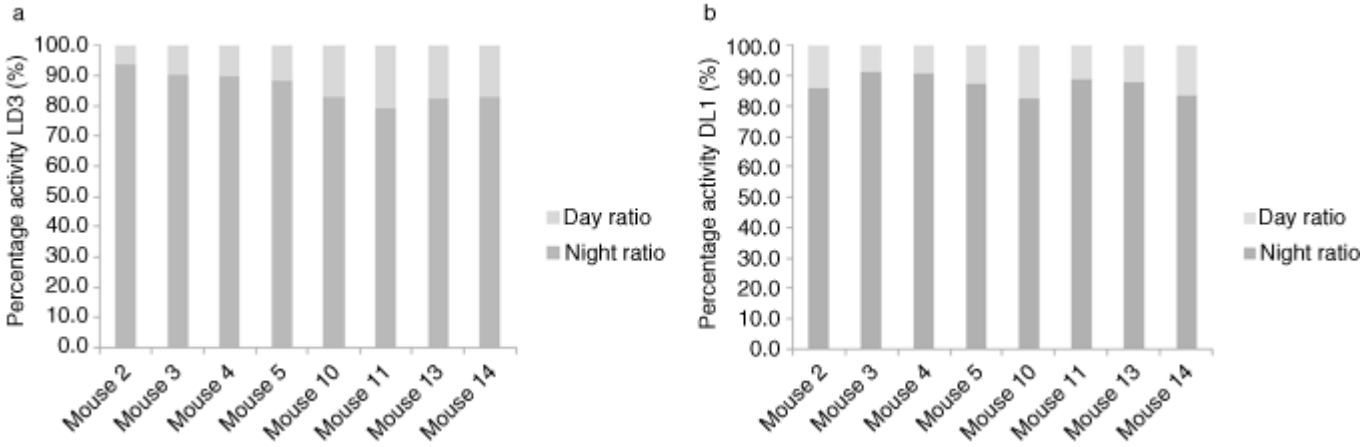

Figure 7.

Bar graph showing the percentage of activity for the spiny mouse, *Acomys spinossismus* from southern Africa during light and dark phases of (a) LD2 and (b) DL1.

Long and Short day Cycles

Activity profiles continue showing an activity peak on a long day cycle 27 ± 6.80 minutes after the lights were switched off. Activity patterns showed clear onsets with a mean (± SD) phase angle of 0.167° ± 0.09 while the offsets were less precise, but more distinct in all animals than during LD1 (Fig. 8). Activity commenced at 10 ±

5.66 minutes after the lights went off. The animals displayed a mean (± SD) percentage of 79.7% ± 5.8% activity during the dark phase of the light cycle, (Fig. 9). The percentage of activity during the dark phase of the long day cycle was significantly less than LD1 (Z=3.01; T=0; n=7; P<0.01).

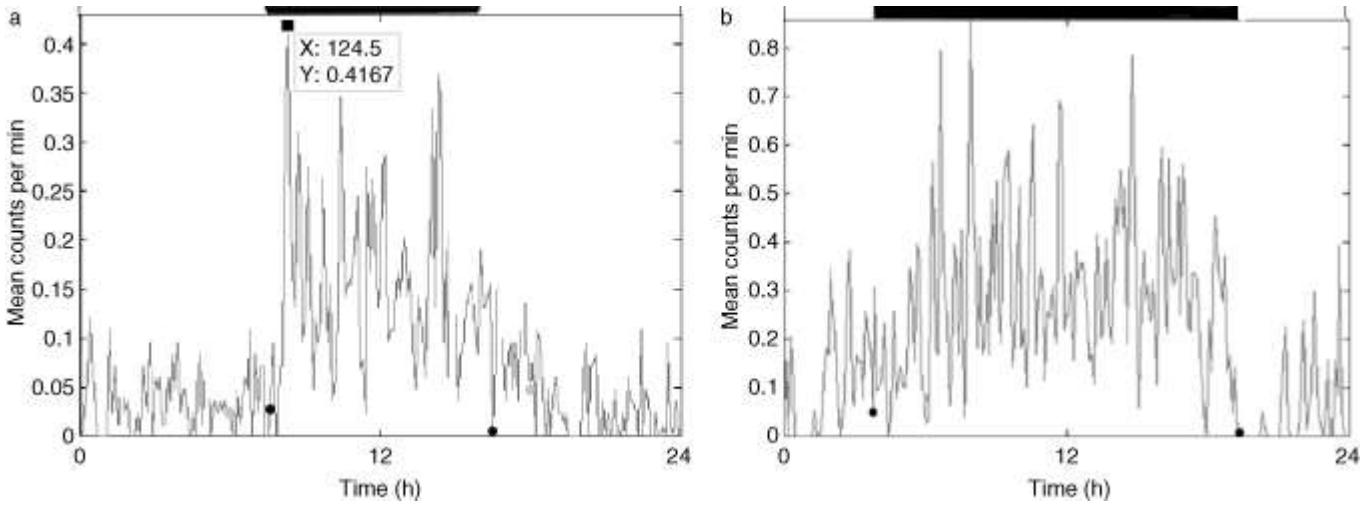

Figure 8.

Activity profile of the spiny mouse, *Acomys spinossismus* from southern Africa during light and dark phases of (a) the long day cycle and (b) the short day cycle.

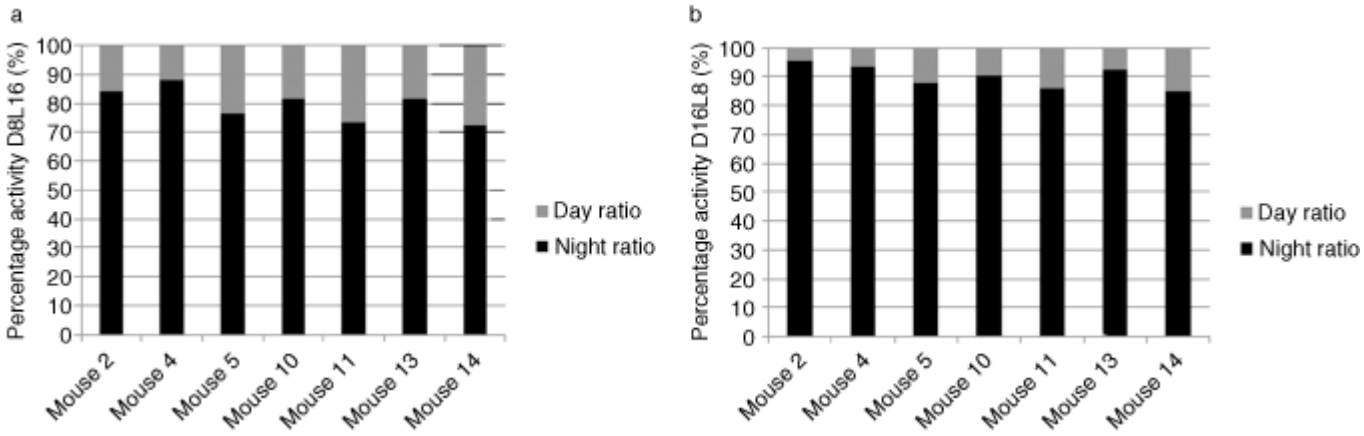

Figure 9.

Bar graphs showing the percentage of activity for the spiny mouse, *Acomys spinossismus* from southern Africa during light and dark phases of (a) the long day cycle and (b) the short day cycle.

The animals required an average of five days until they re-entrained to the new lighting regime with the onsets becoming earlier by 48 ± 8.3 minutes each day (Fig. 10). During the short day cycle there was a mean (± SD) onset of activity

32 ± 26.7 minutes after the lights went off, however activity increased more gradually and there were two activity peaks for each animal. The first peak was 3.9 ± 0.46 hours after the dark phase started (phase angle 59.25° ± 8.29) while the second varied considerably between animals. The offsets became imprecise for all the animals. Dark phase activity (± SD) is 90.11% ± 4.01% (Fig. 9). There was no significant difference in dark phase activity between the short day cycle and LD1 (Z=0.92; T=11; n=7; P=0.47).

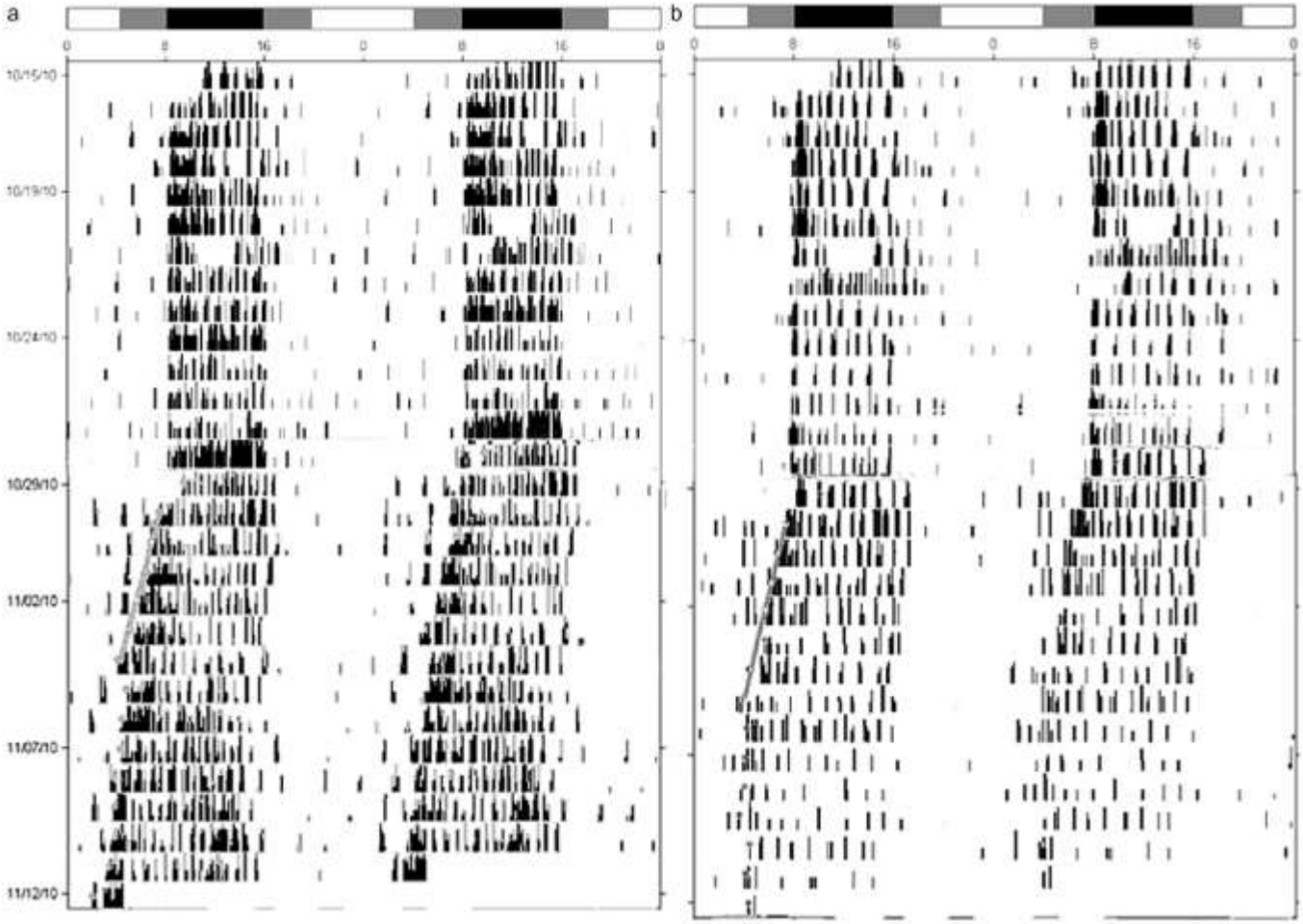

Figure 10.

Actograms of mice 2 and 4 for the long day cycle followed by the short day cycle. (a) Here a distinct offset is seen during the long day cycle and less distinct offsets are apparent during the short day cycle. (b) Offsets are not as distinct as in (a).

Neither long day nor short day activity percentages correlated with TAC's (r = 0.59; n = 8; df = 1 for the long day cycle and r = 0.33; n = 8; df = 1 for the short day cycle). However the total activity for both were significantly less than for either LD1

or LD2; total long day activity was about half of the total short day activity (Total activity count D8L16 ± SD = 1470.43 ± 1029.21;total activity count D16L8 ± SD = 2505.71 ± 2895.43) and there was considerably more variation in the total short day activity than any other cycle.

Discussion

The circadian clock is a self sustaining, genetically programmed mechanism which synchronizes with changing environmental conditions and allows for the optimal performance of the organism (Albrecht, 2002) and represents part of the adaptation of species to their environment (Enright. 1970; Daan & Aschoff, 1975). While activity patterns may change in response to varying environmental conditions and seasonal fluctuations (Hoogenboom *et al*., 1984; Tester, 1987), constant laboratory conditions allow for the expression of endogenous rhythms and for the investigation of individual entraining factors, in this case, light. All experimental animals used in this study exhibited nocturnal activity during all of the light cycles. In congruence with these findings, all mice were captured during the night, indicating that under natural conditions, these animals are also active during the night. These findings complement those for the Cape spiny mouse, as well as the majority of spiny mouse species occurring in the northern hemisphere (Powell, Belitsky & Rathbun, 1981; Weber & Hohn, 2005; Cohen, Smale & Kronfeld-Schor, 2009). In contrast, the golden spiny mouse, *Acomys russatus* displays diurnal activity under natural field conditions, but in the laboratory, with environmental factors such as competitors, predators and extreme temperatures removed, it shifts its locomotory activity pattern to nocturnal (Cohen *et al*., 2009).

Locomotory activity of the spiny mouse from southern Africa shows good entrainment to the light-dark cycle. Onsets are very distinct with a peak in activity shortly after the onset. Offsets were not as clear-cut, implying that the most important entraining factor is the transition from light to dark. Both the golden and common spiny mice also show definite onsets of activity shortly after darkness but in contrast to the spiny mouse from South Africa offsets are more precise and before the commencement of the light phase (Weber & Hohn, 2005; Cohen *et al*. 2009).

Food availability in mesic environments is generally higher than in the drier and harsher regions in which the golden and common spiny mice occur naturally. Therefore, the more pronounced activity peak exhibited shortly after the beginning of the dark phase and the tapering off of activity to less precise offsets of activity in the southern African spiny mouse may be a reflection of food availability in the environment, since the southern African spiny mouse may be able to acquire sufficient food in a shorter time period than these other species.

Activity patterns are flexible within and between species. For example, golden spiny mice exhibit diurnal activity in the wild, but the activity profile appears to be related to temperature and possibly food availability since it differs between winter and summer (Cohen *et al*., 2009). This flexibility may account for the activity patterns observed during the long and short day cycles in the southern African spiny mouse since summer coincides with the rainy season where these mice occur.

The influence of foraging conditions on energy balance of mammals is both the ultimate and proximate cause of seasonal breeding in many mammalian species (Bronson, 2009). Ovulation has been found to be sensitive to both temperature and food restriction in small mammals, although mice have been seen to ovulate at low temperatures provided their food intake is increased (Manning & Bronson, 1990).

Acomys spinosissimus are found in summer rainfall areas with cold, dry winters and in accordance with the above trend, has been found to breed seasonally (Medger *et al*., 2010; Medger *et al*., 2011a) with photoperiod being an important regulator (Medger *et al.,* 2011b). From these results it may follow that when food availability decreases in winter (short day cycle) these animals spend more time and energy on acquiring food during the longer dark phase. However, the absence of predators, competitors and temperature and humidity changes in the laboratory may also have influenced this.

Spiny mice from southern Africa showed an immediate response in the onset of their activity to an inverse in the light cycle. The offset, however, shifted much slower such that the activity was only fully entrained after approximately nine days. Re-entrainment experiments conducted by Weber and Hohn (2005) on common

spiny mice (*Acomys cahirinus*) indicated rapid phase shifts in both the onsets and offsets of activity. These mice exhibited very definite offsets that coincided with the onset of the light phase. However, these experiments were conducted over a period of months compared to the current experiment where light cycles were maintained for two weeks only. The offsets of activity in spiny mice from southern Africa appear to become more defined the longer they were kept under laboratory conditions. This may be due to the constant supply of food and the absence of predators giving them the freedom to move about more or spread out their activity over a longer time period the longer they are in the laboratory.

Under constant conditions, all mice in the present study displayed endogenous rhythms. Most of these free-running rhythms were shorter than 24 h, as predicted for nocturnal animals by Aschoff (1960). However, some, like their northern cousins the golden and common spiny mice, showed free-running rhythms slightly longer than 24 h (Weber & Hohn, 2005; Cohen *et al*., 2009).

The entrainment of locomotory activity to a specific phase of the day may be as a result of either physiological or morphological constraints (Mistlberger & Holms, 2000) and commonly reflects the time most advantageous to the animal, i.e., when food resources are most abundant and either attainable or when predators are least active (Saarikko & Hanski, 1990; Brandt & McCay, 2005).

The endogenous rhythm of locomotory activity was revealed once the activity rhythms of all animals free-ran in the absence of a time-giver (DD cycle). The starting point of the free-run also coincided with the phase angle of entrainment during the LD cycle which suggests that the light-dark cycle was most likely the principle entraining agent rather than the rhythm being the consequence of masking (Aschoff, 1981).

In conclusion, *A. spinosissimus* was found to be primarily nocturnal exhibiting a small amount of intermittent activity during the day. The environmental light-dark cycle plays an important role in entraining the locomotor activity rhythm in *A. spinosissimus* to the phase of the day most favorable to them. The free running rhythm was on average, shorter than 24h.

Acknowledgements

I would like to thank D. Swanepoel, K. Medger, P.R. de Bruin and L.P. Snyman for helping with the trapping and care of animals. L. Verbrugt and C. Purchase assisted and gave advice on cages and maintenance of the mice. A. Harrison and L de Vries helped with statistical analyses. K. Burger assisted with the construction of cage lids and maintenance features. We acknowledge funding from the DST-NRF for funding the South African Research Chair of Mammalian Behavioural Ecology and Physiology to NCB.

REFERENCES

ALBRECHT, U. 2002. Regulation of mammalian clock genes. *J. Appl. Physiol.* **92**:1348-1355.

ASCHOFF, J. 1960. Exogenous and endogenous components in circadian rhythms. *Symp. Quant. Biol.* **25**:11-28.

ASCHOFF, J. (1981). Freerunning and entrained circadian rhythms. In *Handbook of Behavioral Neurobiology: Biological Rhythms*: 81-93. Aschoff, J. (Ed.) New York: Plenum Press.

BEARDEN, H.J., FUQUAY, J.W. & WILLARD, S.T. 2004. *Applied AnimalReproduction*. Pearson Education, Inc., Upper Saddle River, New Jersey.

BENSTAALI, C., MAILLOUX, A., BOGDAN, A., AUZéBY, A. & TOUTOUI, Y. 2001. Circadian rhythms of body temperature and motor activity in rodents. Their relationships with the light-dark cycle. *Life Sci.* **68**:2645-2656.

BRADY, J. 1979. *Biological Clocks*. Edward Arnold Publishers. London.

BRANDT, A.J. & McCAY, T.S. (2005). Temperature and photoperiod effects on activity of the northern short-tailed shrew (*Blarina brevicauda*). *Bios*. **76**, 9-14.

BREYTENBACH, G.J. 1982. *Small mammal responses to environmental gradients in the Groot Swartberg of the Southern Cape*. MSc. Thesis. University of Pretoria.

BRONSON, F.H. 1985. Mammalian reproduction: an ecological perspective. *Biol. Reprod.* **32**:1-26.

BRONSON, F.H. 2009. Climate change and seasonal reproduction in mammals. *Phil. Trans. R. Soc. B.* **364**:3331-3340.

COHEN, R. & KRONFELD-SCHOR, N. 2006. Individual variability and photic entrainment of circadian rhythms in golden spiny mice. *Physiol. Behav.* **87**:563-574.

COHEN, R., SMALE, L. & KRONFELD-SCHOR, N. 2009. Plasticity of circadian activity and body temperature rhythms in golden spiny mice. *Chronobiol. Int.* **26**:430-446.

DAAN, S. & ASCHOFF, J. 1975. Circadian rhythms of locomotor activity in captive birds and mammals: variations with season and latitude. *Oecologia* **18**:269-316.

ENRIGHT,J.T. 1970. Ecological aspects of endogenous rhythmicity. *Annu. Rev. Ecol. Syst.* **1**:221-238.

GOLDMAN, D. 1999. The circadian timing system and reproduction in mammals. *Steroids* **64**: 679-685.

HASTINGS, M. H., MEAD, S. M., VINDLACHERUVU, R. R., EBLING, F. J. P., MAYWOOD, E. S. & J. GROSSE. 1992. Non-photic phase shifting of the circadian activity rhythm of Syrian hamsters: the relative potency of arousal and melatonin. *ScienceDirect* **591**: 20-26.

HOOGENBOOM, I., DAAN, S., DALLINGA, J.H. & SCHOENMAKERS, M. 1984. Seasonal change in the daily timing of behaviour of the common vole, *Microtus arvalis. Oecologia* **61**:18-31.

JACOB, N., VUILLESE, P. & PéVET, P. 1997. Photoperiod does not act on the suprachiasmatic nucleus photosensitive phase through the endogenous melatonin, in the Syrian hamster. *Neurosci. Lett.* **229**: 117-120.

KAKIHANA, R. & MOORE, J.A. 2004. Circadian rhythm of corticosterone in mice: The effect of chronic consumption of alcohol. *Psychopharmacology* **46**:301-305.

KIMCHI, T. & TERKEL, J. 2002. Seeing and not seeing. *Neurobiol.* **12**: 728-734.

KUMAR, V. (1997). Photoperiodism in higher vertebrates: an adaptive strategy in temporal environment. *Indian J. Exp. Biol.* **35**, 427-437.

LAAKSO, M.L., LEINONEN, L., JOUTSIMIEMI, S.L., PORKKA-HEISKANEN, T. & ALILA, A. 1995. Locomotor activity and melatonin rhythms in rats under non-24-h lighting cycles. *Physiol. Behav.* **57**: 849-856.

LIN, Y., HAN, M., SHIMADA, B., WANG, L., GIBLER, T.M., AMARAKONE, A., AWAD, T.A., STORMO, G.D., VAN GELDER, R.N. & TAGHERT, P.H. 2002. Influence of the period-dependent circadian clock on diurnal, circadian, and a periodic gene expression in *Drosophila melanogaster* **.** *Proc. Nat. Acad. Sci. USA* **99**:9562-9567.

MANNING, J. & BRONSON, F.H. 1990. The effects of low temperature and food intake on ovulation in domestic mice. *Physiol. Zool*. **63**:938-948.

MEDGER, K., CHIMIMBA, C.T. & BENNETT, N.C. 2010. Seasonal reproduction in the female spiny mouse from South Africa. *J. Zoo.* **282**:163-170.

MEDGER, K., CHIMIMBA, C.T. & BENNETT, N.C. 2011a. Seasonal changes in reproductive development in male spiny mice (*Acomys spinosissimus*) from South Africa. *South Africa. Mammal. Biol*. doi:10.1016/j.mambio.2011.11.001.

MEDGER, K., CHIMIMBA, C.T. & BENNETT, N.C. 2011b. Reproductive photoresponsiveness in male spiny mice from South Africa. *J. Zoo*. DOI: 10.1111/j.1469-7998.2011.00872.x

MISTLBERGER, R.E & HOLMES, M.M. 2000. Behavioral feedback regulation of circadian rhythm phase angle in light-dark entrained mice. *Am. J. Physiol.* **279**:813-821.

MOSKO, S.S. & MOORE, R.Y. 1978. Neonatal suprachiasmatic nucleus ablation. Absence of functional and morphological plasticity. *Proc. Nat. Acad. Sci. USA* **75**:6243-6246.

PÉVET, P. 1988. The role of the pineal gland in the photoperiodic control of reproduction in different hamster species. *Reprod. Nutr. Dev.* **28**:443-458.

PITTENDRIGH, C.S. & MINIS, D.H. (1964). The entrainment of circadian oscillators by light and their role as photoperiodic clocks. *Am. Nat.* **98**:261- 294.

POWELL, J.A., BELITSKY, D.W. & RATHBUN, G.B. 1981. Demography and activity patterns of some small mammals from the Cape province, South Africa. *J. Mammal.* **62**:646-649.

REITER, R.J. 1988. The melatonin rhythm – its message and its significance. *Neuroendocrinology Lett.* **10**: 218.

REUSS, S. 1996. Components and connections of the circadian timing system in mammals. *Cell Tissue Res.* **285**: 353-378.

RUSAK, B. 1977. The role of the suprachiasmatic nuclei in the generation of circadian rhythms in the golden hamster, *Mesocricetus auratus. Comp. Physiol.* **118**:145-164.

SAARIKKO, J. & HANSKI, I. (1990). Timing of rest and sleep in foraging shrews. *Anim. Behav.* **40**: 861-869.

SCHUMANN, D.M., COOPER, H.M., HOFMEYER, M.D. & BENNETT, N.C. 2005. Circadian rhythm of locomotor activity in the four-striped field mouse, *Rhabdomys pumilio*: A diurnal African rodent. *Physiol. Behav.* **85**:231–239.

SKINNER, J.D. & CHIMIMBA, C.T. 2005. *The Mammals of the Southern African Subregion*. Cambridge University Press, Cambridge.

SMIT, B., BOYLES, J.B., BRIGHAM, R.M. & MCKECHNIE, A.E. 2011. Torpor in Dark times: Patterns of heterothermy are associated with the lunar cycle in a nocturnal bird. *J. Biol. Rhythms* **26**:241-248.

SOKAL, R.R. & ROHLF, F.J. 1981 *Biometry: The Principles and Practice of Statistics in Biological Research*. 2nd Ed. W.H. Freeman & Co., New York.

STEPHAN, F.K. & ZUCKER, I. 1972. Circadian rhythms in drinking behavior and locomotor activity of rats are eliminated by hypothalamic lesions. *Proc. Nat. Acad. Sci. USA* **69**:1583-1586

TESTER, J.R. 1987. Changes in daily activity rhythms of some free-ranging animals in Minnesota. *Can. Field-Nat.* **101**:13-21.

TUREK, F.W. & CAMPBELL, C.S. 1979. Photoperiodic regulation of neuroendocrine-gonadal activity. *Biol. Repro.* **20**:32-50.

WEBER, E.T. & HOHN, V.M. 2005. Circadian activity in the spiny mouse*, Acomys cahirinus. Physiol. Behav.* **86**:427-433.

YELLON, S.M., TAMARKIN, L., PRATT, B.L. & GOLDMAN, B.D. 1982. Pineal melatonin in the Djungarian hamster: Photoperiodic regulation of a circadian rhythm. *Endocrinology* **111**: 488-492.