

A tale of two jirds: the locomotory activity patterns of the King jird (*Meriones rex*) and Lybian jird (*Meriones libicus*) from Saudi Arabia

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ABSTRACT

The animal-environment interaction is complex, and the ability to temporally organise locomotor activity provides adaptive and survival advantages. We investigated daily and circadian locomotor activity patterns of two jird species from Arabia occurring in dramatically different environments to determine the environmental effect on activity. The King jird occurs in mountainous regions of Azir where climatic conditions are cool and wet, while the Libyan jird inhabits low-lying hot sandy deserts where temperatures exceed 45°C during summer.

Six King jirds and nine Libyan jirds were subjected to a 12L:12D light cycle, a period of constant darkness (DD) and an inversed 12D:12L light cycle. Five of six King jirds and all Libyan jirds showed entrainment of their activity to the light cycles, most animals exhibited nocturnal activity. All entraining jirds showed circadian rhythmicity, with the periods of the rhythms very close to 24 hours. Entraining jirds inversed their activity patterns when the light cycle was inversed. The two jird species displayed comparable amounts of nocturnal activity in all light cycles presented. The King jird showed larger intraspecific variability than the Libyan jird, which may reflect more plasticity in its circadian clock, allowing it to adapt quicker to environmental changes.

Key words: circadian rhythm, King jird, light-dark cycle, locomotor activity, Libyan jird,

Meriones

INTRODUCTION

The natural environment is complex and changes considerably over time (Morgan 2004). Some changes are erratic and unpredictable while others show distinct temporal patterns. Cyclical changes of the environment allow organisms to adapt to predictable events. In an ecological context, behavioural adaptations are particularly relevant. Temporal organisation of activity to coincide with the most favourable part of the environmental cycle has obvious selective benefits (Morgan, 2004). The most predictable environmental change is the 24 day-night cycle, and indeed daily activity rhythms are a well-known phenomenon in all mammalian species (Kwon *et al.*, 2011).

Daily activity rhythms are biological in origin and are generated by endogenous pacemakers (Turek, 1994). The endogenous biological clock of mammals is located in the suprachiasmatic nucleus (SCN) in the anterior hypothalamus (Froy, 2007; Okamura *et al.*, 2002; Stephan and Zucker, 1972). In the absence of external time cues, circadian rhythms free-run with the innate period (τ) of the biological clock, that is normally close to, but not exactly 24 h (Aschoff, 1981; Refinetti, 2006). The free-running period of organisms is generally species-specific but there can be intra-specific variability (Aschoff, 1981; Pittendrigh and Daan, 1974; Refinetti, 2006). Endogenous rhythms entrain to external cues to remain synchronised with the external environment (Aschoff, 1981; Goldman, 1999). The daily light-dark cycle may be considered as the primary synchronizer of circadian rhythms (Pittendrigh and Minis, 1964; Quintero *et al.*, 2003).

The expression of circadian rhythms can be influenced by both biotic and abiotic factors in the environment (Morgan 2004). Biotic factors frequently entail interactions between species such as competition and predation (DeCoursey, 2004; Hughes *et al.*, 1994), while abiotic factors may include environmental factors such as light conditions and temperature (Halle, 2000; Ruoff and Rensing, 2004).

The nocturnal and diurnal environments differ significantly in their biological characteristics (Morgan 2004). Different selective pressures are present, and dependent on these, animals may change their preference for nocturnal or diurnal activity (Hoogenboom *et al.*, 1984; Lockard, 1978; Haim and Rozenfeld, 1993).

In this study, we investigate two closely related rodent species, the King jird and the Libyan jird, both of which are resident in Saudi Arabia, but occur in vastly different habitats. The King jird is a rock dwelling rodent that inhabits the slopes of the high altitude Asir mountains on the southwestern side of the Arabian peninsula (Harrison and Bates, 1991), where its range extends from near Mecca south into Yemen. This species has been reported at altitudes ranging from 1 350 to 2 200 m asl (Stuart 2008). Climatic conditions in the mountains are moderate, the experimental animals were collected near the Raydah protected area where the climate is generally cool and wet with frequent cloud cover (Birdlife International, 2012; Janin and Besheer, 2003). Vegetation in the Raydah areas consists of Juniper forests on the higher slopes and more deciduous trees and bushes lower down (BirdLife International 2012), hence providing more cover and a more reliable food source for animals inhabiting it (Abulfatih, 1979, 1981). The King jird lives in large burrows among bushes, frequently shared with other rodents and lizards. Very little information could be sourced for the King jird, but it has been reported to be active in the evening and early morning (Stuart, 2008).

The Libyan jird occurs widespread in the Arabian peninsula. This area consists of sandy desert and semi-desert habitats (Aulagnier *et al.*, 2008). The Libyan jird lives in burrows with multiple entrances constructed under shrubs (Lewis *et al.* 1965). Desert regions in Saudi Arabia are characterised by an extreme span of ambient temperatures, little or no rainfall, intense solar radiation and a low primary production (Schmidt-Nielsen, 1997; Degen, 1997). Mammals inhabiting these environments have evolved both physiological and

behavioural adaptations to survive the extreme temperatures and lack of water (Macfarlane, 1968). A fossorial lifestyle is the norm for small desert living rodents who spend their days in burrows or caves and forage for food during the night. The burrows provide a refuge for food storage and also enable them to regulate their body temperature and the humidity in the burrow prevents excessive water loss. By managing times of activity and inactivity, small mammals can avoid overheating and desiccation during the hottest times of the day. Sporadic reports of locomotor activity patterns of Libyan jirds are ambiguous about the active time of individuals of this species. The Libyan jird has been described as diurnal (Roberts, 1977) and nocturnal by different sources (Vesey-Fitzgerald 1953).

It is clear that a working knowledge of locomotor activity patterns in jirds is lacking, therefore this paper sets out to shed new light on this paucity of information. The aim of the study was therefore firstly to characterise the locomotor activity rhythms of the two species under a controlled 12L:12D light cycle, then to determine whether either species expressed an endogenous circadian rhythm under constant conditions. In addition, we investigated whether the jirds could shift their activity according to an inverse in the light cycle to determine whether the transition between light and dark triggers activity. We predicted that, since the Libyan jird occurs in a habitat with more severe temperature fluctuations, it will be more strictly nocturnal than the King jird. The Libyan jird was expected to display an endogenous period (τ) of shorter than 24 hours, as is common in nocturnal species, while the King jird, should it display diurnal activity, was expected to have a τ of longer than 24 hours (Aschoff 1979).

MATERIAL AND METHODS

General

The rodents used in this experiment consisted of six King jirds (*Meriones rex*) and nine Lybian jirds (*Meriones libicus*). The King jirds (5 males and 1 female; mean body mass \pm SEM: 198 ± 11.5 g) were collected near the Raydah Protected Area near Abha City, in south western Saudi Arabia ($18^{\circ}00'N$, $24^{\circ}46'E$), and the Lybian jirds (5 males and 4 females; mean body mass \pm SEM: 187.2 ± 24.5 g) were trapped near Thumamah, North of Riyadh ($25^{\circ} 07'N$, $46^{\circ} 49'E$). The jirds were trapped with cage live traps (Strauss *et al.*, 2008) baited with bread and peanut butter. After capture, the animals were transported to the animal facility at the Department of Zoology, College of Science, King Saud University, Riyadh, Saudi Arabia where the experimental procedures were carried out. Animals were allowed to acclimatize for approximately one month before experiments commenced. The experimental protocol was evaluated by the Animal Use and Care of the University of Pretoria, ethics clearance number EC013-12 and EC015-12.

The jirds were housed individually in plastic containers (50x 40x 40cm) and provided with wood shavings and tissue paper as nesting material. Animals were fed on pelleted poultry food from the Arabian Agricultural Services Company (Arasco, Riyadh, Saudi Arabia) every 14 days at the end of the cycle. The diet was supplemented with carrots and cucumber when light cycles were changed. Food and water was provided *ad libitum*, and a few drops of multivitamins were added to the drinking water. During the feeding times the general health and condition of the animals was monitored.

The experimental room was temperature controlled at $25 \pm 1^{\circ}C$ and the room was light controlled which enabled us to create different light regimes for the experimental period.

Experimental procedures

Animals were maintained on a 12L:12D cycle (6:00 – 18:00L) for 14 days to determine how well they entrain to light cycles. This was followed by a 14 day DD cycle in

order to determine whether the birds have endogenous free running rhythms of locomotor activity. Subsequently the lights were switched back to the original 12L:12D cycle to re-entrain the animals, after which the light cycle was inverted (12D:12L) for 14 days to investigate whether and how fast the animals change their activity according to the new light cycle.

Activity measurements

An infrared captor (Quest PIR internal passive infrared detector; Elite security products (ESP), Electronic lines, UK) was fitted above each of the cages in which the animal was housed. These sensors were placed in the middle of each cage to detect any movement that the animal made in any area of the cage. A reading was taken once every minute and the activity measurements were captured by the program Vital View on a computer system (Vital View™, Minimitter Co., Inc., Sunriver, OR, USA; www.minimitter.com).

Data analyses

Activity was depicted as double plotted actograms with ActiView Biological Rhythm Analyses 1.2 software (Minimitter Co., Inc., Sunriver, OR, USA; www.minimitter.com) so that activity patterns could be visualised. The phase angle (difference in time between the onset of activity and beginning of dark phase) and was calculated for each animal. To determine peak activity times, activity profiles were generated in Clocklab (ClockLab™, Actimetrics, Evanston, IL, U.S.A.). Microsoft Excel Macro's (Microsoft® Office Excel® 2007) were used to determine percentage activity during the day and night phase for each light regime per animal. The circadian period of locomotor activity rhythms during DD were determined using Clocklab. To determine whether the amount of activity during the different phases was significantly different from one another, Statistica 9.0 (© StatSoft, Inc. 1984-

2009) was employed. Due to small sample sizes, non-parametric statistics were used for all calculations.

RESULTS

12L:12D

Five of the six King jirds entrained their locomotor activity to the 12L:12D cycle presented, the remaining individual displayed activity throughout the 24 hour period. All entraining animals showed a preference for activity during the dark phase of the light cycle ($78.3 \pm 6.9\%$)(Fig.1, 2a). The peak activity time for the jirds was slightly before the middle of the dark phase ($n=5$, mean = $23h26 \pm 0h38$). Two individuals displayed clear onsets of activity but less defined offsets, two more exhibited clear offsets while the onsets were less clear and one individual distributed its activity throughout the dark phase of the light cycle with no clear on or offsets.

All nine Lybian jirds showed entrainment of their activity but, a large amount of intra-species variability was present. Six of the nine jirds showed two bouts of activity, one individual displayed 3 bouts of activity, and two animals exhibited activity throughout the entire dark phase of the light cycle. Eight of the nine animals showed more activity during the dark phase of the light regime ($78.5 \pm 5.7\%$)(Fig.1, 2b). The peak activity time was seven hours after onset of the dark phase ($n=9$, mean = $0h58 \pm 0h59$). Three individuals displayed clear on and offsets, four animals exhibited distinct offsets, but not onsets, and the remaining two animals showed discernible onsets but not offsets. The mean phase angle for the onsets was $18h01 \pm 0h04$ while the mean phase angle for offsets was $6h37 \pm 0h15$. The amount of activity during the dark phase of the light cycle did not differ significantly between the two species (Mann-Whitney U test, $n_1=6$, $n_2=9$, $U=24$, $Z=0.29$, $p=0.77$).

DD

All King jirds that entrained their activity to the light cycle showed circadian rhythmicity, with the periods of the rhythms very close to 24 hours ($n=5$, mean = 23h56 \pm 0h03, range 23h50-24h05). The mean percentage of activity during the subjective night was 76.5 \pm 7.7%, which is almost similar compared to the dark phase activity of the first LD cycle (Wilcoxon matched paired test $Z = 1.78$; $T=2$; $n = 6$; $p = 0.074$)(Fig.1, 3a).

All Lybian jirds displayed free-running rhythms in constant darkness, the periods were, as in the King jirds, close to 24 hours ($n=9$, mean = 23h57 \pm 0h04, range 23h33-24h09). The mean percentage of activity during the subjective night was comparable to that observed in the King jird (74.6 \pm 4.3%). The percentage of activity during the subjective night was not significantly different from activity displayed during the dark phase of LD1 (Wilcoxon matched paired test $Z = 0.888$; $T = 15$; $n = 9$; $p = 0.37$)(Fig. 1, 3b). There is no significant difference in the amount of activity during the subjective night between the two species of jird (Mann-Whitney U test, $n_1=6$, $n_2=9$, $U=23$, $Z=0.41$, $p=0.68$).

LD and inverted LD

Three king jirds showed a higher percentage of activity during the dark phase of the second LD cycle compared to the first LD cycle, and three exhibited a lower percentage of activity compared to the first LD cycle. The mean percentage of activity between LD1 and LD2 did not differ significantly (Wilcoxon matched paired test $Z = 0.734$; $T = 7$; $n = 6$; $p = 0.463$).

All King jirds with discernible rhythms shifted their activity according to the new light cycle. After inverting the light cycles, re-entrainment of visible rhythms of the two animals that showed clear on- and offsets of locomotor activity, took place in about 4 days. The mean percentage of activity during the dark phase of DL was 71.1 \pm 17.5%. The percentage of activity displayed during the dark phases of LD2 and DL was significantly different (78.5 vs

71.1%) from one another (Wilcoxon matched paired test $Z = 2.2$; $T = 0$; $n = 6$; $p = 0.028$) (Figure 1, 4a).

No significant difference in the amount of activity during the dark phase between the two species (Mann-Whitney U test, $n_1=6$, $n_2=9$, $U=25$, $Z=-0.17$, $p=0.86$).

There was no significant difference in the percentage of activity during the dark phase of LD1 and LD2 in the Lybian jird (Wilcoxon matched paired test $Z = 0.059$; $T = 22$; $n = 9$; $p = 0.95$). All Lybian jirds re-entrained to the inversed light cycle. Time for re-entrainment of locomotor activity was on average around 6 days, slightly longer than observed in the King jirds. When the percentage of activity during the dark phase of the DL cycle was compared to the LD2 cycle, a significant difference was apparent (Wilcoxon matched paired test $Z = 2.073$; $T = 0$; $n = 9$; $p = 0.038$). However, when the days during re-entrainment were excluded, there was no significant difference in the amount of activity exhibited during the dark phases of LD2 and DL (Wilcoxon matched paired test $Z = 1.717$; $T = 8$; $n = 9$; $p = 0.086$) (Figure 1, 4b).

There are no significant differences in the amount of activity during the dark phase between the two species in this light cycle (Mann-Whitney U test, $n_1=6$, $n_2=9$, $U=26$, $Z=0.59$, $p=0.95$).

DISCUSSION

Environmental factors are not constant, but vary considerably over time. By anticipating cyclic changes in the environment, animals can optimise their survival by arranging their activity temporally to occur at the most beneficial times.

Both jird species investigated entrained their activity rhythms to light cycles and showed a preference for nocturnal activity. Although King jirds exhibited more activity during the dark phase of the light cycle, more intra specific variation was observed than in the

Libyan jird, as some individuals displayed a substantial portion of activity during the day. This finding is in agreement with Stuart (2008), and considering the natural climatic conditions of the environment this species inhabits, some daytime activity could be explained by the more favourable conditions for foraging during the day.

Similar to the King jird, Libyan jirds were demonstrated to be active predominantly during the dark phase of the light cycles. This result contrasts with that of Roberts (1977) who reported Libyan jirds to be diurnal. Nocturnal activity appears sensible in this species given the high daytime temperatures, and there was indeed less variability between individuals than seen in the King jird. For small mammals inhabiting desert areas, the largest challenges for survival are the extreme temperatures and the low availability of water (Schmidt-Nielsen, 1997; Al-Helal, 2003). Several other jird and gerbil species that occur in hot dry areas have been investigated, and have also been described to exhibit primarily nocturnal activity (Demas *et al.*, 2001; Gould and McKay 1998; Klaus *et al.*, 2000). Since the majority of rodent species show a preference for nocturnal activity (Demas *et al.*, 2001), harsh daytime climatic conditions may merely reinforce in desert species a common evolutionary trait for rodents as a whole.

It is important to note that laboratory conditions as well as the methods used to assess activity may influence the resulting activity patterns. For instance, the Mongolian jird displays crepuscular activity under natural conditions (Stutz, 1972, Pietrewicz *et al.*, 1982), but when it has access to a running wheel, its activity pattern is nocturnal (Weinert *et al.*, 2007). Likewise, temperature and lighting conditions (square wave vs natural light) may have an effect on activity rhythms (Boulos *et al.*, 1996, Tang *et al.*, 1998). It has also been suggested that high sensitivity towards external factors (such as noise) can cause variable locomotor activity patterns (Klaus *et al.*, 2000).

Free-running rhythms of locomotor activity have, so far, not been described for either the King jird or the Libyan jird. Our results show that all entraining animals from both species displayed endogenous rhythms very close to 24 hours. In general, the onsets and offsets of activity became less precise during constant conditions however, we did not find the amount of intra-specific variability in free-running length reported in the Mongolian gerbil by Klaus *et al.* (2000). Both the King jird and the Libyan jird displayed comparable amounts of activity during constant conditions and the first LD cycle. Both species exhibit free-running rhythms very close to, but slightly shorter than 24 hours, confirming a functional circadian clock for both species. The importance of circadian rhythms in both nocturnal and diurnal animals is illustrated by the work of DeCoursey *et al.* (1997, 2000) where free-living chipmunks and squirrels with ablated circadian clocks (SCN's) were shown to have a significantly reduced survival rate as a result of them emerging aboveground at inappropriate times. The SCN appeared to prevent surface activity during times of greatest predation risk (Zucker 1983). Obviously, nocturnality does not exclude predation as a number of birds of prey (several species of owl) and other carnivores (red fox, sand cat, common genet etc.) also display nocturnal activity (Clements 2000, Mallon & Budd 2011).

All entraining animals from both species inverted their activity according to the shift in the light cycle. The King jird re-entrained its activity on average within 4 days while re-entrainment in the Lybian jird generally took place in 6 days. Pohl (1978) suggested that the direction and rate of re-entrainment is dependent on species differences in the characteristics of the circadian systems and its sensitivity to light changes. Phase shifts normally occur in the direction of the zeitgeber (environmental cyclic variable) shift (Aschoff *et al.*, 1975), which in this case could be either, since the zeitgeber shifted by 12 hours.

The King jirds did not show a very directional pattern of re-entrainment. After the inversion of the light cycle, two of the 5 entraining animals became arrhythmic before showing more

activity during the new dark phase after a few days. Two animals appeared to shift their activity with a phase advance and the remaining animal first showed a phase delay, then a phase advance. Lybian jirds exhibited clear delays in their activity until they were fully re-entrained with the new cycle. When investigating several mammalian and avian species, it was discovered that after 12 hour phase shifts, the majority of individuals re-entrained by phase delays (Pohl, 1978). In nocturnal rodents, re-entrainment following a phase delay normally occurs faster than after a phase advance (Aschoff *et al.*, 1975; Halberg *et al.*, 1971; Pittendrigh and Daan 1976, Schöttner *et al.*, 2011). The difference in rate of re-entrainment between the two species may be ascribed to species differences in the plasticity of the circadian clock. Changes in weather can cause temporary variation in temperature and light intensity (Dubruille and Emery, 2008), and faster re-entrainment to cyclic rhythms would have obvious survival advantages.

This study provides the first description of locomotor activity rhythms for the King jird and the Lybian jird. Both species display nocturnal activity, the King jird shows more variability in activity in all light cycles presented. This difference may be related to the different habitats in which these two species occur. Although most rodents are nocturnal, Lybian jirds inhabit harsh desert environments where it is imperative for these small mammals to confine their activity periods during the night in order to avoid overheating and dehydration. In contrast, King jirds occur on mountain slopes in the south western parts of Saudi Arabia. Temperatures are milder and there is more ground cover, therefore King jirds are not as restricted to nocturnal dwelling to ensure survival since climatic conditions may favour some daytime activity. In the laboratory under controlled conditions, the King jird displays a more plasticity of the circadian clock, which may allow it to be more adaptable to changes in the environment than the Lybian jird. However, the laboratory environment is highly artificial, and frequently yields different results to those seen in the natural environment.

Complementary field studies are needed to shed some additional light on the locomotor activity patterns of these species in their natural habitat.

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FIGURE LEGENDS

Figure 1 Mean percentages of activity (\pm SEM) during the dark phase of LD and DL and subjective darkness for DD for the King jird and the Lybian jird.

Figure 2(a) A double plotted actogram of a well-entrained locomotor activity rhythm of a King jird showing a distinct onset, (b) an example of a Lybian jird displaying two distinct bouts of activity with clear on and offsets of activity. The bar at the top of the actograms illustrates when lights were on and off.

Figure 3(a) An example of a free running rhythm of a King jird with a period slightly shorter than 24h. (inset) is the periodogram showing the period of the rhythm at 23.83h. (b) An example of a free running rhythm of a Lybian jird with a period slightly longer than 24h. (inset) Periodogram of the same individual showing the period of the rhythm at 24.03h.

Figure 4(a) An actogram of a King jird that illustrates the delayed transition between LD and DL (27-31 October); (b) An example of a Lybian jird to show the transition period between LD2 and LD. The inversion of the lights are indicated with inversed white and black bars for the light and dark phases half way down the figure.

Figure 1:

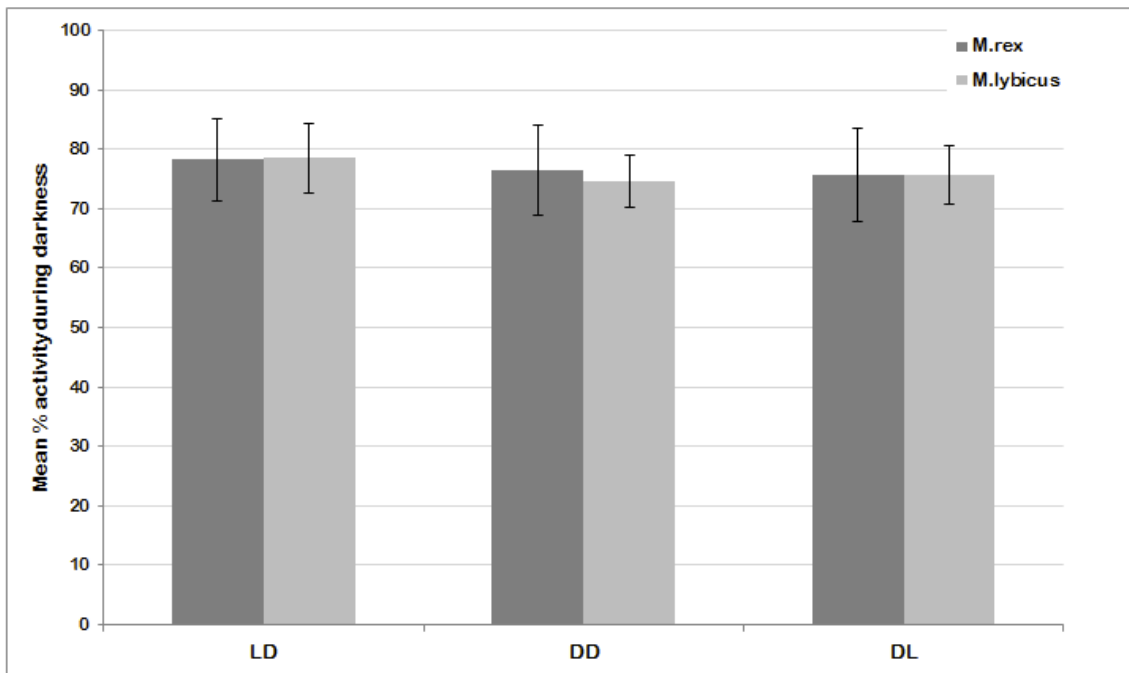


Figure 2a:

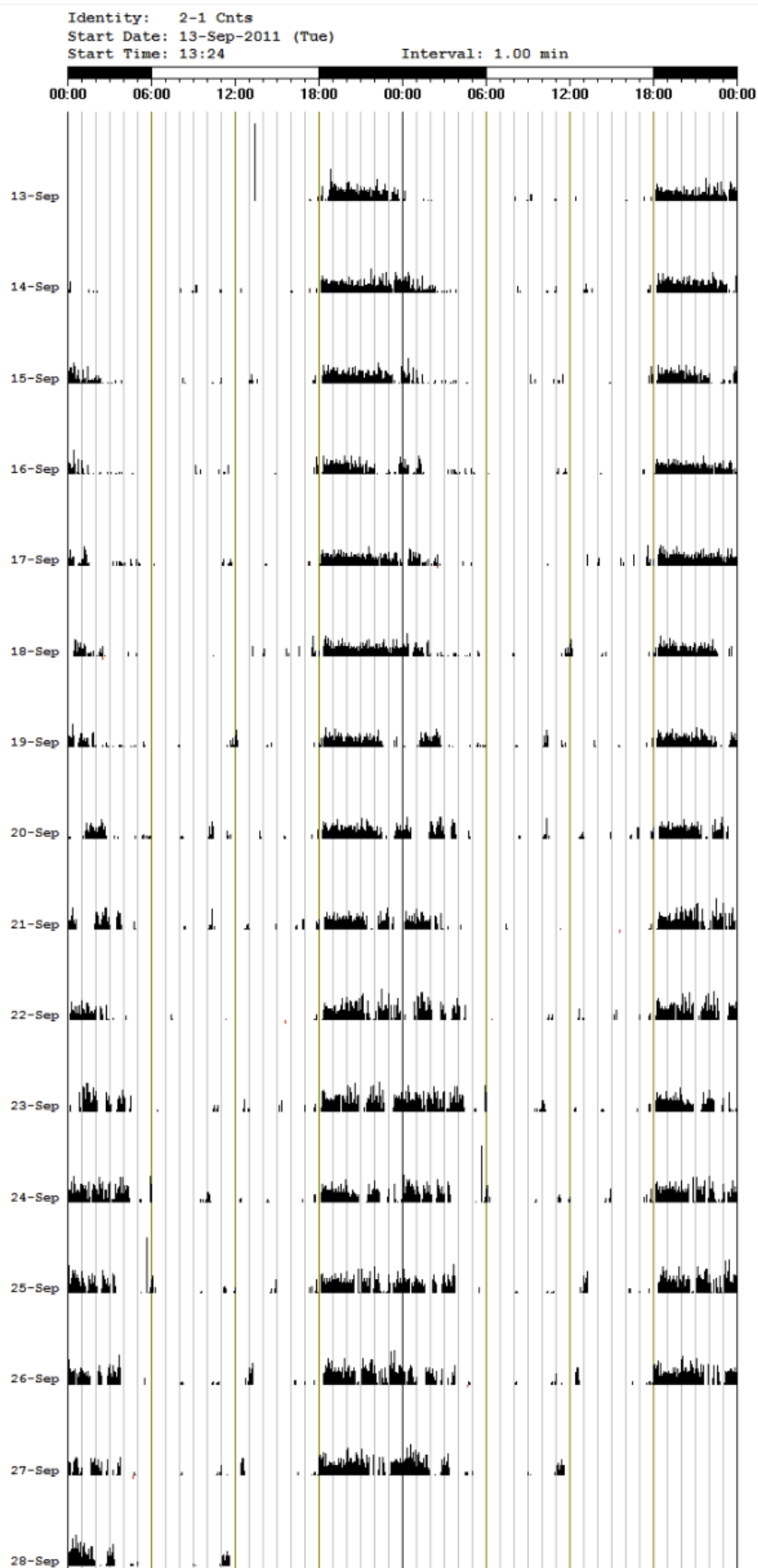


Figure 2b:

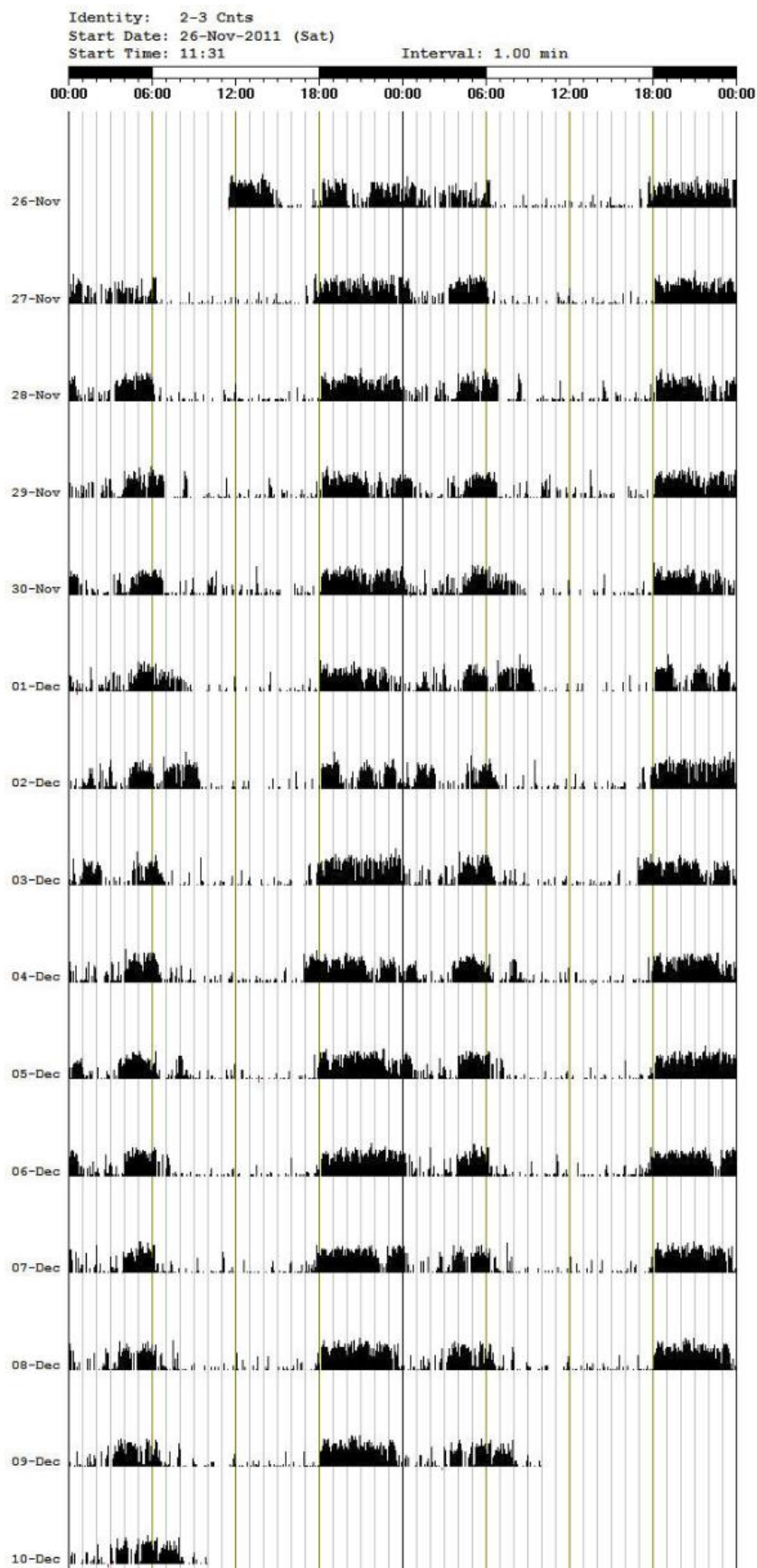


Figure 3a

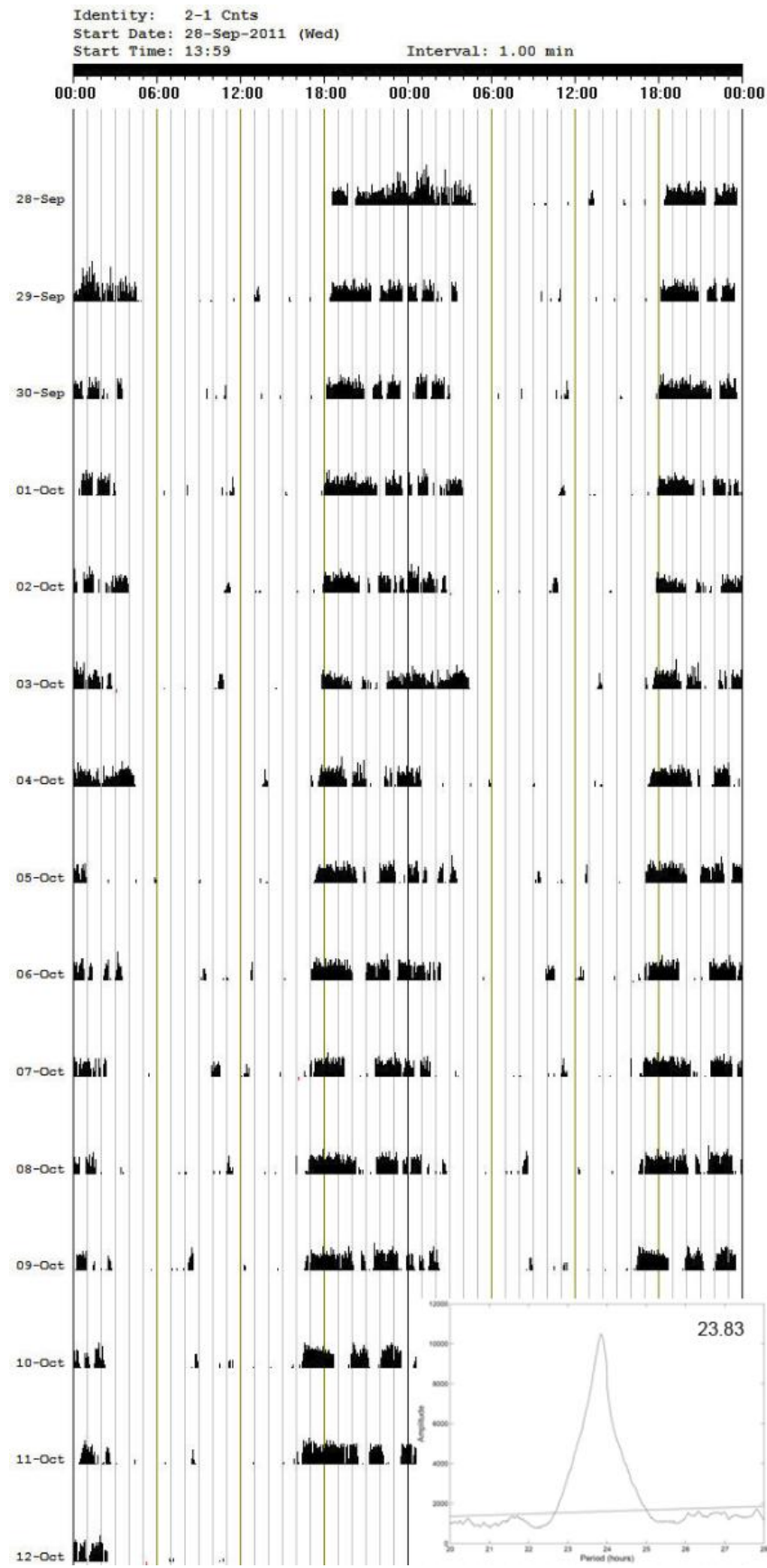


Figure 3b:

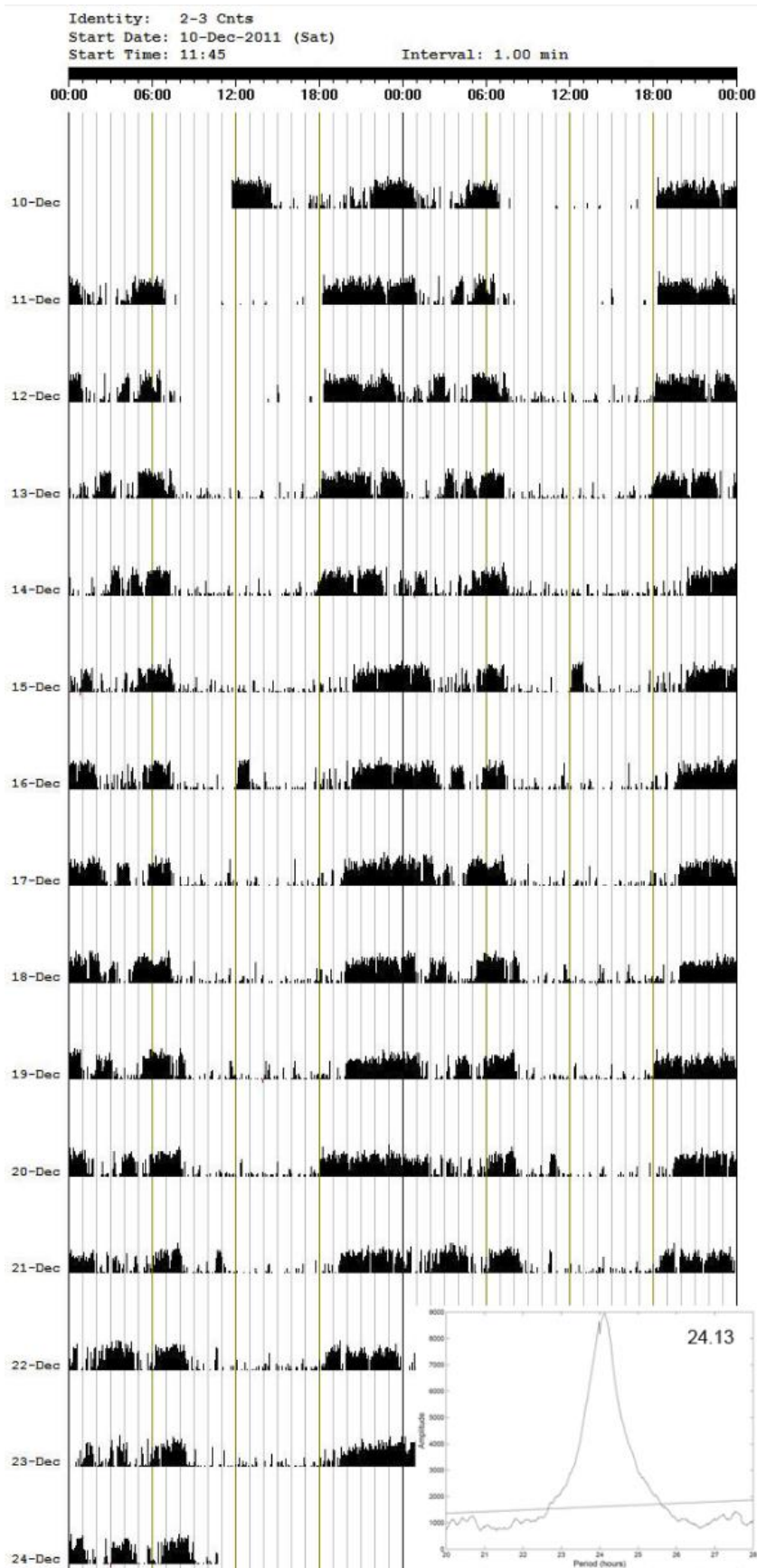


Figure 4a

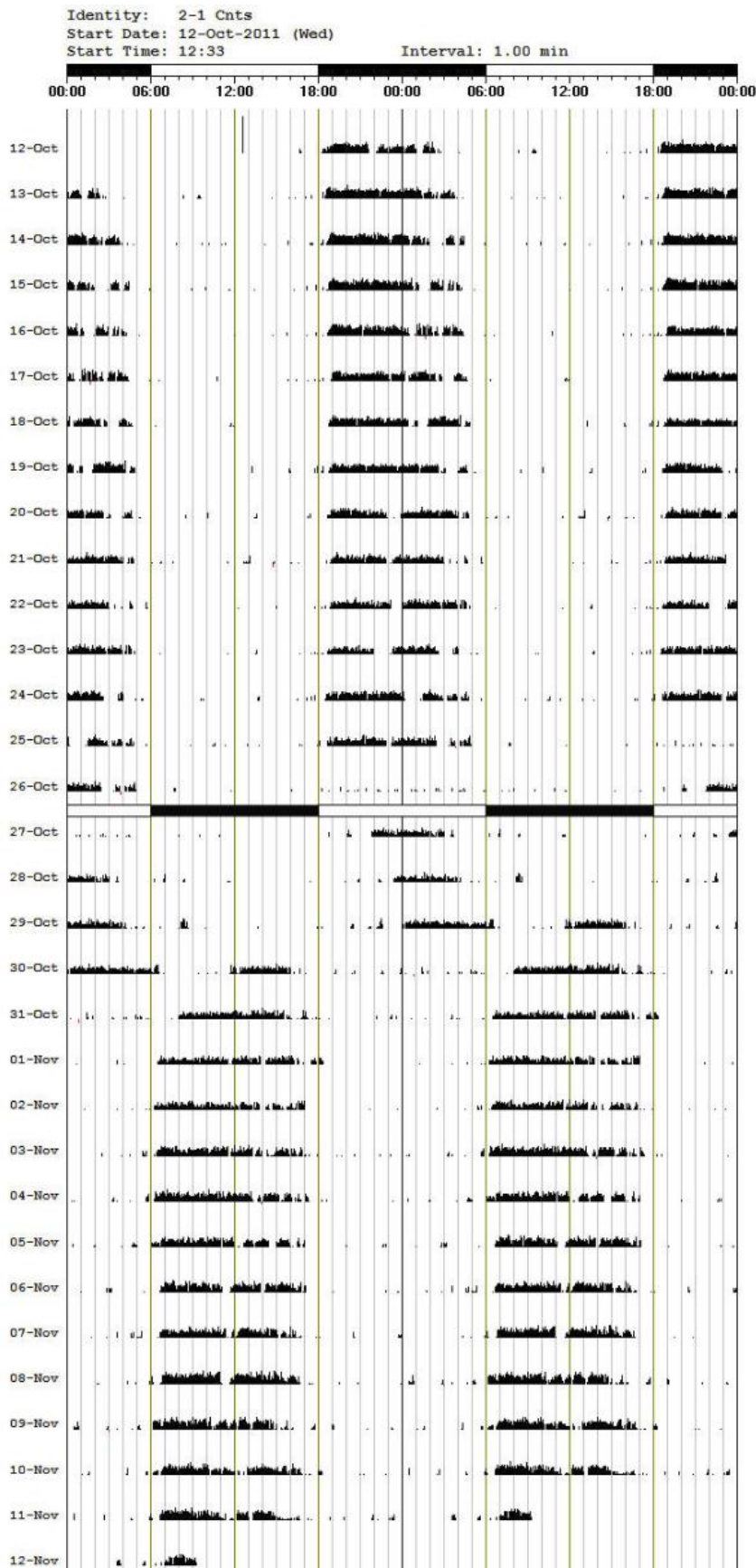


Figure 4b

