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Hicham Farsi, Driss Harti, Mohamed Rachid Achaâban, Mohammed Piro, Mohammed Ouassat, et al.. Seasonal variations in locomotor activity rhythm and diurnal activity in the dromedary camel (*Camelus dromedarius*) under mesic semi-natural conditions. *Chronobiology International*, 2022, 39 (1), pp.129 - 150. 10.1080/07420528.2021.1984936 . hal-03843903

**HAL Id: hal-03843903**

**<https://cnrs.hal.science/hal-03843903>**

Submitted on 8 Nov 2022

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# Seasonal variations in locomotor activity rhythm and diurnal activity in the dromedary camel (*Camelus dromedarius*) under mesic semi-natural conditions

Chronobiol Int. 2022 Jan;39(1):129-150.

doi: 10.1080/07420528.2021.1984936.

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## **ABSTRACT**

The dromedary camel (*Camelus dromedarius*) is a large ungulate that copes well with the xeric environment of the desert. Its peculiar adaptation to heat and dehydration is well-known. However, its behavior and general activity is far from being completely understood. The present study was carried out to investigate the ecological effect of the various seasons on the locomotor activity (LA) rhythm and diurnal activity of this species. Six adult female camels were maintained under mesic semi-natural conditions of the environment during four periods of 10 days in each season: autumn, winter, spring and summer. In addition, three female camels were used to test the effect of rain on the LA rhythm during a period of 18 days during the winter. The animal's LA was recorded using the locomotion scoring method. Camels displayed a clear 24.0h LA rhythm throughout the four seasons. Activity was intense during Day-time (6–22 fold higher in comparison to night) and dropped or completely disappeared during nighttime. Mean daytime total activity was significantly higher in the summer as compared to winter. Regardless of the season, the active phase in camels coincided with the time of the photophase and thermophase. Furthermore, the daily duration of the time spent active was directly correlated to the seasonal changes of photoperiod. The diurnal activity remained unchanged over the four seasons. For each season, the start and the end of the active phase were synchronized with the onset of sunrise and sunset. At these time periods, temperature remained incredibly stable with a change ranging from 0.002 to 0.210°C; whereas, changes of light intensity were greater and faster with a change from 0.1 to 600 lux representing a variation of 3215–7192 fold in just 25–29 min. Rainfall affected the pattern of the LA rhythm with occurrence of abnormal nocturnal activity during nighttime disturbing nocturnal rest and sleep. Here we show that the dromedary camel exhibits significant seasonal changes of its activity within daylight hours. However, the diurnal pattern remains unchanged regardless of the season; whereas, abnormal nocturnal activity is observed during periods of rain. The activity onset and offset in this species seems to be primarily driven by the changes in light intensity at dusk and dawn.

## **KEYWORDS**

Camel; locomotor activity rhythm; seasonal changes; diurnality; temporal niche switching; daily ambient temperature cycle; light intensity

## Introduction

Several vertebrate species have developed different strategies to regulate behavioral activity over the 24 h cycle. This temporal niche partitioning is dictated by the survival needs required by animals to meet or escape specific ecological pressures of biotic and abiotic factors (Aschoff et al. 1971; Castillo-Ruiz et al. 2012; Cloudsley-Thompson 1961; Kronfeld-Schor et al. 2017; Sih 1980). Daily changes in these environmental factors shape the activity and behavior of animals to a specific pattern which can be nocturnal, diurnal, crepuscular or even cathemeral (Refinetti 2008). In mammals, the daily activity pattern throughout the season is shaped by three major mechanisms (Chiesa et al. 2010): (a) a central circadian pacemaker located in the hypothalamic suprachiasmatic nucleus that drives the endogenous rhythm entrained by zeitgebers in the external environment, mainly by the light–dark cycle (Challet 2007); (b) Masking effect of different factors that either positively or negatively determine the phase predominance and the shape of locomotor activity pattern, regardless of the central pacemaker control; and finally, (c) switching mechanisms downstream from the clock that are implicated in temporal niche partitioning of the activity (nocturnal or diurnal patterns) without any changes in the central clock properties.

Temporal niche switching is displayed by some species to overcome compromised survival conditions, by shifting their pattern from diurnality to nocturnality/or crepuscularity activity or vice versa (Brown and Kotler 2004; McNamara 1987; van der Vinne et al. 2014; Vivanco et al. 2010). It is an important adaptive strategy for individuals and species survival (Refinetti 2008) and was reported in a wide range of mammals (Mrosovsky and Hattar 2005), including small rodents (Daan et al. 2011; Fenn and Macdonald 1995; Hut et al. 2011; Levy et al. 2007; Shkolnik 1971; van der Vinne et al. 2019), many carnivores (Lourens and Nel 1990; Merrill and Mech 2003) and some primates (Fernández-Duque et al. 2010; Kleitman and Engelmann 1953). Literature reports on the existence of temporal niche switching cases under the harsh environment of the desert are extremely scarce. Such adaptive strategy was well documented in the Arabian oryx (*Oryx leucoryx*) in which a temporal niche switching occurs between seasons with diurnal activity during the cooler winter and nocturnal/crepuscular activity during the hotter summer and intermittent patterns during spring and autumn (Davimes et al. 2017, 2016). Such changes in activity pattern appear to be linked to high ambient temperature ( $T_a$ ) and heat experienced by the Arabian oryx during the summer season (Davimes et al. 2017; Hetem et al. 2012a, 2012b).

The dromedary camel (*Camelus dromedarius*) is another ungulate of the desert and one of the most adapted species to this harsh biotope. This large domesticated mammal is permanently exposed to environmental conditions that can be life-threatening. These conditions include low or no patterns of precipitation, a scarcity of water and food, extreme solar radiations, heat stress and high amplitudes of  $T_a$ . To cope with such xeric environment, this species employs specific adaptive processes in order to avoid heat and to economize water (Ben Goumi and Faye 2002; Bengoumi et al. 1993; Bouâouda et al. 2014; Schmidt-Nielsen et al. 1957; Wilson 1984; Yagil 1985). Heterothermy is one of the fascinating mechanisms of adaptation of the camel to heat stress and dehydration that allows water economy (Bouâouda et al. 2014; Schmidt-Nielsen et al. 1957). Under such conditions, dromedary camel switches from endothermic homeothermy to become heterothermic with daily rectal temperature rising up to 42°C and dropping during night to 34°C with an over a range of 6–8°C (Schmidt-Nielsen et al. 1957). Behavioral changes were also reported under such heterothermy. Indeed, with progressing dehydration, camels expose their body to a surface as small an area as possible to the solar radiations by assuming a sitting position on the ground and their trunk oriented lengthwise in the direction of the solar radiations; while, at night, they dissipate passively the overloaded heat by convection and also by conduction (Schmidt-Nielsen et al. 1957; Schmidt-Nielsen 1959; for review see Tibary and El Allali 2020).

Much has been reported about the fascinating adaptive mechanisms displayed by the camel; however, its behavior and activity have not been fully studied to date. Recent data from our team (Farsi et al. 2020, 2018) revealed that, under natural conditions, camel exhibits a clear rhythm of activity

corresponding to a pattern of diurnal activity. However, timing management of the daily activity pattern throughout the changing seasons is still not documented.

In the present study, we assumed that, as the Arabian oryx, the dromedary camel could show a temporal niche switching of its activity throughout the seasons. To achieve this, locomotory activity rhythm in the camel was characterized under mesic semi-natural conditions over the four seasons of the year. The study aimed also to investigate the temporal relationship between the pattern of activity of the camel and the environmental changes, such as  $T_a$  and light intensity that may entrain this pattern, in addition to the effect of rain during the winter season.

## Material and methods

### Animals and experimental design

Six non-pregnant adult female camels (Identified as camel 1–6) originating from southern Morocco (latitude 23° 43'N, 15° 57'O) were used for the present study. The age of animals varies from 7 to 10 years and their mean mass was  $486.0 \pm 33.0$  kg. They were individually housed in outdoor enclosures of 100 m<sup>2</sup> (10 m × 10 m) at the Hassan II Ind Agronomy and Veterinary Medicine Institute of Rabat (Latitude: 34°01'N, Longitude: 6°50' W) where they were maintained under mesic seminatural conditions. The enclosures were devoted from any roofs and, therefore, no shade was provided in order to mimic the desert conditions where dromedaries are directly exposed to sun radiations and natural environmental changes. Prior to the experiments, each animal undergoes in its enclosure a phase of 2 weeks of adaptation. During the whole experiments, camels were not able to see each other but were allowed to hear the rest of the group.

The climate of Rabat region is warm to hot and dry during summer ( $15.3 \pm 3.23^\circ\text{C}$ – $49.1 \pm 1.70^\circ\text{C}$ ) and mild damp and cold during winter ( $08.3 \pm 0.74^\circ\text{C}$ – $36.7 \pm 1.73^\circ\text{C}$ ). Camels were able to move freely in their enclosures. They received a balanced food source (Maraa for Camelids, Alf Sahel, Morocco) and barley straw ad libitum and had free access to water. All animal procedures adopted in the present study comply with the ARRIVE (Animal Research Reporting of In Vivo Experiments) guidelines. The study was in agreement with the Hassan II Ind Agronomy and Veterinary Institute of Rabat and Moroccan Ministry of Agriculture recommendations which are in accordance with international ethical standards (European Union Directive 2010/63/EU) legislation and recommendations in the field of chronobiology (Touitou et al. 2006).

### Locomotor activity recording

Video-recordings were performed using high-resolution cameras equipped with infrared emitters (Dahua® HACHFW1200RM camera – Dahua Technology Co., Ltd, Zhejiang, China). The recorded videos were stored into a Digital Video Recorder (Dahua DVR (DHIHCVR5108H-S2, Dahua Technology Co., Ltd, Zhejiang, China) providing a large storage capacity of 1 Terabyte. For each enclosure, three cameras were positioned at a high of 2.5–3 m providing three viewpoints (frontal and two lateral views from the back, one from the right and the other from the left) covering the pen area to easily and clearly follow the camel's movements.

The LA rhythms were recorded in each of individual camel using the validated video-locomotion scoring technique (Farsi et al. 2020, 2018). This technique uses six scores of activity with different amplitudes that are visualized throughout an analysis of recorded video sequences of each camel on a computer screen. The assignment of the six scores according to time in minutes was carried out by two evaluators well-trained in behavioral scoring using an Excel document. The scores correspond to different activity states following a predefined scale, where:

- Score 0: corresponds to a camel in a sitting position and not moving;
- Score 1: is a sitting position with slight movements;
- Score 2: represents a camel in a standing position but not moving;
- Score 3: is a standing camel just moving its limbs with no real locomotion;
- Score 4: corresponds to a camel walking with exploration of the surrounding area; and

- Score 5: is assigned to a camel with intense locomotor activity or in agitated state.

The LA rhythms were measured separately in each camel using a time set of 1 min. Total rest of animal corresponds to the sitting position in the sternal recumbency; while, inactivity/activity threshold was considered when camels switch from score 2 to score 3. While; scores of 3, 4 and 5 were considered for calculating intense activity.

#### Experiment 1: seasonal rhythm of LA

Locomotor activity rhythms were recorded in camels during the four seasons. Each period lasted ten days during summer, autumn, winter and the spring seasons (Table 1). The experiment took place under outdoor conditions of the natural environment and during clear sky and sunny days. For each period, the average of the LD-cycle, sunrise and sunset times, times of morning civil twilight start and of evening civil twilight end, changes of Ta, humidity and precipitations quantities were recorded or identified (Table 1). The annual photoperiodic variation, at this location, is 04:32 h; while, the annual changes of the recorded Ta under direct solar radiations varied between 6 and 15°C for minimums and 31 and 49°C for maximums. Relative humidity of ambient air fluctuated between 40% and 82%, measured by a hygrometer (Model STHW, Thermo Hygrometer electronic). Air Ta was measured every 1 min using a data logger, Ibuttons (DS1922L, Dallas Semi-Conductor, USA). These devices were calibrated in water bath prior to use. The devices were programmed with a resolution of 0.0625°C then suspended in the air inside the enclosures (At a height of 2 m) and exposed directly to solar radiations from sunrise to sunset. Light intensity was measured at the night–day and day–night transitions every 1 min using a luxmeter (Testo 540, France). Sunrise and sunset times as well as civil twilight start and end were obtained from various freely accessible databases including those of Time-and-Date-AS limited liability company (Stavanger, Norway: <https://www.timeanddate.com/>) and of the regional Direction of Meteorology of Rabat, Morocco.

#### Experiment 2: rhythm of LA during rainy days of winter

This experiment was carried out one year after experiment 1. Video recordings were realized for locomotor activity rhythms scoring in 3 camels (Camels 1, 2 and 3) during 18 consecutive days during the winter (10th–27th February, 2017). The three other camels (camels, 4, 5 and 6) were discarded from the study because of their inconvenient healthy state (affected with a chronic infectious disease) impacting their general activity. The three used camels were maintained under the same outdoor conditions as in the previous experiment. The average of LD-cycle, sunrise and sunset times, morning civil twilight start and evening civil twilight end, changes of Ta, humidity and rainfall data were similarly measured as in experiment 1 and described in Table 2.

LA rhythm was recorded according to the same method used in the previous experiment. Data analysis The LA rhythm data were plotted either as simple curves using Sigma-Plot software (Sigmaplot v12.0, Systat, Chicago, IL) or as actograms using the software Actogram Plotter® (Refinetti R, Circadian Rhythm Laboratory, University of South Carolina, <http://www.circadian.org/software.html>).

LA rhythm parameters such as period, robustness, amplitude and mesor were determined by a nonlinear least squares method using the following softwares: Cosinor, Acro and LSP software (Refinetti R, Circadian Rhythm Laboratory, University of South Carolina, <http://www.circadian.org/software.html>). This Cosinor analysis was performed by using the following mathematical equation:

$$f = y_0 + a \times \cos[2\pi \times (t - \phi)/\tau]$$

Where f is LA at time t, : y<sub>0</sub> is the mesor, a is the amplitude, φ is the acrophase and τ is the period. For each parameter, the analysis provides a calculation based on a confidence interval of 95% probability. Similarly, the regression significance level is given. These parameters were averaged for all the 6 camels and presented as Mean±SEM.

The robustness has been largely used in the circadian studies to describe how regular a circadian rhythm is (Refinetti 2004; Refinetti et al. 1994). As described by Nelson et al. (1979), the robustness of the LA rhythm was calculated using cosinor rhythmometry method. It is automatically computed by

Cosinor software as the percentage of variance accounted for by the rhythm. The robustness and the other parameters of the rhythm were calculated for each individual 10 days rhythm of LA and then by averaging (Mean  $\pm$  SEM), for each season, the six animals.

#### Cosinor

The cosinor fittings were too approximate to determine the acrophases of the scoring data (Farsi et al. 2018). Therefore, the acrophase parameter was concurrently determined from the following exponential mathematical equation (Vivien-Roels et al. 1997; Bothorel et al. 2002; Farsi et al. 2018) and using scoring averaged data of every 5 min of each animal during each season:

$$f = y_0 + (y_{\max} / ((1 + \exp(2.7 \times (\phi_1 - x))) \times / ((1 + \exp(2.7 \times (x - \phi_2))))))$$

The  $f$  representing LA variation with time  $x$ , :  $y_0$  is the basal level measured during daytime,  $y_{\max}$  is the amplitude of the diurnal pick of LA. The  $\phi_1$  and  $\phi_2$  represent the inflection point and the time point at which the 50% of the maximal increase and the 50% of the decline were reached respectively. The duration of the LA peak corresponds to the difference between  $\phi_1$  and  $\phi_2$ . Since the locomotion scoring and its best fitting waves were in regular square shape, the acrophase was calculated as the half of this duration:  $\phi_2 - \phi_1 / 2$  (Farsi et al. 2018).

#### Onset and offset of activity

In order to compare if the beginning and the end of the activity rhythm coincide with the night–day and day–night transitions, the onset and offset of activity were calculated and compared respectively with the time of these transitions. The onset corresponds to a phase-angle difference in minutes between the time of the beginning of activity and the time of the night-day transition (i.e. sunrise time) while the offset of activity is the phase-angle difference in minutes between the time of the end of activity and the time of the day–night transition (i.e. sunset time). The onset and offset of activity in each day of each season were averaged for all camels and presented as Mean  $\pm$  SEM.

#### Total activity mean

Is calculated based on the inactivity/activity threshold (switch from score 2 to score 3) which considers the general activity and not only locomotor activity. For each season, this parameter was calculated separately for each nighttime and each daytime as the sum of scores 3, 4 and 5 of each individual camel and averaged (Mean  $\pm$  SEM) thereafter for all the six camels in each season. Active phase duration

Was determined for each season by calculating the difference in hours between the time of the onset and the offset of activity. It was first determined individually for each day, then averaged for each camel in a season and averaged, thereafter, for all camels during each season (Mean  $\pm$  SEM).

#### The midpoint of the active phase

Was defined as the clock time between the time of onset and the offset of the activity. It was calculated daily for each camel and then averaged for the 6 camels in each single season.

#### Activity amount per hour

Corresponds to  $C_d$  in the bellow D-index formula. For each active phase, this parameter was calculated as the sum of scores 3, 4 and 5 divided by the day-length in hours per day (defined by civil twilights at dawn and dusk). It was first calculated for each individual camel and then averaged (Mean  $\pm$  SEM) for the six camels in each season.

#### Midday phase angle

Corresponds to phase-angle differences in minutes between midday time of each season and the daily beginning (onset) and end (offset) of activity and with the acrophase. Each phase angle was calculated in each season for each camel and then averaged for all camels. Data were also presented as Mean  $\pm$  SEM.

Diurnality index (D-index = D)

Was calculated to determine if the camel diurnality is stable throughout the four seasons. The following equation (Hoogenboom et al. 1984) was used to calculate the D-index:

$$D = (Cd/Td - Cn/Tn)/(Cd/Td + Cn/Tn)$$

Where Cd and Cn were initially defined for the common vole (*Microtus arvalis*) by Hoogenboom et al. (1984) as the activity counts in day-time and at night and Td and Tn are their corresponding trap exposure times. In the present study, Cd and Cn were defined as the activity counts per hour during the daytime and at nighttime:

$D = (Cd - Cn)/(Cd + Cn)$  (Daan et al. 2011; Davimes et al. 2017); where: Cd = quantities of total activity per day divided by the day-length in hours per day (defined by civil twilights at dawn and dusk).

Cn = quantities of activity per night divided on the night-length in hours per day (defined by civil twilights at dawn and dusk). D-index was calculated for each season and for each individual and, thereafter, averaged (Mean  $\pm$  SEM) for all camels. D-index ranges from -1 to +1. According to Daan et al. (2011), values close to -1 represent a dominance of nocturnality; while, values close to +1 correspond to a pattern of diurnality. Finally, when D-index is around 0, it denotes of equal distribution of activity between night and day, indicating therefore a crepuscular pattern.

Frequencies of scores per hour

Were calculated as the daytime and nighttime daily average of the total number of registrations of each score in each camel. This average was divided by the duration (in hours) of each phase (daytime and nighttime) and averaged for each season for all the six camels. A one-way ANOVA analysis followed by the Holm-Sidak post-hoc test were used to compare different parameters between the different seasons (Inter-seasons comparison). Such inter-season differences were searched for all the LA rhythm parameters in addition to D-index, the duration of the active phase, activity amount per hour and the midpoint time of the active phase. One-way ANOVA was also used to test in each season (Intra-season comparison), the equality of means of activity onsets and offsets around day-night and night-day transitions (Intra-season comparison: day to day).

A repeated measurement two-way ANOVA (RM ANOVA2) analysis followed by a Holm-Sidak posthoc test were used to test the equality of variances between the onsets and offsets across the seasons (Interseason comparison). This analysis was also applied to determine statistical differences between nights and days in the total activity mean and frequencies of scores throughout the four seasons (Inter-seasons comparison). It was used also for the active phase to compare Midday phase angles (onset, offset and acrophase) between the seasons.

The Spearman Rank Correlation was used to calculate the strength of association by ranks between the distributions of locomotion scoring data and the Ta. The correlation equal to 1 ( $r_s = 1$ ) reveals a strong relationship between the two variables. The correlation was performed on a 24 h educed rhythm in each season obtained by averaging first the LA rhythms of the 6 camels and, thereafter, the obtained average rhythm of 10 days into a 24 h rhythm. The Ta was averaged as well from the data of 10 days of each season to obtain a 24 h educed cycle. In order to search for a possible correlation between the 2 variables (Ta and locomotion scores) in equal conditions, the data of the 24 h educed cycle of Ta were sorted out by assigning them to the six categories of LA scores (0–5 in an increasing direction) according to their frequencies. The spearman rank correlation was, thereafter, applied to compare by ranks the arranged categories of Ta with the corresponding scores (Farsi et al. 2018).

Individual and mean data of the active phase duration was presented during the four seasons according to the seasonal changes of day length. A linear Regression equation  $f = y_0 + a \times x$ , was used to determine the statistical correlation (R) between the two variables. A perfect correlation has a coefficient R equal to 1.

A  $P \leq 0.05$  was considered statistically significant in all statistical tests.



## Results

### Seasonal changes in the locomotor activity rhythm in the camel

Under the outdoor natural environmental conditions of the study area, camels displayed a LA rhythm, clearly expressed throughout the four seasons (Figure 1). The period was stable and equal exactly to 24 h (Table 3). The diel rhythm showed a high regularity expressed throughout with an elevated percentage of robustness in all the seasons (Table 3).

Compared to the other seasons, the mesor during the summer was significantly higher (Table 3); while, the amplitude in the winter was significantly higher. All the four seasons showed an intense activity in the camels during daytime and a strongly reduced activity during nighttime (Figures 1 and Figure 2). Scattered and scarce nocturnal movements were observed during the four seasons. Throughout the year, daily locomotor activity in the camel starts to increase early in the morning from/around sunrise and remains elevated throughout the day and then decreases toward the end of the evening around sunset to finally disappear at night (Figures 1 and Figure 2). During daytime, camels alternate between standing position with movements (score of 3) and a state of locomotion with exploring the surrounding environment (score of 4); while, the sitting positions (scores of 0 and 1) were completely absent. However, dominant behavior during nighttime corresponds to camels on rest state, laying down in a sternal recumbency. Comparison of the frequencies across the seasons (Figure S1) showed that score 3 is frequently the most observed behavior ( $P < 0.001$ ) during daytime in all seasons, followed by score 4; except for the winter in which score 4 became predominant as compared to score 3.

Regardless of the season, the active phase in camels coincides with the time of the photophase and thermophase, i.e. the light and warm phases of the day (Figures 1 and Figure 2). Furthermore, the daily duration of the time spent active was correlated with the seasonal changes of day-length (Figure 3 and Table 4). Comparison of this active phase has shown interseasonal significant differences with highly extended duration noticed when days are longer. Hence, during the summer camels spent much more time active when compared to other seasons (Table 4). Inter-seasonal significant differences were also observed in the acrophase of the camel LA rhythm. Indeed, acrophase was significantly ( $P \leq 0.05$ ) delayed in autumn compared to the other seasons (Table 3). However, these seasonal changes remained small and did not exceed 38 min over a year. In fact, for all camels studied, the acrophase of activity occurred in the middle of the day regardless of seasons. Moreover, comparison of the midpoint time of the active phase showed no significant difference between the four seasons occurring near to midday ( $P > .05$ ) (Table 4).

### Diurnal activity throughout the four seasons

Figures 1 and Figure 2 illustrate the existence of a clear diurnal activity pattern and a nocturnal period of rest in the camel. In fact, the diurnal activity of the camels was unchanged throughout the four seasons. This was also highlighted throughout the calculation of the D-index and the total activity mean. The D-index of all camels was higher throughout the four seasons:  $0.89 \pm 0.018$  during autumn,  $0.89 \pm 0.016$  in winter,  $0.91 \pm 0.012$  in spring and finally  $0.90 \pm 0.008$  for summer (Figure 4a). ANOVA-1 test did not show any significant differences between the seasons. The values obtained were close to the extreme limit of D-index (i.e., 1.0) and, therefore, emphasized the existence of a prominent diurnal activity phase in the camel throughout the year.

For all seasons, the mean of total activity showed values of 6–22 fold higher ( $P \leq 0.001$ ) during the days when compared to nights (Figure 4b). This confirms a constant yearly period of diurnal activity in the camel. Although this diurnal pattern of activity was unchanged, seasonal differences were observed in the total amount of activity (Figure 4b and Table 4). Indeed, RM-ANOVA 2 showed that the mean of total activity during daytime was significantly higher ( $P \leq 0.001$ ) during summer ( $576.40 \pm 10.60$ ) compared to winter ( $386.60 \pm 11.04$ ) (Figure 4b and Table 4). However, no significant differences were seen between the other seasons. Moreover, the ANOVA-1 did not show any significant differences in the activity amount per hour through seasons. Similarly, mean nighttime total activity did not show

any significant differences between seasons (winter:  $20.36 \pm 1.8$ ; autumn:  $25.81 \pm 3.1$ ; spring:  $27.30 \pm 7.5$  and summer:  $12.10 \pm 1.73$ ) ( $P > 0.05$ ).

Activity onset and offset in relation to environmental changes of light intensity and air Ta

Assessment of activity onset and offset (Figure 5a,b) shows that, for all seasons, the start and the end of the active phase were respectively synchronized with the sunrise and sunset times. Moreover, in each season, one-way ANOVA (Intra-season comparison) showed that the daily activity onsets and offsets respectively around the night-day and day-night transitions did not show any statistical differences between successive days, which indicate a significant equality of the means around each transition. However, the RM-ANOVA (Inter-season comparison) showed significant differences between the onsets and offsets across all the seasons, with the higher differences ( $P \leq 0.001$ ) observed between winter and summer. Inter-individual variations of onsets and offsets angle phase exist, particularly during winter (Figure 5b); but, these remain within a small interval of time (maximum of 35 min) around day-night and night-day transitions.

In addition, RM-ANOVA showed that the midday phase angle of the active phase revealed a higher significant difference ( $P \leq 0.001$ ) with the onsets and offsets across all the seasons (Table 4). However, midday phase angle with the acrophase indicate a significant difference only between the autumn with winter, spring and summer ( $P \leq 0.01$ ) (Table 4).

The potential correlation between the assigned locomotor scores and the daily variation of Ta was analyzed throughout the four seasons. Figure 6 shows a time course 3D representation of LA scores and daily Ta in representative camels. Despite the fact that the different activity scores were encountered at all levels of ambient temperature, the camels were more active (scores 2, 3, 4 and 5) under the highest Ta (yellow-orange-red colors) and less active (scores 0 and 1) when the environment was cold (blue-green colors) (Figure 6). This correlation was attested by the Spearman Rank test (Figure S2) which showed a strong degree of correlation between high activity scores (3, 4 and 5) with high ambient temperatures ranging from 23 to 42°C for summer and from 16–18°C to 33–34°C for winter, spring and autumn. Meanwhile, low activity scores (0, 1 and 2) were correlated with low ambient temperatures ranging from 18 to 23°C for summer and from 9–11°C to 16–17°C for winter, spring and autumn. The correlation coefficient ( $r_s$ ) was high regardless of the season (ranging from 0.81 to 0.86, Table 5). Pairing the two variables showed a very highly significant positive correlation ( $P \leq 0.0001$ ) in all camels.

The results in Figure 1 and Figure 2 show that once the active phase starts in early morning, the levels of activity remain stable and higher regardless of the continual increase of the day-time light intensity and of Ta. The most important changes of the activity pattern are noticed around the day–night and night–day transitions where light intensity and Ta dramatically decreased and increase, respectively. It appears that environmental changes occurring around these time-point transitions are dominant in the control of activity pattern of the camel. To verify if these changes of Ta and light intensity trigger the onset and offset of activity, the assigned locomotor scores were analyzed in correlation to these factors around the day–night and night–day transitions (Figure 7). This analysis includes data of 60 min before and after sunrise and sunset times. The results indicate that at night–day and day–night transitions, when activity respectively suddenly rises or drops, Ta remains stable and displays insignificant variations, ranging from 0.002°C to 0.210°C (Table 6, Figures 1 and Figure 2). However, changes of light intensity are greater and faster than of Ta (Figure 7), varying (average of the four seasons) from 0.1 to 560.7 lux for the interval between the start of morning civil twilight to sunrise time and from 453.6 to 0.1 lux between sunset time to the end of evening civil twilight. These important changes of light intensity represent a variation of 3000 to 7000 fold in only 25 to 29 min. Therefore, it appears that the sudden rise and drop of LA in the camel, seen respectively at the night–day and day–night transition, is primarily driven by the important changes of light intensity, since Ta remained almost unchanged at these moments of the day.

Precipitations disturb the rhythm of LA during winter

During rainfall, camels exhibited a diurnal rhythm of LA with the maximum of activity observed during day-time with Ta of  $14.9 \pm 2.1^\circ\text{C}$ ; while, at night, animals lied down for rest under Ta of  $11.2 \pm 0.9^\circ\text{C}$ .

However, the observed changes in the climate during this experiment, especially rainfall, affected the pattern of LA rhythm (Figure 8). Indeed, whilst precipitation did not impact the amount of activity during day-time which is usually higher at this phase (Day 2 in Figure 8a and day 1 and 2 in Figure 8b and finally day 2 in Figure 8c), their occurrence during nighttime caused abnormal nocturnal activity (3<sup>rd</sup>, 5<sup>th</sup> and 7<sup>th</sup> nights in Figure 8a; 2<sup>nd</sup> and 3<sup>rd</sup> nights in Figure 8b and 5<sup>th</sup> night in Figure 8c). The rain induced a higher level of nocturnal activity that lasted as long as the rain fell. Such behavior is highlighted on the 5<sup>th</sup> night in Figure 8c showing clearly that when rainfall ends, the induced activity drops immediately and the camel returns to its normal nocturnal rest. This effect of rainfall on camel activity is further highlighted by the calculated robustness for the examples of Figure 8a,b, where regularity of the locomotory rhythm ranged between 28.8% and 33.7%. In addition, compared to the former experiment, the D-index during these wet periods of winter decreased to 0.4–0.5.

## Discussion

The present study is the first investigation undertaken to characterize the seasonal changes of LA rhythm in the dromedary camel. Our results showed that camel exhibits a clear diurnal rhythm of LA that persists throughout the four seasons and with an active phase coinciding with the time of the photophase and thermophase. Mainly, the daily duration of the time spent active was directly correlated to the seasonal changes of photoperiod with the start and the end of the active phase synchronized with the onset of sunrise and sunset.

The sample size of animals ( $n = 6$ ) enrolled in the protocols of the present study may appear, to some extent, small and may constitute a limitation to attain statistical significant conclusion. However, unlike small mammals (rodents) and laboratory animals, the use of great number of large mammals, either domestic or wild ones in intricate experimentation, constitutes a challenge, both under controlled conditions and in the wild. Actually, most of studies including the present one, on specific species like camel and some wild animals, have to deal with difficult access to a large size of specimens. This is probably why a number of 6 animals (and sometimes less, in the case of invasive and complicated experiments) is still used and accepted for publication (Charan and Kantharia 2013) providing sufficient exploratory analysis of biological phenomenon.

Based on ecological investigations, personal observations and the reports of nomads, diurnal activity in the dromedary camel was first described in the early reports of Gauthier-Pilters (1958), Köhler-Rollefson (1991) and Khan et al. (1998). The first experimental investigation into the pattern of locomotor activity in the camel provides strong evidence that this species is diurnal (Aubè et al. 2017). However, this study was formulated on a discontinuous ethogram and, furthermore, was limited to only two consecutive days of recording. Farsi et al. (2018), Farsi et al. (2020) provided the first demonstration of diurnal activity in dromedary camel. Recording of locomotory activity rhythm has been difficult due to several technical constraints meet in large mammals and particularly in this species (El Allali et al. 2018). In the present study, a successful continuous recording of LA rhythm totaling 294 days has been performed over the four seasons of the year. Moreover, the current study has the advantage of monitoring LA rhythms under outdoor environmental conditions; while, most other studies were conducted under controlled environment.

The obtained results revealed that under semi-natural environmental conditions at the study area, camels displayed a clear daily LA rhythm with an exact period of 24.0h. Similar daily rhythms have been demonstrated in several large mammals, including the goat, sheep, horse, Arabian oryx and African elephant (*Loxodonta africana*) (Bertolucci et al. 2008; Davimes et al. 2017; Giovanni et al. 2010; Gravett et al. 2017; Hetem et al. 2012a; Hut et al. 1999; Piccione et al. 2008a, 2008b, 2010). Regardless of season, the active phase in camels coincides with the time of the photophase and to a much lesser extent the thermophase. Furthermore, the daily duration of the time spent active was proportionally correlated with the seasonal changes of daytime length. Also, the results showed that, in the camel, the active phase starts in the early morning at night-day transition (sunrise) and ends in the late evening at the day–night transition (sunset). Diurnal laboratory animals (García-Allegue et al. 1999;

Hut et al. 1999; Refinetti 2008; Schumann et al. 2005; Weinert et al. 2007) exhibit quite similar characteristics of LA rhythm as those reported in the present study.

Captivity seems to deeply affect the general activity of animals (McPhee and Carlstead 2010; Queiroz and Young 2018). According to the first behavioral study carried out on dromedary camel under laboratory conditions, Aubè et al. (2017) have suggested that, in order to preserve animal welfare and health, the camel housing system should include paddocks and not only boxes. Indeed, if maintained in their boxes, camels may not have enough space to walk and forage and could exhibit stereotypic movement expressing chronic mild stress and develop legs edema. Therefore, the constrained spaces for camels could significantly affect the percentage of daily activity. In the current study, camels presented a clear diurnal pattern of activity that was confirmed by various measures and significant parameters. This robust diurnal LA rhythm was obtained under specific captive conditions, including individual housing of camels in a spacious outdoor enclosure of 100 m<sup>2</sup>, directly exposed to natural environmental cues (Ta, solar radiations, natural light of LD cycle, rain, and humidity) and having free access to water and food. In the natural desert biotope, camels spend 8–10 h per day grazing and an equal time ruminating (Gauthier-Pilters 1958). When food biomass quantity and quality are reduced, camels spread out over large areas to find vegetation.

The activity pattern exhibited by the camel may reflect an effect of its domestication and a chronotype control imposed by humans in the breeding management system. The proper nature of the activity remains completely unknown and probably requires studying in the field without human influence. For many reasons including those discussed above, such investigations are still difficult to conduct. Nevertheless, using farm camels and minimizing human impact and interferences, the present study allowed a continuous quantification of the LA rhythm in this species throughout the four seasons of the year as well as demonstrated diurnal activity. This corroborates the data of a phylogenetic investigation (Wu et al. 2017), confirming the existence of diurnal traits in the ancestors of the dromedary as well as in wild Bactrian camel and alpaca. The only still living wild species of genus *camelus*, the *Camelus ferus* was shown to be diurnal with the highest activity occurring during the day-time between 10:00 h and 16:00 h (LST) (Xue et al. 2018). Meanwhile, other groups of camelids including the llama have been shown to also be diurnal (Riek et al. 2017, 2019).

Results from the first set of observations showed that the diurnal activity of the dromedary camel was maintained throughout the year, in all seasons. Although the daily period of LA rhythm remained exactly on 24 h, the duration of the active phase of this rhythm underwent important seasonal changes. Indeed, it was either extended or reduced depending on the day length. The active phase was longer in summer and shorter in winter. Such seasonal variations have also been reported for other species such as the Arabian oryx and the goat (*Capra hircus*) (Davimes et al. 2017; Piccione, 2008b; Hetem et al. 2012b) and was mostly reported in several species of mammals and birds (Daan and Aschoff 1975). In a recent study, Metzger et al. (2019), who investigated the LA rhythm of mice over a calendar year maintained under natural outdoor conditions, showed that the duration of the active phase as well as the chronotype, its stability and the total daily activity displayed clear seasonal differences in the melatonin-proficient C3H strain; whereas, the melatonin-deficient C57Bl strain lacked such pronounced seasonal variations. This seasonal plasticity appears to depend on the production of melatonin. In the camel, the observed seasonal differences in activity duration resulted from changes in the onset and offset of the activity that follow seasonal variations in the timing of sunrise and sunset. Regardless of how the active phase is shortened or extended, the acrophase, which usually shows inter-seasonal significant differences, remained relatively constant throughout the seasons (Variation did not exceed 38 min over a year). Relative unchanged acrophase recorded throughout the year has been also reported by Daan and Aschoff (1975) in three mammalian species including Tree shrew, golden hamster and Southern Flying Squirrel, as well as in athletic horses by Bertolucci et al. (2008). Significant coincidence of the activity onset and offset in camels with the respective day-night and night-day transitions was also maintained throughout the four seasons. Daan and Aschoff (1975) have reported that large seasonal fluctuations in the day-to-day variability of activity timing are more frequent at high latitudes when comparing Arctic Circle conditions (latitudes of 66°42'N and 66°42'N) to temperate European regions (latitude of 47° 58' N). This statement is in

agreement with our results that showed a good stability in activity onset and offset at lower latitudes of 34°00'47"N.

The current study demonstrates the switch between activity and rest phases which occurs in camels around the day-night and night-day transitions, where light intensity and  $T_a$  seem to undergo great changes. These environmental cues were carefully examined during time sets in order to assess which of the cues trigger the activity onset and offset. The analysis revealed the existence of a very low variability in the  $T_a$  ranging from 0.002 to 0.210°C. As stated by Darian-Smith and Johnson (1977) and Zhang (2015), the interval of this  $T_a$  variability is so minor that it may not be perceived by animals. Therefore, these insignificant changes in  $T_a$  do not explain why, at the transition from night to day, resting camels on sternal recumbency get up suddenly and start their daily activity and why, at the transition from day to night, the activity of the camels is unexpectedly interrupted, entering instantly into the nocturnal rest phase. In our previous studies (El Allali et al. 2013; Farsi et al. 2020), we have shown that, in the camel, the central circadian clock and its three outputs, the body temperature, locomotor activity and melatonin secretion rhythms, are entrained by  $T_a$  cycle. The no-involvement of  $T_a$  in the triggering of the activity onset and offset in the present study is not inconsistent with the previous demonstration of its entrainment of the circadian clock. Indeed, the activity onset and offset are driven by the circadian clock and are even observed in the absence of any environmental temporal perception (Free running rhythm: constant conditions). Application under DD of  $T_a$  cycle and its reverse (Farsi et al. 2020) resynchronize the time of the activity onset and offset and entrain, therefore, the rhythm.

However, these trials were conducted under controlled indoor conditions with no light (DD regime); meanwhile, we have shown previously (Khalid et al. 2013) that  $T_a$  entrainment is abolished when LD-cycle is applied. The present study was conducted under natural conditions of LD cycle and, therefore, the effect of  $T_a$  would be weak, particularly at dawn and dusk when its changes are insignificant. Since the two environmental cues are naturally in phase, we think that, in natural outdoor conditions,  $T_a$  would not drive the activity onset and offset at day-night and night-day transitions but could potentialize the effect of LD cycle during the rest of the day. This is particularly true when the environment is not xeric and camels are not subjected to ecological pressures such as food and water shortage and heat stress inducing heterothermy, which are the conditions in the present study.

On the other hand, the variations in light intensity around civil twilights-sunrise/sunset, ranging from 3000 to 7000 folds in only 25–29 min, are much greater and more rapid than those of  $T_a$ . These changes are perfectly in phase with the time of alternation between activity and rest phases. According to these results, the activity onset and offset in the camel seem to be independent of any direct effect of  $T_a$ ; but, instead, they are in phase with the rapid and important changes in light intensity around dawn and dusk. Such a phenomenon probably reflects a direct action of light on the rhythm rather than a property of the entrainment mechanism of the circadian clock by LD cycle. Daan and Aschoff (1975) have also reported such masking effect of light on the onset and offset activity of some birds and mammals. In mice maintained under natural outdoor conditions (Metzger et al. 2019), activity onset is determined by the evening dusk; whereas, the offset is affected by  $T_a$ . A dual oscillator system has been proposed to explain differential responses to onsets and offsets of activity in the small mammals (see Daan et al. 2001). This model, originally developed for nocturnal rodents, suggests the presence of two coupled circadian oscillators that drive activity and respond differently to light: A morning (M) oscillator that synchronizes the activity to dawn (onset) and accelerated by light and an evening (E) oscillator that synchronizes the activity to dusk (offset) and decelerated by light (Pittendrigh and Daan 1976). At seasonal level, under short days, both oscillators may overlap; while, under long days, the M and E oscillators are even further away and a bimodal activity patterns appear. Several examples of desert small mammals such as arid-dwelling desert hedgehog (*Paraechinus aethiopicus*) uses both the M and E oscillators with LA onset seeming to be strongly driven by E oscillator; while, the offset is less linked to M oscillator (Alagaili et al. 2020). Unlike the King jird (*Meriones rex*), a desert rodent (Alagaili et al. 2013), for the arid hedgehog, the climate conditions are only favor during night; therefore, the LA is restricted to a clearly defined nocturnal pattern with ambient temperature likely driving the E

oscillator (Alagaili et al. 2020). In the camel, there is no evidence of the existence of such dual oscillators and the activity onset and offset is triggered by light intensity in a unimodal pattern. Similar observations were reported on two strains mice, melatonin-deficient C57Bl and melatonin-proficient C3H, suggesting that the mechanisms regulating the activity onset and offset in this species are not dependent of the melatoninergetic system. In the camel, both onset and offset seem to depend on light intensity.

The second set of observations (Experiment 2) indicates that, during periods of rain at night, the pattern of activity was disturbed. The abnormal nocturnal activity seems to correspond to discomfort resulting from the noise of the rain droplets and the dampening of body coat caused by the rain. Dromedary camels are encountered only in areas characterized by a long dry season and short rainy period and they are reported to be sensitive to cold and humidity (Wilson 1984). In the context of the present study, the rain during the night and the consequent nocturnal activity correspond to a disturbance of the LA rhythm rather than a switch in temporal niche. This direct behavioral response to rain may, therefore, be attributed to a masking effect on activity pattern and thermoregulation process. Actually, during the winter nights, rain and low Ta make the body surface very cooler. This could increase the heat loss at the skin surface through convection and conduction and induce reactive hemostasis responses to the cold, particularly through changes of camel's posture and a thermogenesis rise of activity (abnormal nocturnal activity) as well as shivering that we clearly observed in this study. These facts are in accordance with the significant rise of frequency of Score 4 observed in this study during winter, resulting in an increase in locomotion behavioral, which is probably important for thermogenesis and striving against cold during this season.

Temporal niche switching has been reported in a wide range of animals (Mrosovsky and Hattar 2005). Under similar harsh environment of the camel, the Arabian oryx has been shown to display a clear temporal niche switching between seasons (Hetem et al. 2012b; Davimes et al. 2017, 2016). Accordingly, the extreme variations in Ta were found to drive such changes in the pattern of activity. Therefore, the Arabian oryx is diurnal during the cooler winter and nocturnal or crepuscular during the hotter summer period and finally intermittent during spring and autumn (Davimes et al. 2017, 2016). In the present study, the diurnal activity in the camel was maintained throughout the four seasons of the year (Experiment 1). This was particularly highlighted by the D-index that remained high and close to 1.0 over the year. Thus, no seasonal changes in the pattern of activity and no temporal niche switching occurred in the camel, as compared to those reported in the Arabian oryx.

In the hot desert area, that is different from the mesic environment of the present study, camels graze during the day and rest at night. However, during the hottest hours of the day, it is not uncommon to see camels laying down for rest. Such diurnal rest under heat environment is likely displayed to prevent further rise in body temperature induced by the thermogenesis of daytime activity. It was also reported that in the desert dune areas, where soil radiations are very high, herds could be allowed to feed during the night and, hence, increasing nocturnal activity and having rest for the entire day (Gauthier-Pilters 1958). It is, therefore, logical to assume that the absence of any temporal niche switching in the activity of camels in the present study is related to the mesic semi-natural conditions of the environment, which are completely different from the xeric desert biotope, the natural home of the camel. Indeed, under the latitudes of our study area (city of Rabat, located in the center of Morocco, Latitude: 34°00'47"N; Longitude:6°49'57"W), the natural cycles of Ta are not intense enough as is the case of the Sahara and Arabian desert to induce a seasonal changes in the pattern of activity. Several studies in small mammals of arid regions have indicated that responses to various zeitgebers could change when animals are kept under mesic regions. Truly, this fact has been approved in King jird (*M. rex*) and hedgehogs (Alagaili et al. 2013; Fowler and Racey 1990; Saboureau et al. 1979). Indeed, these species were found to be able to adopt or not a strict nocturnal profile of activity, depending strongly on the climate conditions of the region they occupy. This shows the greater plasticity of the circadian clock in these species under different environmental regimes.

In the present study, camels were kept at Rabat where the climate is highly humid (Relative humidity is ranging from 40% during summer to 82% during autumn-winter) comparing to the dry climate of the Sahara and Arabian desert. Such differences were previously reported to affect water economy and

salt balance in the camel (Achaaban et al. 2000; Achaaban et al. 1992). Further research is needed to determine how the dromedary camel responds to the desert habitat characterized by extreme temperatures and excessive solar radiations.

## **Conclusion**

The results obtained from the present work demonstrate, for the first time, that dromedary camel exhibits significant seasonal changes in the daily rhythm of locomotor activity without changing its diurnal pattern. The duration of the active phase depends on seasonal changes in day length and coincides, for all seasons, with the scotophase and of the day–night cycle. This ensues from alterations in the activity onset and offset, associated to seasonal variations of sunrise and sunset times. At these time point sets, activity seems to be driven mostly by the light intensity rather than by Ta changes. To approve such hypothesis, other trials involving different demonstration approaches should be undertaken. Moreover, sparse uncommon nocturnal activity can be triggered by rainfall. This behavioral response does not correspond to a temporal niche switching, but rather appears to be a transitory disturbance of LA rhythm induced by rainfall. Beyond the environmental outdoor conditions of the present study, further studies are required to decipher whether a harsh desert habitat, including heat stress and dehydration, can affect the temporal niche of activity in the camel.

## **Acknowledgements**

The authors are grateful to Hassan II Agronomy and Veterinary Medicine Institute (Rabat, Morocco) and the Institute of Cellular and Integrative Neurosciences (CNRS and University of Strasbourg, France) for supporting this study.

## **Disclosure statement**

The authors declare no competing interests.

## **Funding**

This work was supported by the Hassan II Institute of Agronomy and Veterinary Medicine of Rabat-Morocco and the International Foundation for Science [IFS: Research Grant Agreement N°: I-3-B-6082-1].

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## **Author contributions**

HF performed the experiments; analyzed and interpreted the data and drafted the manuscript. DH performed the experiments; analyzed and interpreted the data. MRA Analyzed and interpreted the data and drafted the manuscript. MP, MO and BB contributed reagents, materials, analysis tools or data and drafted the manuscript. PP and EC conceived and designed the experiments; analyzed and interpreted the data and drafted the manuscript. KE conceived and designed the experiments; analyzed and interpreted the data; contributed reagents, materials, analysis tools or data and drafted the manuscript.

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**Table 1.** Parameters characterizing the four seasons periods of locomotor activity rhythm recording in camels during the experiment 1 (Camels:  $n = 6$ ).

Recording periods	LD Cycle	Sunrise*	Sunset*	Morning civil Twilight Start*	Evening civil Twilight End*	Air $T_a$ (°C) Min–Max Under sun radiations	Humidity (%)	Rainfall (mm)
<b>Winter</b> December 23 <sup>th</sup> 2015 – January 01 <sup>st</sup> , 2016	09:54 L – 14:06D	07h31	17h25	07h03	17h53	08.3 ± 1.73–36.7 ± 0.74	82.1	0.0
<b>Spring</b> March 26 <sup>th</sup> – April 04 <sup>th</sup> , 2016	12:31 L – 11:29D	07h15	19h46	06h50	20h12	06.4 ± 1.44–31.2 ± 1.47	77.7	0.0
<b>Summer</b> June 30 <sup>th</sup> – July 09 <sup>th</sup> , 2016	14:21 L – 09:39D	05h21	19h42	04h52	20h11	15.3 ± 3.23–49.1 ± 1.70	40.3	0.0
<b>Autumn</b> October 23 <sup>th</sup> – November 1 <sup>st</sup> , 2016	10:56 L – 13:04D	07h42	18h39	07h17	19h04	10.2 ± 3.17–35.8 ± 0.59	82.9	0.0

\*The time is given in Greenwich Mean Time (GMT).

**Table 2.** Parameters characterizing the rainfall periods of Experiment 2 (Camels:  $n = 3$ , camel 1, 2 et 3).

Recording period	LD Cycle	Sunrise*	Sunset*	Morning civil Twilight Start*	Evening civil Twilight End*	Air $T_a$ (°C) Min-Max Under sun radiations	Humidity (%)	Rainfall (mm)
	11:05 L-12:55D	07h07	18h13	06h42	18h39	07.5–36.7	[80.0–90.1]	[4.1–11.0]

\*: The time is given in Greenwich Mean Time (GMT).

**Table 3.** Parameters (Mean  $\pm$  SEM) of the locomotor activity rhythm in six camels during the four seasons of the year (Experiment 1).

Saison	Period (h)	Acrophase (h)	Mesor	Amplitude	Robustness
Winter	24.0 $\pm$ 0.01	12:28 $\pm$ 0.05	1.58 $\pm$ 0.06	2.13 $\pm$ 0.18	58.7 $\pm$ 1.8
Spring	24.0 $\pm$ 0.03	12:36 $\pm$ 0.06	1.33 $\pm$ 0.10	1.30 $\pm$ 0.24	44.1 $\pm$ 3.0
Summer	24.0 $\pm$ 0.05	12:52 $\pm$ 0.02	1.82 $\pm$ 0.15	1.76 $\pm$ 0.38	59.2 $\pm$ 2.3
Autumn	24.0 $\pm$ 0.04	12:09 $\pm$ 0.04	1.54 $\pm$ 0.12	1.27 $\pm$ 0.36	36.6 $\pm$ 2.7

Note: One-way ANOVA analysis was used for the calculation of the statistical differences concerning the parameters of LA rhythm across the four seasons of the year. Vertical black lines with asterisks indicate the statistical comparison between two seasons. The asterisks indicate the degree of statistical significance. "\*\*\*\*" ( $P \leq 0.001$ ) extremely significant; "\*\*\*" ( $P \leq 0.01$ ) very significant.

**Table 4.** Seasonal changes of the active phase parameters (Mean  $\pm$ SEM) in the dromedary camel (Experiment 1).

Phase active markers							
Season	Midpoint time	Duration	Total activity mean	Activity amount per hour	Midday phase angle (min) for:		
					Activity onset	Activity offset	Acrophase
Winter	12:28 $\pm$ 0,005h	09,88 $\pm$ 0,24 h	386,60 $\pm$ 11,04	39,12 $\pm$ 1,51	279 $\pm$ 0,08	343 $\pm$ 0,06	-48 $\pm$ 0,05
Spring	12:20 $\pm$ 0,007h	12,34 $\pm$ 0,21h	400,00 $\pm$ 11,78	32,41 $\pm$ 1,81	419 $\pm$ 0,05	418 $\pm$ 0,08	-52 $\pm$ 0,02
Summer	12:34 $\pm$ 0,001h	14,34 $\pm$ 0,16h	576,40 $\pm$ 10,60	40,19 $\pm$ 0,37	358 $\pm$ 0,04	493 $\pm$ 0,03	-54 $\pm$ 0,04
Autumn	12:31 $\pm$ 0,003h	11,00 $\pm$ 0,28h	302,21 $\pm$ 08,07	35,47 $\pm$ 2,62	333 $\pm$ 0,09	369 $\pm$ 0,04	-22 $\pm$ 0,06

Note: One way ANOVA analysis was used to compare Midpoint time, duration of active phase, total activity mean and activity amount per hour. Two-way repeated measures ANOVA analysis was used to compare Midday phase angles (onset, offset and acrophase) between the seasons. Vertical black lines with asterisks indicate the presence of significant statistical differences between two seasons. The asterisks indicate the degree of statistical significance: "\*\*\*" ( $P \leq 0.01$ ) very significant. "\*\*\*\*" ( $P \leq 0.001$ ) extremely significant.

**Table 5.** Results of the spearman rank test correlation between the scores of activity and Ta cycle levels.

Seasons	$r_s$ Correlation coefficient	<i>P</i> value
<b>Winter</b>	0.818 ± 0.021	<i>P</i> < .0001
<b>Spring</b>	0.863 ± 0.040	
<b>Sumer</b>	0.845 ± 0.028	
<b>Autumn</b>	0.810 ± 0.015	



**Table 6.** Variation in the ambient temperature around day–night and night–day transitions (time of activity onset and offset) during the four seasons of the year.

	Night–day (Activity onset)	Day–night (Activity offset)
<b>Winter</b>	$0.025 \pm 0.005^{\circ}\text{C}$	$0.031 \pm 0.043^{\circ}\text{C}$
<b>Spring</b>	$0.110 \pm 0.050^{\circ}\text{C}$	$0.210 \pm 0.011^{\circ}\text{C}$
<b>Summer</b>	$0.002 \pm 0.019^{\circ}\text{C}$	$0.088 \pm 0.047^{\circ}\text{C}$
<b>Autumn</b>	$0.016 \pm 0.005^{\circ}\text{C}$	$0.100 \pm 0.019^{\circ}\text{C}$

## Legends to figures

**Figure 1.** Rhythm of the locomotor activity (Blue curve) of a representative camel (Camel 1) under the natural conditions of the (a) Winter; (b) Spring; (c) Summer; (d) Autumn seasons (Experiment 1). The activity was measured every minute for 10 consecutive days using the locomotion scoring technique. Each score is presented with different amplitudes (from 0 to 5). The air ambient temperature under direct solar radiations is shown at the top of the figure (Red curve). The black and white bars at the top of the figure correspond respectively to the succession of the dark and light phase of the LD-cycle. The time of successive days is indicated at the bottom of the figure in hours and days.

**Figure 2.** Actograms of the locomotor activity in a representative camel (Camel 3) in relation to the seasonal changes of the LD-cycle and of the daily ambient temperature cycle (Experiment 1). The activity was measured every minute for 10 consecutive days per season using the locomotion scoring technique. Each score is presented with different amplitudes (from 0 to 5). Each line corresponds to 24 h of activity starting at 00:00 h and ending at 24:00 h. The lines and black points indicate the existence of a locomotor activity rhythm: scores of 1–5 inducing an increase in the thickness of the lines. White or on-line vacuum shows no activity thus representing a score of 0. The black and white bars correspond respectively to the dark and light phase of the LD-cycle of each season. Colored bars indicate the daily changes of air ambient temperature cycle.

**Figure 3.** Seasonal variations in the active phase duration of the camel in relation to the day length changes (Experiment 1). Red line and triangles represent the Mean ( $\pm$ SEM) of the active phase duration in the 6 camels, while each colored circle represent a daily active phase duration in each individual camel (camels 1 to 6). Each color represents one individual camel. The linear Regression equation  $f = y_0 + a \times x$ , was used to determine the statistical correlation (R) between the two variables. A perfect correlation has a coefficient R equal to 1. Dashed gray line represents the best line of correlation with  $y = -0.061$  and  $a = 1.007$ . Results of the one-way ANOVA analysis followed by the Holm-Sidak post-hoc test comparing the active phase duration between the four seasons are given at the right bottom angle of the figure.

**Figure 4.** Diurnality index and total activity mean of the dromedary camel during the Experiment 1. (a) Diurnality index (D-index) presented as the mean (Mean $\pm$ SEM) of the six camels of experiment 1 according to the four seasons of the year. Each bar indicates the D-index level for winter, spring, summer and autumn. D-index which is close to 1 and to -1 indicate, respectively a diurnality and a nocturnality; while, values around 0 correspond to the crepuscularity. (b) Total activity mean ( $\pm$ SEM) of the six camels in experiment 1 during day (D) and night (N) of each season of the year. This parameter was calculated separately by summing all activity bouts (Scores 3, 4 and 5) occurring during the day and night for each individual camel and averaged thereafter for all the six camels in each season.

**Figure 5.** Onset and offset of the LA rhythm of the camels in correlation to the night-day and day-night transitions of each of the four seasons of the year (Experiment 1). (a) Onset and offset during 10 consecutive days through the four seasons. Each blue point represents the average (M $\pm$  SEM) of the six animals within each day for ten days in each season. (b) Seasonal changes of the average of onsets and offsets: blue points correspond each to an individual camel's average of the 10 days data in a season; while, red points and lines are the means (M $\pm$  SEM) of all the 10 days data and all the six camels. The onset corresponds to a phase-angle differences in minutes between the time of the beginning of activity and the time of the night-day transition (i.e. sunrise time); while, the offset of activity is the phase-angle differences in minutes between the time of the end of activity and the time of the day-night transition (i.e. sunset time). The black and white bars at the top of the figures

correspond respectively to a segment of the dark and light phase of the LD-cycle around sunset and sunrise.

**Figure 6.** 3D representation of the activity scores in relation to the levels of Ta and time (24 h) during winter, spring, summer and autumn (Experiment 1) in representative camels (winter from camel 1 and spring, summer and autumn from camel 6). The black points on the curve represent the activity scores; the colored plane represents the variations of the ambient temperature (under solar radiations). Red–orange–yellow colors correspond to high temperatures of the season; while, blue–green colors correspond to the low temperatures.

**Figure 7.** Relationship between the activity levels (onset and offset) and the changes in the natural light intensity and air ambient temperature around night–day and day–night transitions in each of the four seasons. Changes in the seasonal time of sunrise and sunset and of morning civil twilight start and the evening civil twilight end are given on the figure. Clock time is given in Greenwich Mean Time. Each red line corresponds to 1 min activity score of a representative camel (Camel 4) around sunrise and sunset of one day chosen randomly in each season. Changes in the light intensity is given numerically and also highlighted by the colored panel with a transition between the black-gray and white color for respectively a gradient of transition from darkness to light.

**Figure 8.** Rhythm of the locomotor activity (Blue curve) of camels under the natural conditions of the Experiment 2. Video recordings were realized for locomotor activity rhythms scoring in 3 camels during 18 consecutive days in the winter. Each camel was selected as a representative example for 6 different rainy days among the experimental period: (a) Camel 1: 10th–15th February, 2017, (b) Camel 2: 16th–21th February, 2017 and (c) Camel 3: 22th–27th February, 2017). The activity was measured every minute using the locomotion scoring technique (scores 0–5). Activity during rain is labeled in the figure with an Orange color. The air ambient temperature is shown at the top of the figure (Red curve). The black and white bars at the top of the figure correspond respectively to the succession of the dark and light phase of the LD-cycle. The rainy orange clouds symbols indicate the moments of precipitations.

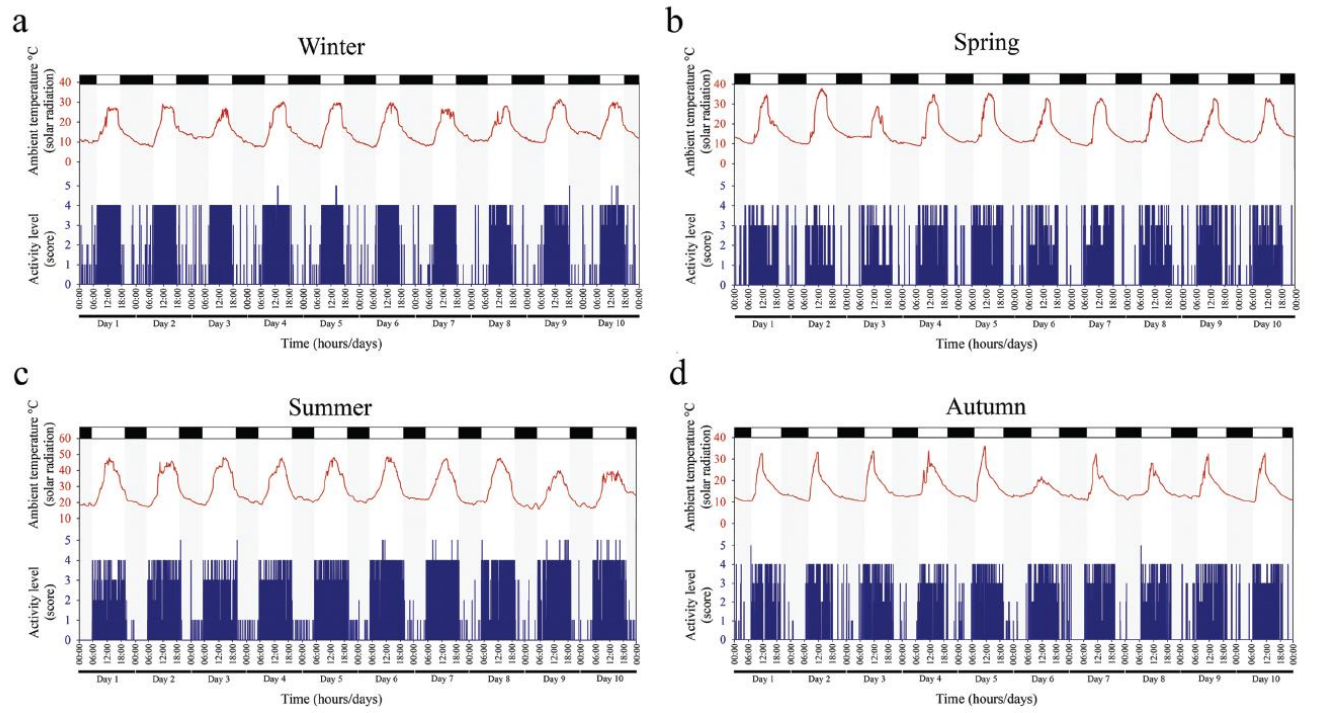


Figure 1

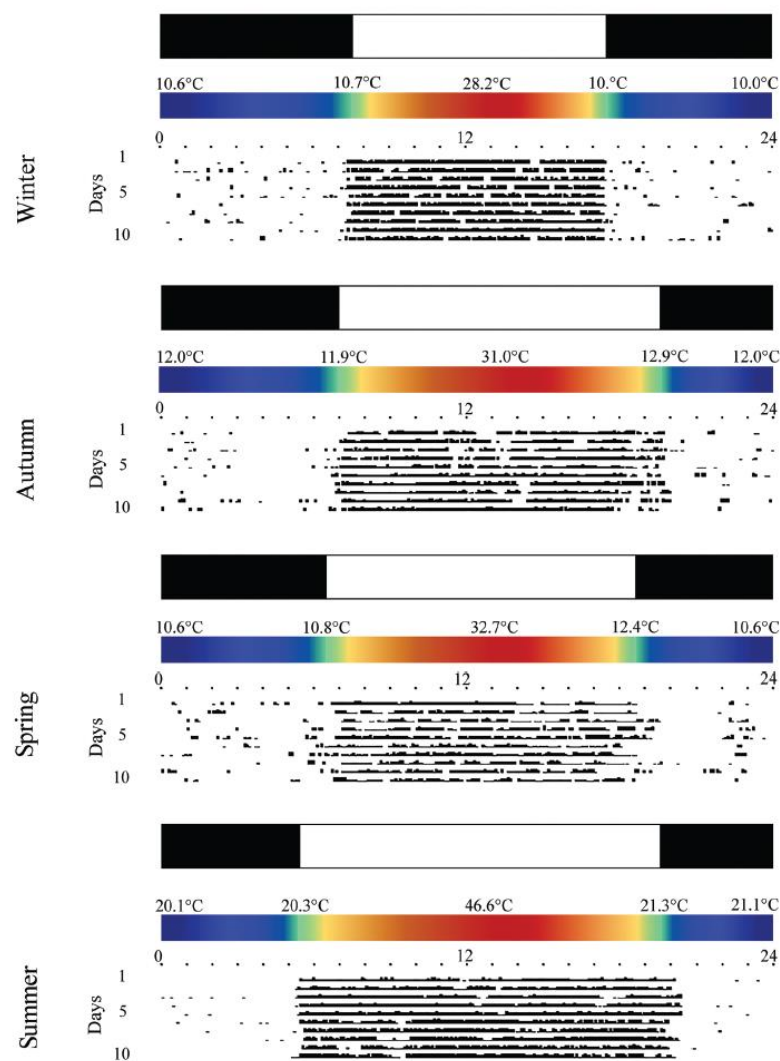
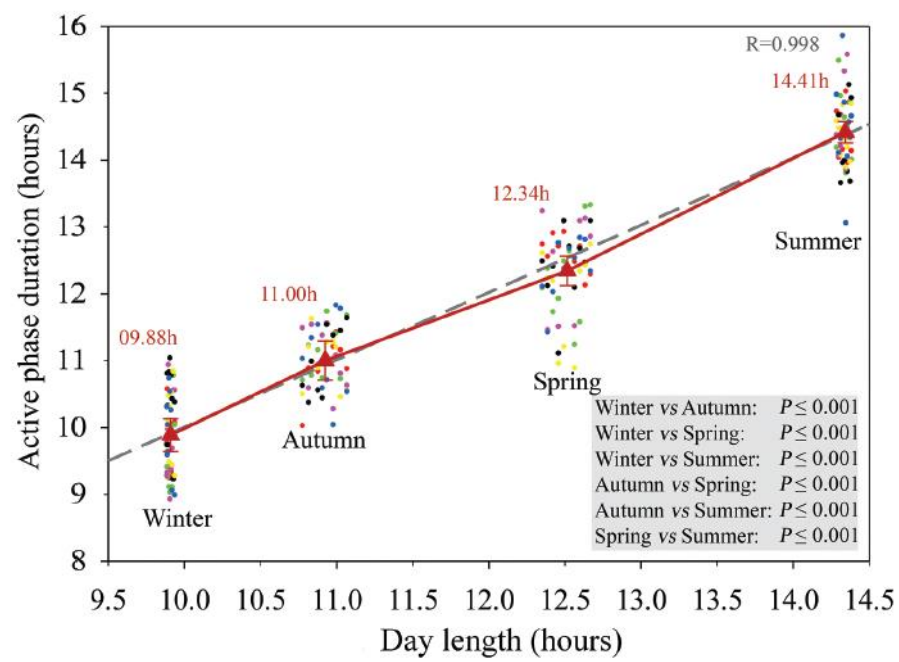
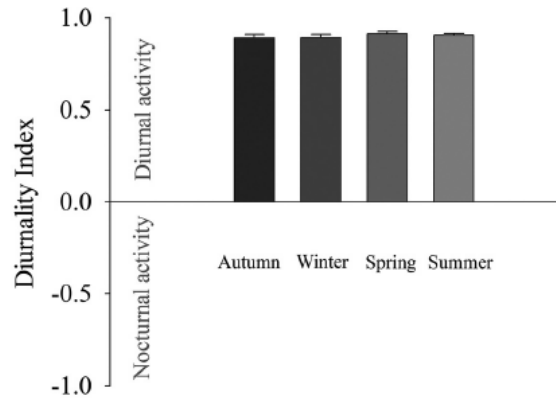


Figure 2

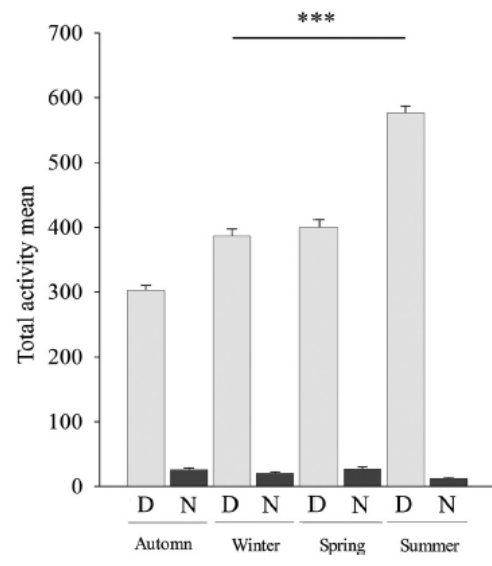


**Figure 3**

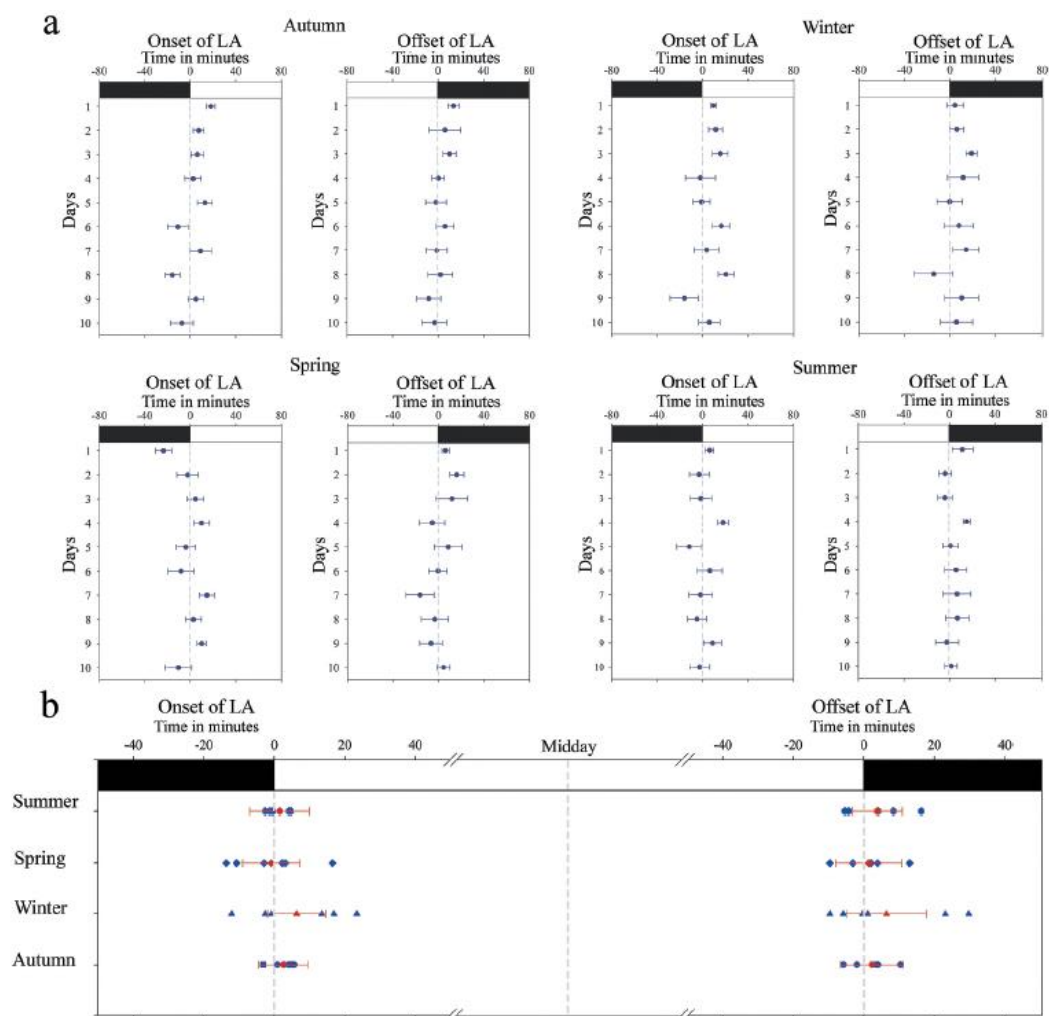
**a**



**b**



**Figure 4**



**Figure 5**



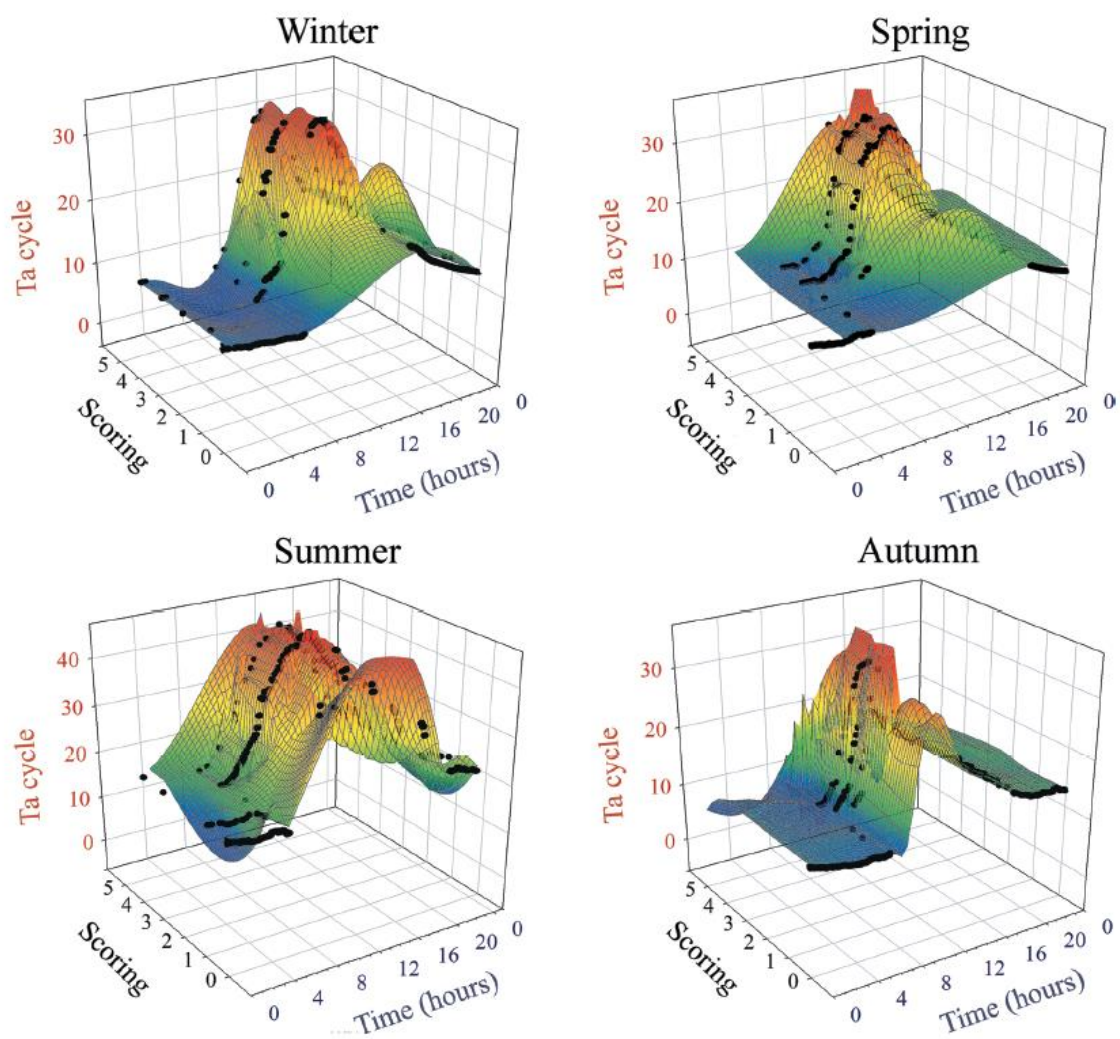


Figure 6

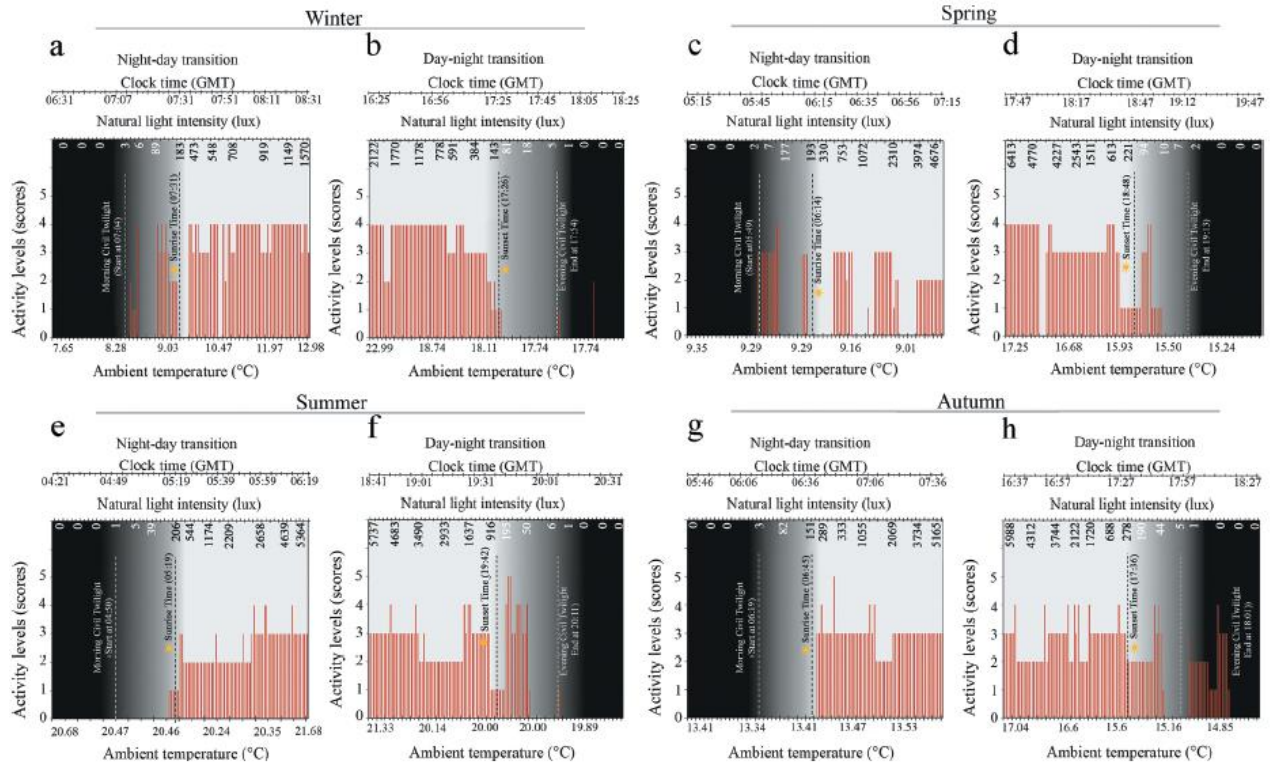
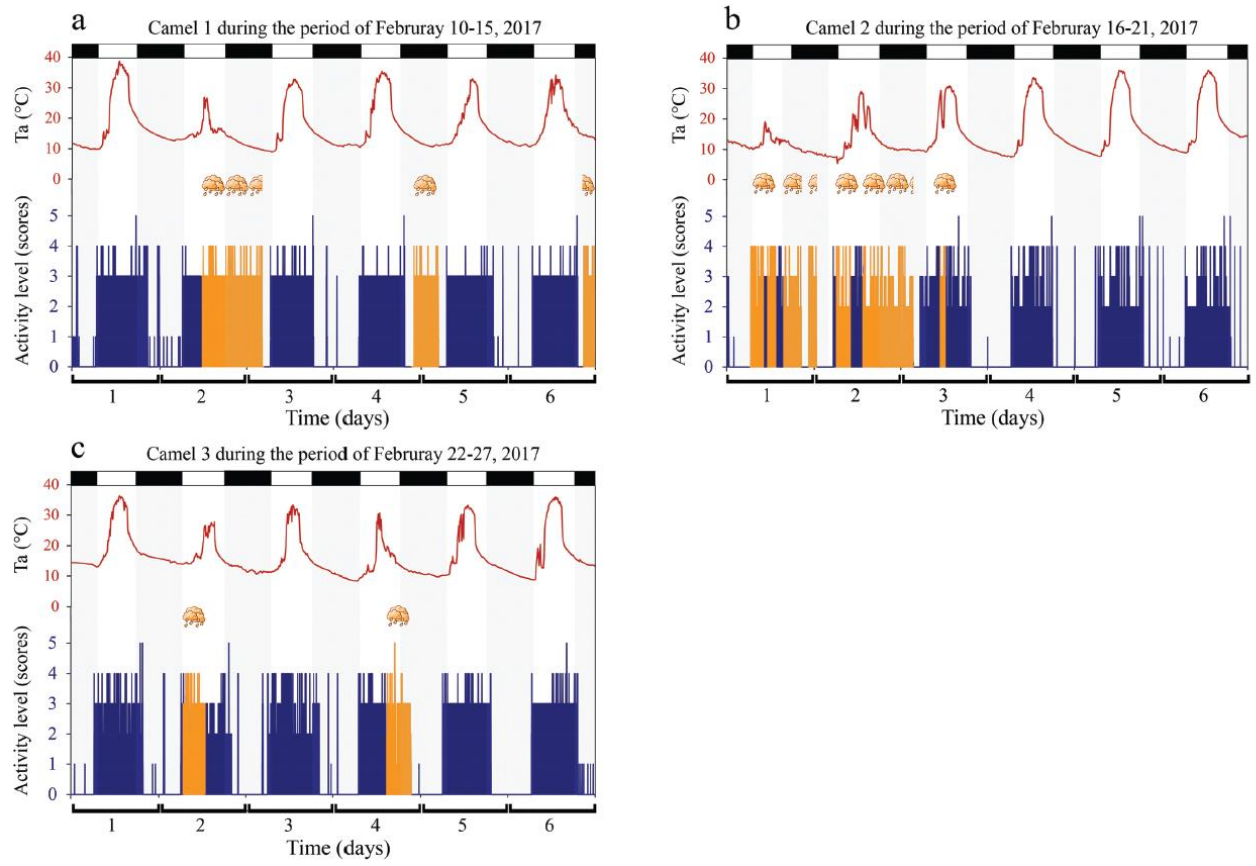


Figure 7



**Figure 8**