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Sleep pattern in the dromedary camel: a behavioral and polysomnography study

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Abstract

Study Objectives: To investigate sleep patterns in the camel by combining behavioral and polysomnography (PSG) methods.
Methods: A noninvasive PSG study was conducted over four nights on four animals. Additionally, video recordings were used to monitor the sleep behaviors associated with different vigilance states.
Results: During the night, short periods of sporadic sleep-like behavior corresponding to a specific posture, sternal recumbency (SR) with the head lying down on the ground, were observed. The PSG results showed rapid shifts between five vigilance states, including wakefulness, drowsiness, rapid eye movement (REM) sleep, non-REM (NREM) sleep, and rumination. The camels typically slept only 1.7 hours per night, subdivided into 0.5 hours of REM sleep and 1.2 hours of NREM sleep. Camels spent most of the night being awake (2.3 hours), ruminating (2.4 hours), or drowsing (1.9 hours). Various combinations of transitions between the different vigilance states were observed, with a notable transition into REM sleep directly from drowsiness (9%) or wakefulness (4%). Behavioral postures were found to correlate with PSG vigilance states, thereby allowing a reliable prediction of the sleep stage based on SR and the head position (erected, motionless, or lying down on the ground). Notably, 100% of REM sleep occurred during the Head Lying Down-SR posture.
Conclusions: The camel is a diurnal species with a polyphasic sleep pattern at night. The best correlation between PSG and ethogram data indicates that sleep duration can be predicted by the behavioral method, provided that drowsiness is considered a part of sleep.

Statement of Significance

The Sahara Desert is considered among the harshest biotopes on earth, where the lives of many species are constantly under threat. Sleep behavior/polysomnography (PSG) studies in this biotope are extremely scarce. The intriguing question concerns the importance of sleep for large desert mammals while they must cope with heat and dehydration. In the dromedary camel, a desert animal, sleep and its associated behavioral states have not yet been investigated. The aim of the present study was to characterize sleep behaviors and to perform noninvasive electrophysiological recordings of sleep in the camel. A noninvasive technique of PSG together with behavioral analysis showed that the dromedary camel is a diurnal species with a polyphasic sleep pattern.

Key words: dromedary camel; sleep; sleep behaviors; polysomnography; EEG; EMG; EOG; vigilance states; NREM sleep; REM sleep; rumination

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Introduction

All studied mammals to date have been shown to sleep. Although the complete function and evolution of sleep are still not fully understood, notable progress has been made over the last decades, allowing improved comprehension of its neurological and physiological roles and mechanisms. Sleep is defined as a state of body rest corresponding to a reversible natural loss of sensorimotor interactions with the environment [1]. In terms of electrophysiology, two distinct cyclic sleep stages have been identified in mammals and birds: non-rapid eye movement sleep (NREM sleep, also called slow-wave sleep [SWS]) and rapid eye movement sleep (REM sleep, also called paradoxical sleep). Using polysomnography (PSG), a combination of electroencephalography (EEG), electromyography (EMG), and electrooculography (EOG), it is possible to distinguish NREM sleep and REM sleep from each other and from other vigilance states. Briefly, NREM sleep is characterized by low-frequency activity and a high-amplitude EEG signal (SWS) resulting from the cortical synchronization of neuronal activity [2], whereas REM sleep exhibits an EEG with fast activity and variable amplitude, sharing similarities with the wakefulness pattern. In addition, REM sleep is well defined by the presence of typical rapid eye movements in EOG of large amplitude and muscle atonia in EMG mixed with typical muscle twitch [3]. Wakefulness shows EEG traces with high-frequency and low-voltage activity related to neuronal activation or desynchronization. In addition to the former vigilance states, drowsiness, which is a transient state between sleep and wakefulness, has been observed in the majority of species [4]. However, the criteria defining drowsiness often remain inconsistent. Sleep architecture, which refers to the organization, distribution, and duration of sleep episodes and also to the phasing of sleep across the daily cycle, varies considerably among mammalian species [5].

The dromedary camel (*Camelus dromedarius*), belonging to the superorder of Cetartiodactyla, copes well with the harsh desert biotope [6]. Specific physiological and anatomical characteristics allow this animal to live in areas where the survival of other species is threatened. We have recently shown that activity time partitioning of this species exhibits a diurnal pattern [7–9]. Unlike other domesticated animals, no previous sleep studies have been conducted on this species. The present study was performed to investigate sleep in the dromedary camel to reveal its architecture and associated behaviors. To achieve this, we focused on:

1) Describing nocturnal behaviors/postures in this species.
2) Studying sleep and other vigilance states during the night using polysomnographic recordings (EEG, EMG, and EOG).
3) Determining correlations between the sleep states defined by PSG and the observed sleep postures.

Methods

Animals

The present study was conducted at the Hassan II Agronomy and Veterinary Medicine Institute of Rabat (Latitude: 34°01′N, Longitude: 6°50′W) on four clinically healthy nonpregnant adult female camels. Females were preferred to males because of the bad temper of males and to avoid their aggressiveness and restlessness, particularly during the breeding season. The female camels were aged between 7 and 10 years and weighed 467 ± 39 kg. The animals were maintained under natural outdoor environmental conditions within individual open enclosures (100 m^2), where they were able to move freely. They were fed with a compound food (Maraa for Camelids, Alf Sahel, Morocco) and barley straw ad libitum and also offered water ad libitum.

Experimental design

All experiments carried out in the present study were in agreement with the Hassan II Agronomy and Veterinary Institute of Rabat and Moroccan Ministry of Agriculture recommendations, which comply with the ARRIVE (Animal Research Reporting of In Vivo Experiments) guidelines and the European Union Directive 2010/63/EU.

PSG was performed on camels under outdoor conditions during the summer solstice (Table 1). The EEG, EOG, and EMG signals were recorded with a noninvasive method using two miniature ambulatory polysomnographic devices: the four-channel Actiwave EEG/ECG device and the 2-channel Actiwave EMG device (CamNtech Ltd, Cambridgeshire, UK). The two Actiwave devices (Figure 1A) measured 3.70 × 2.70 × 8.05 and 2.70 × 2.50 × 8.05 cm and weighed 8.5 and 5.6 g, respectively. They include 24 Mb of internal memory (13 hours of recording for EEG/EOG and 27 hours for EMG) and are fitted with a rechargeable lithium polymer battery providing autonomy. The Actiwave devices were programmed on a computer using its USB reader and software (CamNtech Actiwave Multi Dock, h Ltd, Cambridgeshire, UK). The sampling frequency was 500 Hz with 10-bit resolution.

The cranium, the nape, and a square-shaped surface on the masseter region (just below the zygomatic crest) of each camel were shaved. The shaved skin areas were degreased with alcohol and scrubbed with an abrasive gel (Everi, SPES Medica, Genova, Italy). Eight gold-plated disc electrodes (CamNtech Ltd, Cambridgeshire, UK; diameter: 11 mm, leads: 450 mm, connector: 1 mm; and impedance 10 MΩ) were attached to the head and neck (Figure 1, B and C). They were glued to the skin using an EC3 conductive adhesive gel (Natus Neuro, Middleton, USA) and covered by rubber. The electrodes were then secured by placing a medical sticking plaster on the top (Figure 1C). Two electrodes were used for EEG: one placed over the frontal cortex in the median frontal concavity (approximately 2 cm from the parieto-frontal suture and on the sagittal suture) and the second electrode was placed over the occipital cortex on the caudal planum of the external sagittal crest (approximately 1–2 cm rostral to the external occipital protuberance, and about 2 cm caudal to the lambdoid suture; Figure 1, B and C). Both electrodes were placed on the median plane. The EEG electrodes were positioned directly on the bony surface. The choice of anatomical site for the EEG electrode locations was made based on data from previous studies on domestic animals [10–13]. The occipital electrode position was selected because of the specific posterior dominant alpha rhythm in human EEG. Moreover, the frontal and occipital positions constitute the unique parts of the camel skull where muscular components are less developed, thereby preventing potential myogenic (EMG) artifacts. A reference electrode was placed behind the neck (level of the nuchal ligament; Figure 1B). For EOG, two electrodes were used, one near the upper eyelid of the left eye and the other close to the lower eyelid of the right eye (Figure 1B), with the same

Table 1. Outdoor environmental cues during the PSG study on camels

Recording period	Light-Dark (LD) cycle	Sunrise†	Sunset†	Morning civil twilight start†	Evening civil twilight end†	Air Ta (°C) min–max Under sun radiations	Humidity (%)	Rainfall (mm)
June 20–24, 2020	14:25L–09:35D	05:16 am	07:41 pm	04:47 am	08:11 pm	20.2–39.8	58.5	0.0

Air ambiant temperature (Ta) was measured every 1 min using a data logger, iButtons (DS1922L, Dallas Semi-Conductor, USA). The devices were programmed for 16 bit with a resolution of 0.0625°C. 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/worldclock/) and of the regional Direction of Meteorology of Rabat, Morocco.

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

reference electrode as the EEG at the nuchal ligament. Two electrodes recorded the EMG, one placed on the masseter muscle of the left jaw and the other near the nape on the dorsal musculature of the neck (Figure 1B); the reference electrode was placed at the level of the nuchal ligament behind the external occipital protuberance.

The cables of all eight electrodes were placed caudally and above the neck to join the two Actiwave devices. These devices were placed in small protective boxes that were securely attached to the left side of the neck. All these pieces of equipment were covered with nylon tissue and then with a handmade lightweight polystyrene helmet (Figure 1C) to protect the Actiwave devices and their leads from any possible damage.

During the trials, the camels showed no specific distress or anxiety. They appeared accustomed to their environment and recurrent handling; no sedation was needed. Each camel was allowed a week to adapt to the allocated helmet before the implementation of the PSG system. Recording sequences were obtained separately for each camel at different periods.

Several sleep and awakening sessions were recorded for repeated setup assays. Before each sleep session recording, awake activity was recorded during the day, first to ensure the connectivity of the electrodes and the quality of the electrophysiological signals and, second, to compare it to sleep session recordings. Because the camel is a diurnal species exhibiting nocturnal rest [7–14], and based on preliminary results showing sleep-like behaviors only during nighttime, the recording of polysomnographic signals was performed only during the night. For each camel, a single night recording set was performed from 19:40 to 05:20.

In addition to the EEG, EMG, and EOG recordings, sleep behaviors were simultaneously monitored by observing the animals-specific resting postures. Video recordings of camel movements and behaviors were obtained using two high-resolution cameras equipped with infrared emitters (RAYNESS vision Sony TVL CAMERAS) placed at two opposite angles of the enclosure. This setup offered complete coverage, thus allowing comprehensive monitoring of their behavior. The recorded videos were stored in a Digital Video Recorder (Provision ISRÒ, model: SA-4100HDXþ) for subsequent sequence analysis. The sleep-associated behaviors were monitored using an ethogram and included the following postures and events: rest body position such as recumbency and neck and head positions (head and neck lifted up with no movement or relaxing and placed down on the ground).

Data analysis

The total duration of the polysomnographic recordings from the four camels was 115 hours 17 minutes, consisting of a usable dataset of 30 hours 47 minutes 30 seconds duration for EEG, 35 hours 13 minutes 30 seconds duration for EOG, and 44 hours 50 minutes 00 seconds duration for EMG signals, and a mean duration of 9 hours 14 minutes ± 1 hour 44 minutes per night for each camel. For two EEG electrodes on two separate nights, short episodes (totalizing a mean duration of 2 hours 13 minutes) of unreadable signals were recorded and subsequently excluded. This loss of signal was likely due to the temporary disconnection of the electrode caused by sudden movements of the animals. All readable signals (Table 2) were scored and analyzed. The best traces were used for visualization of the different vigilance states in the camel.

Data from EEG, EMG, and EOG were downloaded from the Actiwave devices as EDF files and then analyzed visually using a sleep scoring program, the freely accessible software Polyman [15]. Polysomnographic signals were displayed and scored in 30-second epochs on Polyman and given a fixed scale: 100 μV both for EEG and EMG, and 250 μV for EOG. The program allows the synchronization of PSG recordings with video recordings to determine the correspondence between vigilance states and behavior postures. Before scoring, both EEG channels were digitally filtered using a band-pass filter with a high-pass cutoff of 0.3 Hz and a low-pass cutoff of 50 Hz.

Polysomnographic scoring was performed by two independent observers according to criteria and events for sleep analysis in humans [16] and animals [10–12, 17–20] (Table 3). Five vigilance states, including wakefulness, drowsiness, NREM sleep, REM sleep, and rumination, were identified (Table 3). When a 30-second epoch contained two different states of vigilance, only the dominant state was scored. This included transient awakening that interrupted NREM sleep and REM sleep bouts for more than 15 seconds, which were considered as wakefulness.

The averages (means ± SEM) of the following parameters were determined each night for the four camels:

- The duration (minutes) of each vigilance state bout.
- The episode number for each state per night.
- The total state time (hours) is calculated as the sum of the duration of all episodes of a specific vigilance state during a night.
- The percentage of time spent in each vigilance state per night is calculated as follows:
  % = total state time of a specific vigilance state/sum of total state times of all the vigilances states.
- REM sleep as a percentage of total sleep is determined as follows:
  % = time spent in REM sleep/sum of REM and NREM sleep times.
- The percentage of transition from one vigilance state to another is calculated as follows:

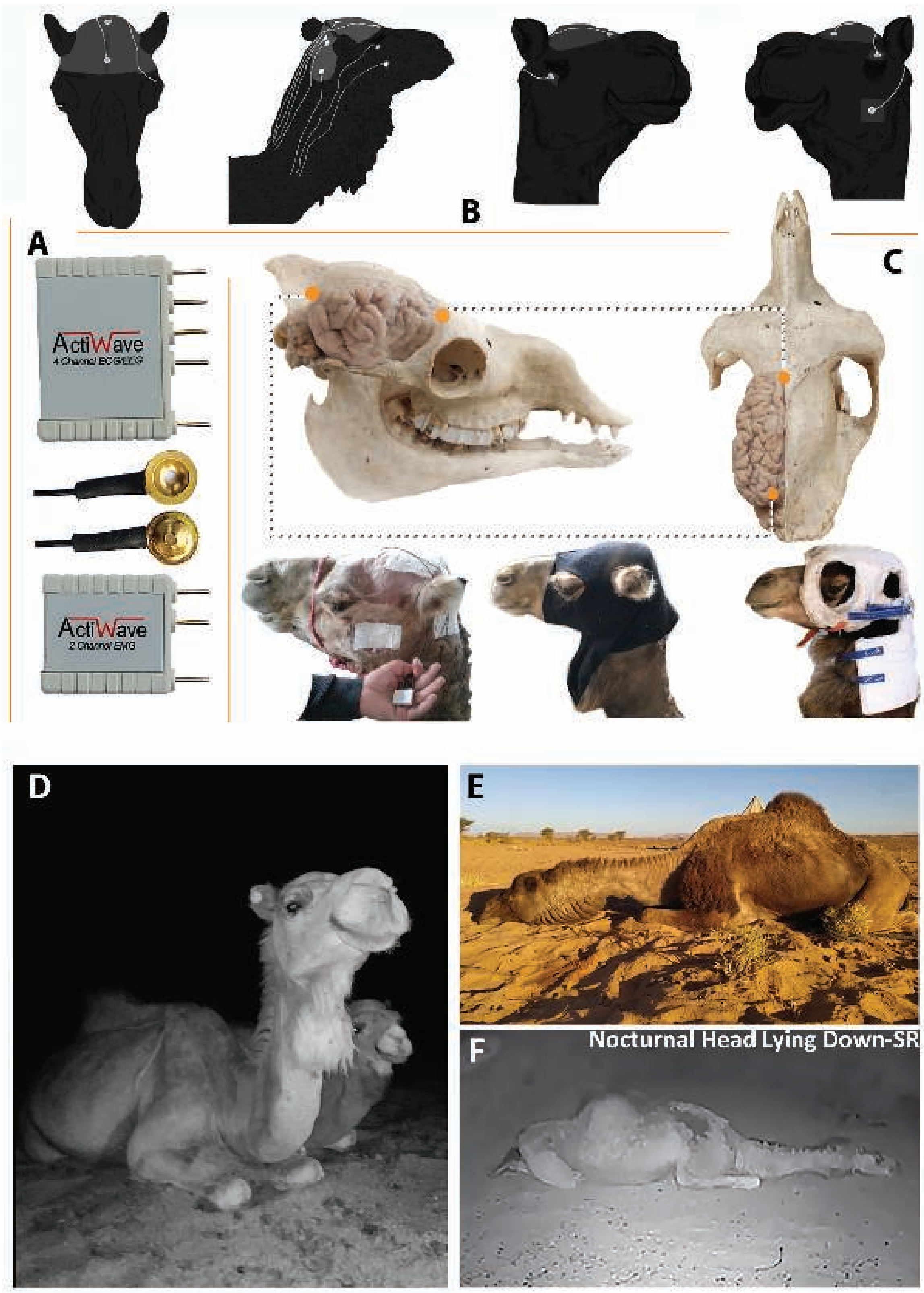

Figure 1. Noninvasive PSG equipment for studying sleep in the camel. (A) Two Actiwave devices (CamNtech-UK) connected with gold-plated disc electrodes used for investigating EEG, EOG, and EMG. (B) Different views of the schematic representation of eight electrodes location on the dromedary head. (C) Upper photographs represent lateral and dorsal views of the camel skull with the brain in the cranial cavity and the location of two EEG electrodes (orange circles). One electrode applied over the frontal cortex in the median frontal concavity and the other over the occipital cortex, on the caudal planum of the external sagittal crest, approximately 1–2 cm rostral to the external occipital protuberance. The lower row in panel (C) shows the attachment of electrodes on the skin by medical plasters and protection of leads and the devices by a nylon cover and then a handmade lightweight polystyrene helmet protects all material. (D)–(F) Behavioral postures in socially housed dromedary before the beginning of the experiments showing the SR with the head and neck erect (D: postures of Moved Head up-SR/Motionless Head up-SR) or laying on the ground (E and F: diurnal and nocturnal Head Lying Down-SR posture).

Table 2. Total readable signal duration for EEG, EOG, and EMG in each camel per night

Recording periods	EEG	EOG	EMG
Camel 1	9 h 19 min 00 s	09 h 19 min 00 s	11 h 20 min 00 s
Camel 2	6 h 01 min 30 s	08 h 12 min 30 s	11 h 10 min 00 s
Camel 3	9 h 24 min 00 s	09 h 24 min 00 s	11 h 12 min 00 s
Camel 4	6 h 03 min 00 s	08 h 18 min 00 s	11 h 08 min 00 s
Total duration per signal	30 h 47 min 30 s	35 h 13 min 30 s	44 h 50 min 00 s
Total (EEG + EOG + EMG)	110 h 51 min 00 s readable signal from 115 h 17 min 00 s of total recorded signal		

Table 3. Polysomnographic signal criteria of EEG, EOG, and EMG used for defining the vigilance states and the used sleep terminology in camels

(A) Criteria† of EEG, EOG, and EMG

	EEG	EMG	EOG
Wakefulness	High-frequency EEG activity, low amplitude but sometimes variable and accompanied by artifacts that expand the voltage and increase the frequency. During awake, movement of the head, jaw, eye, and ear generated artifacts on the EEG signals	High-voltage EMG indicates elevated muscular tone	High amplitude and frequency in EOG signal corresponding to occasional and non-rhythmic movements of the eyes
Drowsiness	Fast EEG activity with reduced amplitude	Muscle tone is still present but the signal is lowered	Amplitude and frequency of EOG are decreased
NREM sleep (SWS)	Low-frequency, high-amplitude activity in EEG with apparition sometimes of the spindle as in stage 2 of human sleep	Muscle tone is reduced: EMG signal with very low amplitude than in wakefulness and drowsiness.	No or very sparse reduced signals of eye movements
REM sleep	Fast frequency and return to a general low amplitude as seen in wakefulness but with often EOG artifacts in the EEG	Muscular atonia: very reduced amplitude with sparse muscle twitches	EOG signal showing the high amplitude of Rapid eye movements
Rumination	High amplitude, low frequency with artifact covered EEG signal	Fast frequency, typical prominent high-voltage rhythm in EMG	Artifact covered EOG signal

(B) Sleep terminology‡ used in the camel

	Definitions
Delta waves	Frequency range from 0 to 4 Hz
Theta waves	Frequency range from 4 to 8 Hz
Alpha waves	Frequency range from 8 to 12 Hz
Beta waves	Frequency range from 12 to 30 Hz
Gamma waves	Frequency range from 30 to 50 Hz
Depolarization	A relatively negative voltage appearing as wave changes in PSG traces
K-complex	An ample surface-positive transient followed by a slower, surface-negative component in EEG signal
Hypersynchronous pattern	A pattern including EEG and EOG traces with high-amplitude rhythmic synchronized discharges related to REM
Slow-wave depolarization in EOG (slow rolling eye movements)	Long gentle and not sharply waves with an initial deflection and lasting more than ≥ 0.5 s in duration
Eye blinks	Conjugate vertical eye movements, 0.5–2 Hz, present in wakefulness
REM	Irregular, sharply, initial deflection waves seen in the EOG signal. Characteristic of the REM stage

†Criteria combined from human (Carskadon and Rechtschafen [21]) and animal (Williams et al. [10]; Kis et al. [12]; Perentos et al. [13]; Bell [17]; Bell and Itabisashi [18]; Hänninen et al. [19]; Scriba et al [20]) sleep studies.
‡Terminology defined by Loomis et al. [22]; Florin Amzica and Mircea Steriade [23]; Carskadon and Rechtschafen [21].

% = (number of transitions from state “a” to state “b”/ total transitions from state a) × 100.

Hypnograms including the different vigilance states scored per night were realized using the Polyman program. In addition, a quantitative EEG method using the power spectrum (PS) calculation, based on fast Fourier transform (FFT) analysis [24], was used to assess each vigilance state. PS analysis was used to plot the average $\log_{10}$ power (μV^2/Hz) vs the frequency (Hz) of each state. The frontal EEG derivation was processed using the free EDF browser software (https://www.teuniz.net/edfbrowser/) to calculate the PS. FTT analysis was conducted with the following parameters [25–27]: Hamming window, FFT number: 500, FFT resolution: 1 Hz, and segment length: 4 seconds. The frontal derivation was selected because it offers a clear EEG signal pattern. Four-second artifact-free epochs of each vigilance state were selected from each camel and displayed at frequencies of 1–30 Hz. Frequencies below 1 Hz were not used for the analysis because of their sensitivity to artifacts. For each specific state, the PS means of all epochs were calculated at different frequencies. This was done for each animal and then averaged for all camels. Data are presented as the means ± standard errors of the mean (SEM).

The raw spectral power values of each epoch and each camel were also used to calculate the average PS corresponding to each frequency band. For each frequency band, one-way repeated-measures ANOVA followed by Holm–Sidak's multiple comparison post hoc test was used to determine the significant differences in the average spectral power between the different vigilance states. In this way, the average spectral powers in the delta (1–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma (30–50 Hz) bands were separately compared between wakefulness, drowsiness, NREM sleep, and REM sleep. Rumination epochs were not analyzed due to numerous artifacts in the EEG signals. Values of $p \leq 0.05$ were considered statistically significant.

Results

Nocturnal sleep-like behaviors

During the night, the camels remained inactive in the sternal recumbency (SR) position (Figure 1D–F), most often preferring a specific location in the enclosure, in front of, or close to the door. Nocturnal resting of the camel was characterized by three behavioral states:

1) Moved Head up-SR: SR position with the head and neck raised straight and moving (rumination, shaking, ear movements, etc.), corresponding to an awakening state.
2) Motionless Head up-SR: SR position with the head and neck raised straight. The head moves slightly or is motionlessness. Video-recording analysis revealed that in this position, camels yawn frequently and that the eyelids are relaxed with eyes remaining mostly opened. This posture probably corresponds to the state of drowsiness.
3) Sleep-like behavior: During nocturnal rest, camels in the recumbent position went through different episodes of drowsiness mixed with arousal and sleep-like behavior. Short periods of sporadic sleep-like behavior corresponding to a specific posture of Head Lying Down-SR were observed. In this posture, the camel was in motionless SR, but the head and the elongated neck were laid on the ground straight along the longitudinal axis of the body (Figure 1F).

Polysomnographic characteristics of camel sleep

For all camels, sustained polysomnographic signals were obtained, defining five different vigilance states: wakefulness, drowsiness, NREM sleep, REM sleep, and rumination. Recording analyses showed that these various states were quite brief and that they often overlapped, resulting in multiple configurations and combinations. In summary, camels exhibited a sleep pattern involving rapid shifts between different vigilance states.

Wakefulness. When the camels were awake, video recordings showed a motionless posture in SR with a polysomnographic signal characterized by fast, low-amplitude, beta-type wave activity in the EEG signal (22–34 Hz with amplitude 9–17 μV) (Figure 2A) and high-frequency horizontal eye movements and blinking in the EOG (Figure 2B). Permanent, high tonic activity was found in the EMG signal, with myogenic artifacts seen in the EEG and EOG signals most likely associated with voluntary movements (Figure 2C), such as head turning and erected ears. In the awake state, when the animal chewed, the activity of the masseter muscle produced a low-frequency, large-amplitude rhythmic signal that disrupted almost all polysomnographic tracings (Figure 2D).

Three major patterns were observed in the signals during wakefulness in the camel:

1. High-frequency, low-amplitude EEG without any artifacts, with a flat EOG pattern and high-amplitude EMG (Figure 2A).
2. Desynchronized EEG, possibly linked to eye, ear, and/or head movements, and myogenic artifacts (Figure 2, B and C).
3. EEG with synchronous artifacts from the masticator muscles when the camels were chewing (Figure 2D).

Drowsiness. Drowsiness is considered a state of transition from arousal to sleep. During this state, the EMG signal is characterized by tonic activity lower than that of the awake state but higher than that during sleep. This EMG activity could vary due to the presence of head and neck movements. The EEG signal was contaminated by myogenic artifacts that were less prominent than in the wakefulness stage (Figure 3A–C). The EEG signal showed activity at 3–8 Hz and theta waves with high amplitude (16–25 μV, up to 50–60 μV at the frontal electrode; Figure 3A–C). Drowsiness is also characterized by the sporadic presence of K-complex waves (Figure 3B). Finally, the EOG pattern showed low-frequency and low-amplitude eye movements (Figure 3, A and B), with occasional high-amplitude but slow-wave depolarizations (2–3 seconds) corresponding to slow rolling eye movements (Figure 3C).

NREM sleep. NREM sleep in the camel showed low-frequency activity (1–4 Hz) corresponding to delta waves, with a high amplitude of 34–76 μV (Figure 4A), occasionally exceeding 100 μV at the frontal electrode (Figure 4). Transient discharges, as reflected by the K-complex waves, were also recorded during the NREM stage (Figure 4D). Muscle tonic activity during NREM sleep was much lower than that during the drowsiness and wakefulness states. Finally, myogenic artifacts were absent from the EEG recordings, and eye movements were either absent or of very small amplitude in the EOG recordings.

REM sleep. REM sleep in the studied camels showed a hypersynchronous pattern defined by fast EEG activity dominated by oscillations at 19–28 Hz (beta wave) with amplitudes of 8–15 μV, interspersed with occasional gamma waves (approximately 47 Hz) and an amplitude of 5–8 μV, clearly seen at the occipital electrode (Figure 5, A and B). The EEG signal was similar to the signal recorded during wakefulness, except for the absence of any muscle activity in the EMG recordings and the presence of characteristic rapid eye movements of large amplitude, between 67 and 450 μV, in the EOG (Figure 5). These rapid eye movements generated strong artifacts in the EEG signal at the frontal electrode (Figure 5, C and D). Muscular atonia was prevalent, giving a flat trace with sporadic phasic EMG bursts (muscle twitch) at 62–153 μV, in some cases exceeding 250 μV (Figure 5D), with a duration of 0.4–0.9 seconds. These bursts were occasionally observed in signals from both the masseter muscle and the dorsal musculature of the neck.

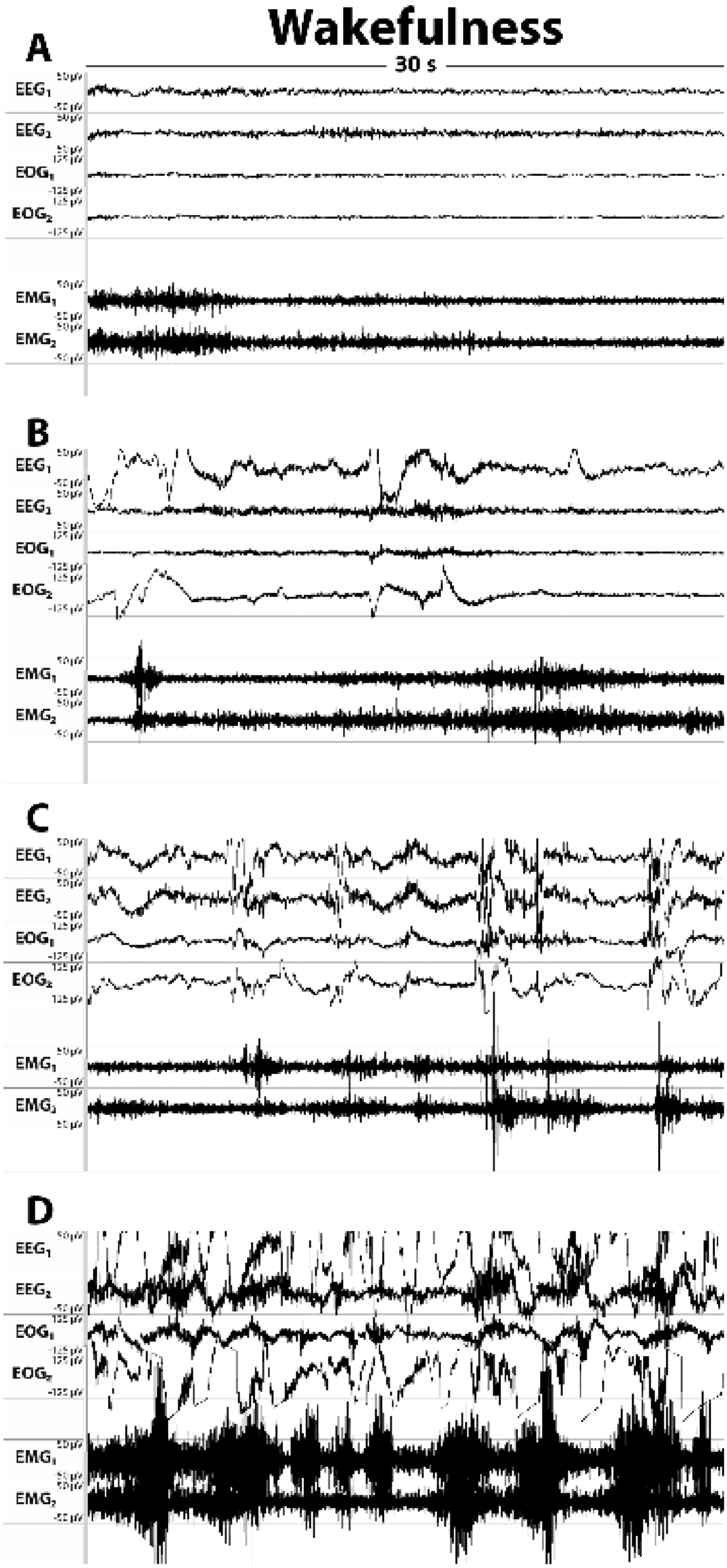

Figure 2. Examples of polysomnographic traces with appropriate frequency analysis during wakefulness state in the camel. (A)–(D) show the major patterns of the polygraphic signals (EEG, EOG, and EMG) that were shaped by different events during wakefulness in the camel. Especially in (D), chewing during arousal has a particular pattern with all traces covered by synchronous artifacts of masticator muscles. EEG1 and EEG2: electroencephalogram waveforms from, respectively, frontal and occipital electrodes, with a calibration of 100 µV. EOG1 and EOG2: electrooculogram waveforms from, respectively, the left and right eye electrodes, with a calibration of 250 µV. EMG1 and EMG2: electromyogram from, respectively, the masseter and nuchal muscles with a calibration of 100 µV. A band-pass filter of 0.3–50 Hz was used for the EEG. The length of the data epochs is 30 seconds.

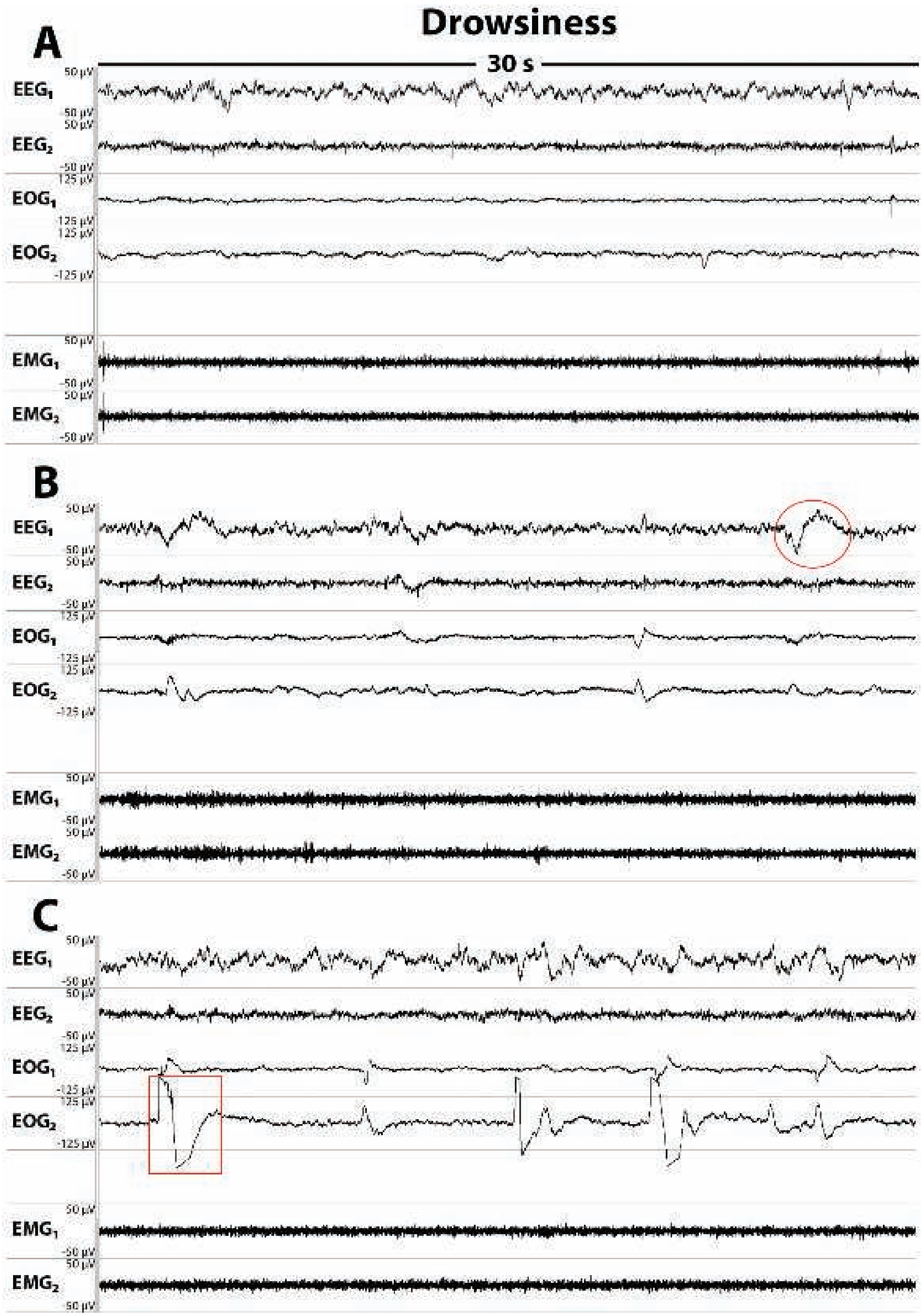

Figure 3. Typical segments of polysomnographic traces with appropriate frequency analysis during Drowsiness state in the camel. (A–C) Polysomnographic patterns examples during Drowsiness state in the dromedary camel. EEG1 and EEG2: electroencephalogram waveforms from, respectively, frontal and occipital electrodes, with a calibration of 100 µV. EOG1 and EOG2: electrooculogram waveforms from, respectively, the left and right eye electrodes, with a calibration of 250 µV. EMG1 and EMG2: electromyogram from, respectively, the masseter and nuchal muscles with a calibration of 100 µV. A band-pass filter of 0.3–50 Hz was used for the EEG. The length of the data epochs is 30 seconds. The K-complex events (denoted in circle), slow rolling eye movements (denoted in square).

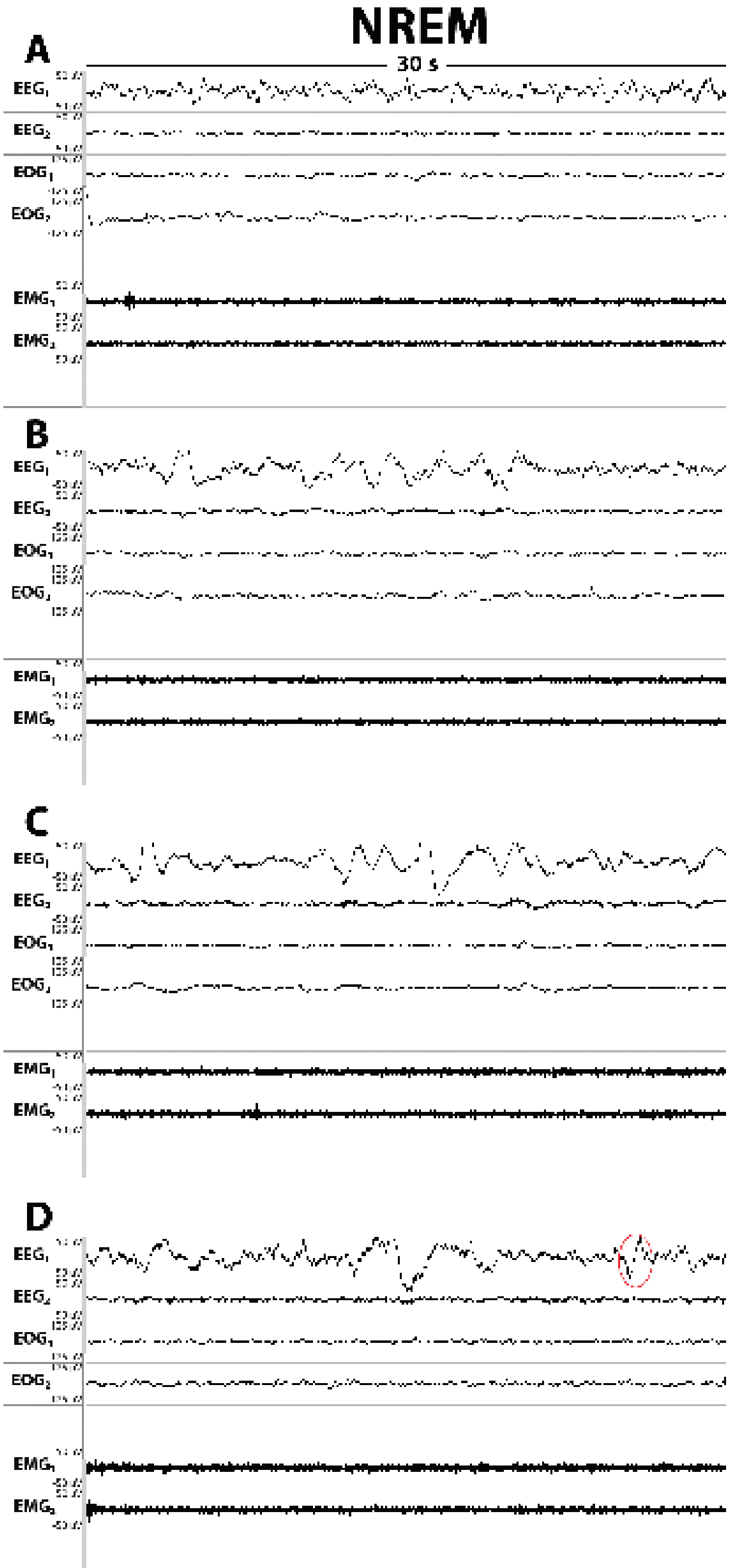

Figure 4. Representative polysomnographic traces with appropriate frequency analysis during the NREM-sleep state in the camel. (A–D) Different patterns and examples noticed during the NREM-sleep state in the camel. EEG1 and EEG2: electroencephalogram waveforms from, respectively, frontal and occipital electrodes, with a calibration of 100 µV. EOG1 and EOG2: electrooculogram waveforms from, respectively, the left and right eye electrodes, with a calibration of 250 µV. EMG1 and EMG2: electromyogram from, respectively, the masseter and nuchal muscles with a calibration of 100 µV. A band-pass filter of 0.3–50 Hz was used for the EEG. The length of the data epochs is 30 seconds. The K-complex event is encircled.

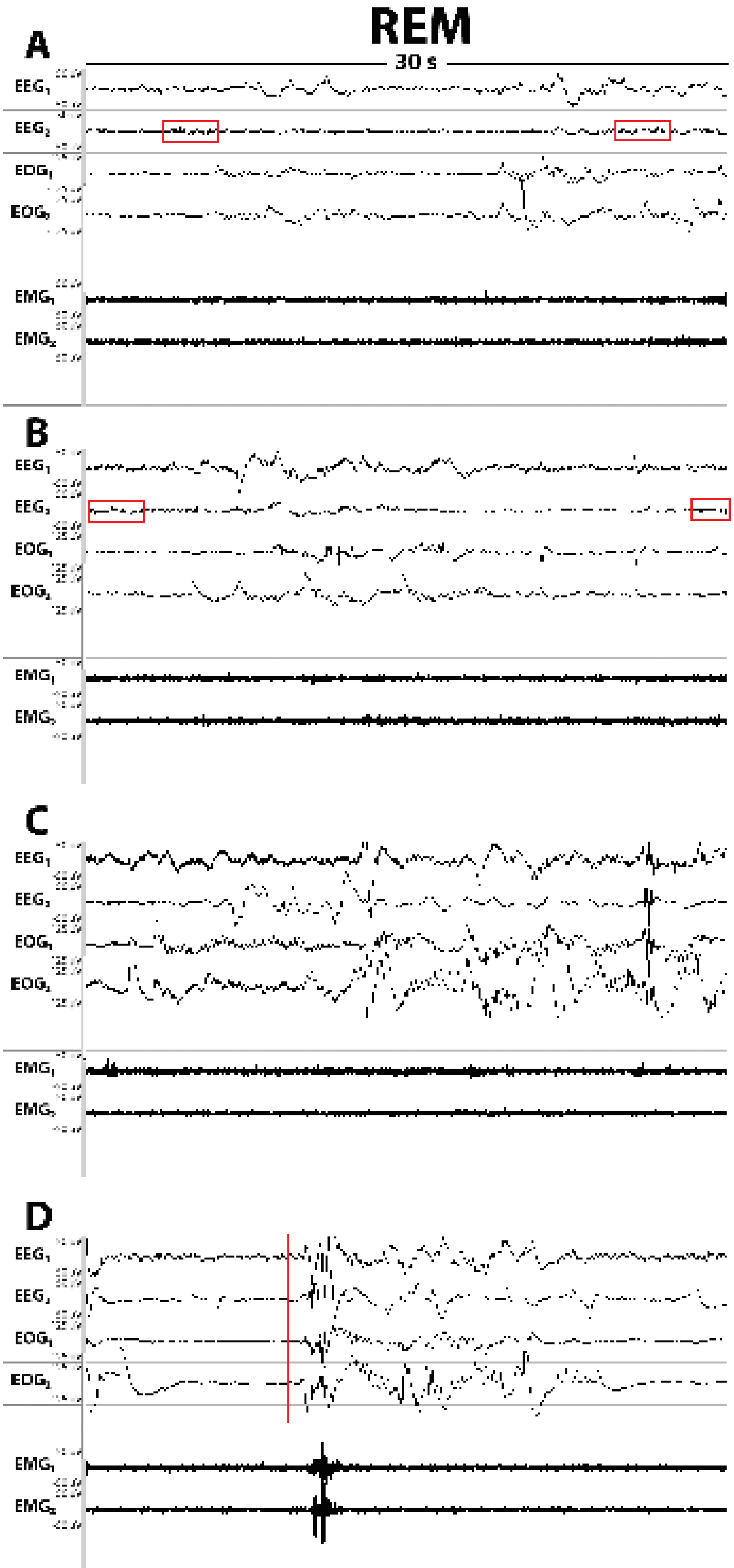

Figure 5. The REM-sleep state characteristics in the camel polysomnographic signals and its appropriate frequency analysis. (A–D) Different examples of polysomnographic signals showing the pattern of the REM-sleep state in this species. EEG1 and EEG2: electroencephalogram waveforms from, respectively, frontal and occipital electrodes, with a calibration of 100 µV. EOG1 and EOG2: electrooculogram waveforms from, respectively, the left and right eye electrodes, with a calibration of 250 µV. EMG1 and EMG2: electromyogram from, respectively, the masseter and nuchal muscles with a calibration of 100 µV. A band-pass filter of 0.3–50 Hz was used for the EEG. The length of the data epochs is 30 seconds. Hypersynchronous EEG/EOG pattern is framed by the two red lines. Occasional gamma waves (47 Hz) transitions (denoted in square).

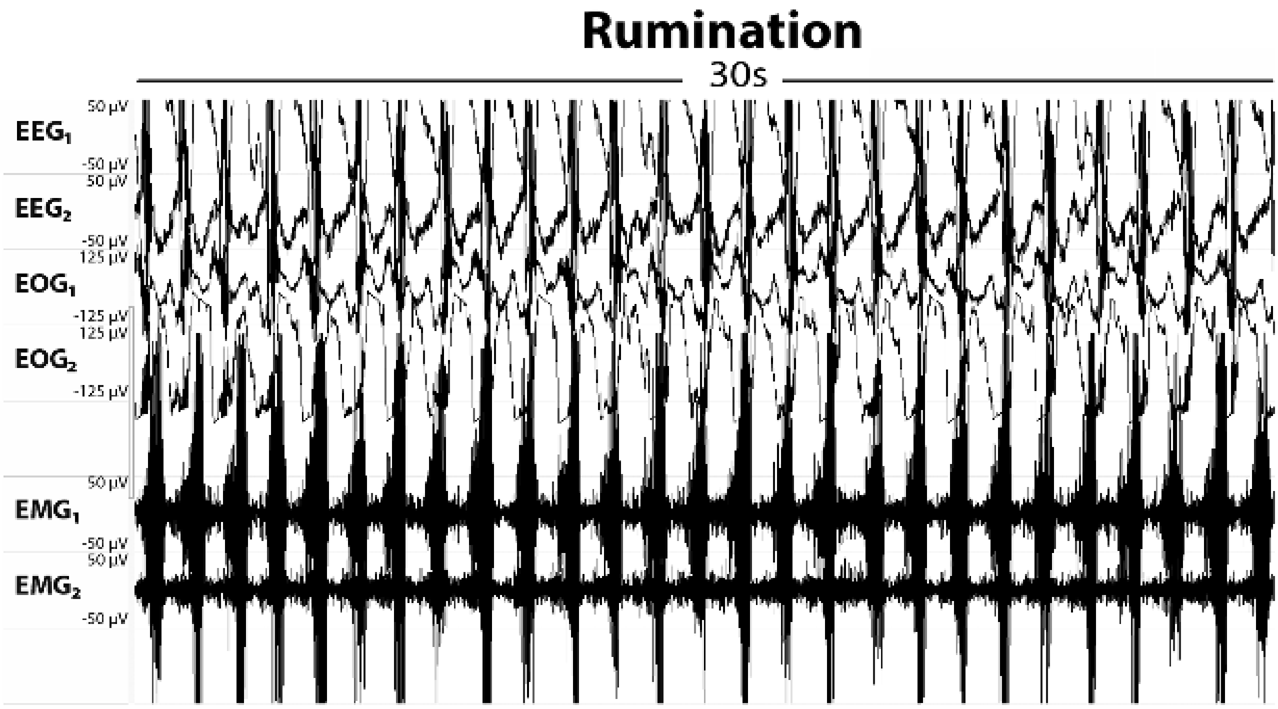

Figure 6. Camel's rumination state example from a polysomnographic traces with its appropriate frequency analysis. The typical pattern of the polysomnographic signal during rumination. EEG1 and EEG2: electroencephalogram waveforms from, respectively, frontal and occipital electrodes, with a calibration of 100 µV. EOG1 and EOG2: electrooculogram waveforms from, respectively, the left and right eye electrodes, with a calibration of 250 µV. EMG1 and EMG2: electromyogram from, respectively, the masseter and nuchal muscles with a calibration of 100 µV. A band-pass filter of 0.3–50 Hz was used for the EEG. The length of the data epochs is 30 seconds.

Rumination. Rumination was considered an independent state because during behavioral scoring, it was associated with both wakefulness and drowsiness, and because EEG recorded during rumination were easily distinguished from the other vigilance states (Figure 6).

Rumination was characterized by fast, rhythmic myogenic depolarizations in the EMG, each lasting for 0.8–1.2 seconds, with a high mean amplitude of 497.7 ± 1.0 µV generated by regular muscle twitching of the masseter and dorsal musculature of the neck (Figure 6). Rumination was completely different from the EMG signal of simple chewing (Figure 2D). Chewing and feeding during wakefulness generated a small rhythmic myogenic signal exhibiting long-lasting (3–5 seconds) and low voltage (not exceeding 313.9 ± 16.1 µV). Rumination provoked intense rhythmic electrical artifacts that pervaded the EEG and EOG signals (Figure 6). The EEG showed low-frequency, high-amplitude signals with a specific pattern of spike-like waves. In the EEG, each rumination bout was preceded by a specific long wave followed by a depolarization corresponding to the eruption of a new bolus.

EEG spectral power. Figure 7 shows that NREM sleep was characterized by maximal EEG spectral power at lower frequencies. At higher frequencies, there was a progressive decrease in the power values. Concerning REM sleep and wakefulness, FTT analysis showed lower EEG spectral power at lower frequencies than drowsiness and NREM sleep. For wakefulness, a small peak at 10 Hz was observed, with a moderate increase in power between 20 and 25 Hz. It is interesting to note that the EEG power in REM sleep also showed a slight elevation between 20 and 30 Hz (Figure 7).

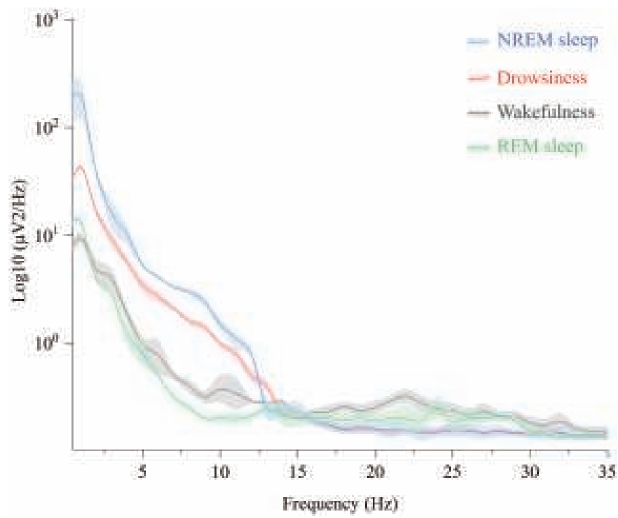

Figure 7. Averaged EEG power spectra (µV2/Hz) plotted on a $\log_{10}$ scale for NREM sleep, drowsiness, wakefulness, and REM sleep for frequencies from 1 to 30 Hz calculated as a mean of the four camels. The light-shaded area along the curves indicates the standard error (± SEM) variation between the frequencies' points.

One-way repeated-measures ANOVA was used to compare the average spectral power in each frequency band between the different vigilance states (Figure 8). Results showed significantly higher spectral power in the delta range (1–4 Hz) for NREM sleep than for drowsiness ($F_{(3,12)} = 63.36$; $p < 0.0001$), wakefulness ($F_{(3,12)} = 63.36$; $p < 0.0001$), and REM sleep ($F_{(3,12)} = 63.36$; $p < 0.0001$). Furthermore, the spectral power was significantly higher for the theta (4–8 Hz) and alpha (8–12 Hz) frequencies

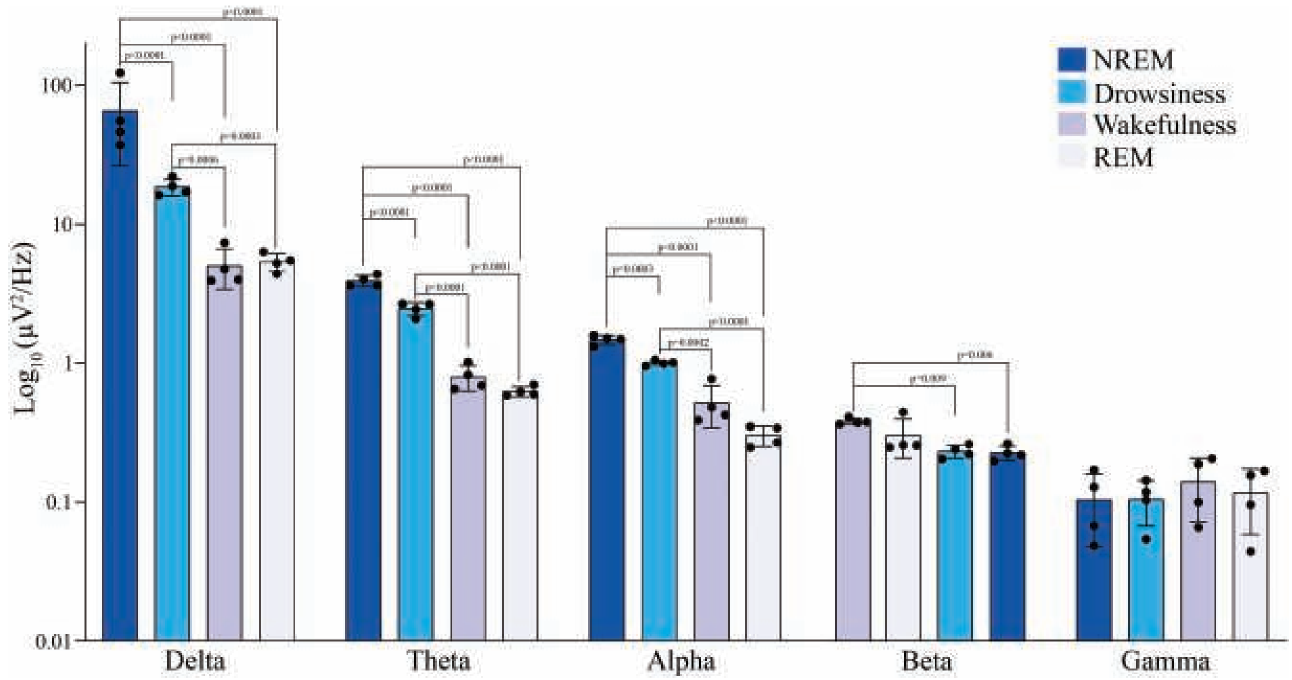

Figure 8. The means (± SEM) of EEG PS for delta, theta, alpha, beta, and gamma bands for each vigilance state of the four camels. Dots in the bar graph represent the individual data points (each point represents the average PS value of one camel for each vigilance state). The spectral power of each frequency range was compared between different vigilance states using repeated-measures ANOVA. Only statistical significances ($p \leq 0.05$) were illustrated with horizontal bars and the corresponding *p* values.

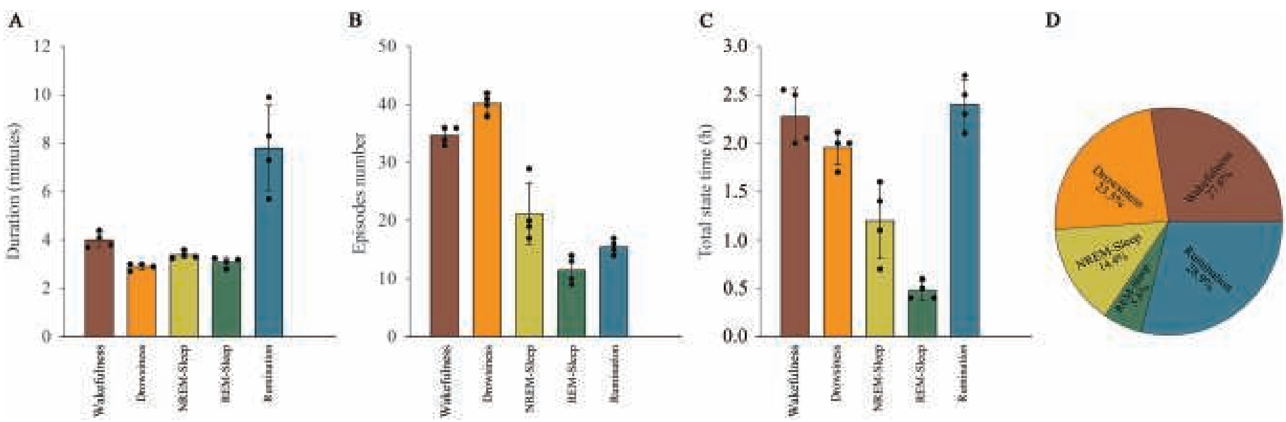

Figure 9. Nighttime dynamics of vigilance states in the camel depicting the duration in minutes (A), episode numbers (B), total state time in hours (C), and the percentage time spent in each of the vigilance states (D). Dots in the bar graph A, B, and C represent the individual data points (each point represents the average value of each camel).

in NREM sleep than in drowsiness ($F_{(3,12)} = 164.4$; $p < 0.0001$ and $F_{(3,12)} = 93.21$; $p = 0.0003$, respectively), wakefulness ($F_{(3,12)} = 164.4$; $p < 0.0001$ and $F_{(3,12)} = 93.21$; $p < 0.0001$, respectively), and REM sleep ($F_{(3,12)} = 164.4$; $p < 0.0001$ and $F_{(3,12)} = 93.21$; $p < 0.0001$, respectively). A significant difference in spectral power was found in the beta (12–30 Hz) frequencies in wakefulness compared with NREM sleep ($F_{(3,12)} = 7.9$; $p = 0.006$) and drowsiness ($F_{(3,12)} = 7.9$; $p = 0.009$).

Nighttime dynamics of vigilance states

Episode duration and number, total state time, and the percentage time spent in each vigilance state per night are shown in Figure 9. The camels spent most of the night ruminating (2.4 ± 0.3 h/night), being awake (2.3 ± 0.3 h/night), and drowsing (1.9 ± 0.2 h/night) (Figure 9C). These three states occupied 87.8% of the night, with 27.6 ± 0.1% for wakefulness, 28.9 ± 0.6% for rumination, and 23.5 ± 0.1% for drowsiness (Figure 9D). The wakefulness and drowsiness bout durations were 4.00 ± 0.41 and 2.90 ± 0.15 minutes, respectively, and both displayed the highest episode numbers per night with 34.7 ± 1.8 and 40.3 ± 1.2, respectively (Figure 9B). From all the analyzed states, rumination exhibited the largest bout duration, with a mean of 7.80 ± 1.78 minutes (minimum 0.5–2 minutes and maximum 5–49 minutes) and an episode number of 15.5 ± 1.5 per night.

The camels slept for approximately 20.0% of the night (Figure 9D). This proportion encompassed several contiguous episodes throughout the night (episode numbers, NREM: 21.0 ± 5.5 vs

REM: 11.3 ± 2.6) with a duration of up to 4 minutes (Figure 9, A and B; NREM: 3.40 ± 0.17 minutes vs REM: 3.05 ± 0.26 minutes). NREM sleep represented 14.4% of the total recording, while REM sleep accounted for only 5.6% (Figure 9D), totaling a state time per night of 1.2 ± 0.4 and 0.5 ± 0.1 hours, respectively (Figure 9C). Therefore, REM sleep constitutes an episodic and infrequent state, with only 29.4% of total sleep time.

Hypnograms (examples from two camels are given in Figure 10, A and B) clearly illustrate the polyphasic sleep nature in this species, with sleep periods interrupted by frequent periods of wakefulness. In addition, sleep was also interrupted by different bouts of drowsiness and rumination. The different vigilance states followed a specific chronology: wakefulness was more dominant during the first two-thirds of the night, most NREM periods occurred during the first and middle parts of the night, and REM sleep was distributed throughout the night, mainly occurring either during the first half (camel in Figure 10A) or the middle of the night (camel in Figure 10B). Similarly, rumination varied from one animal to another, occurring either in the first part of the night (camel in Figure 10A) or shifted to the middle and last parts of the night (camel in Figure 10B).

Transitions between different states of vigilance were calculated as the mean percentage from all camel recordings (Table 4). In most cases, wakefulness switched toward drowsiness (77%), and direct shifting from wakefulness to sleep was unusual (9% for NREM sleep and 4% for REM sleep).

After drowsiness, the camels moved either to an awake state in 48% of cases or to NREM sleep in 37% of transitions. The transition from drowsiness to REM sleep was infrequent, occurring only 9% of the time, and in 6% of the cases, the camels interrupted their drowsiness to ruminate.

After NREM sleep, the camels were immediately awake (37% of cases), drowsy (32% of cases), or moved to REM sleep (17% of cases). Rumination replaced NREM sleep in 14% of transitions. Furthermore, results showed that REM sleep was predominantly followed by wakefulness (50%) or drowsiness (32%), while major transitions from rumination were toward drowsiness (48%).

Correlation between resting positions and sleep

To correlate the nocturnal sleep-like behaviors with sleep and other vigilance states, video recordings of the camels were analyzed jointly with the scoring of polysomnographic signals in 30-second epochs. During this analysis, the SR posture was dominant, with no standing position recorded. The occurrence of the three nocturnal SR behaviors, namely Moved Head up-SR, Motionless Head up-SR, and Head Lying Down-SR, were compared with the vigilance states of wakefulness, drowsiness, REM sleep, NREM sleep, and rumination as recorded by PSG (Table 5, refer A). Results showed that camel wakefulness was mainly associated (79.1%) with the Moved Head up-SR posture, while drowsiness mainly corresponded to the Motionless Head up-SR posture (83.2%). NREM sleep was associated with the former posture in 60% of the cases and with the Head Lying Down-SR position in 39.2% of the cases. REM sleep, during which muscle tonicity is reduced and the musculature of the animal is relaxed, occurred exclusively when the head and neck were lying on the ground (sleep-like behavior of SR). Rumination was mainly observed (89.3%) when the camels exhibited a Moved Head up-SR posture.

Further calculations (Table 5, refer B) showed that the Head Lying Down-SR posture was almost exclusively associated with sleep (60.6% and 23.7% to REM and NREM, respectively), while the Motionless Head up-SR posture corresponded to drowsiness (51.9%) and NREM sleep (37.4%). Finally, the Moved Head up-SR posture was exclusively observed during wakefulness (45.2%) and rumination (51%).

An illustrative, comparative description of the sleep structures recorded by PSG and behavioral observations was performed using hypnograms (Figure 10C). Considering only the Head Lying Down-SR posture as an indicator of behavioral sleep and NREM and REM as indicators of PSG sleep led to an underestimate sleep duration (Figure 10C, refer no. 1), with important mismatches between behavioral and PSG sleep bouts. In the second comparison (Figure 10C, refer no. 2), when considering both the Head Lying Down-SR and Motionless Head up-SR postures as indicators of behavioral sleep, the match between behavioral and PSG sleep (both NREM and REM sleep) was clearly enhanced. This is probably linked to the fraction of the Motionless Head up-SR posture corresponding to NREM sleep (Table 5). However, the best correlation was found when drowsiness was also included as part of the PSG sleep in addition to NREM and REM states, with Head Lying Down-SR and Motionless Head up-SR postures considered as indicators of behavioral sleep (Figure 10C, refer no. 3).

Discussion

The present study aimed at characterizing the sleep pattern in the dromedary camel using noninvasive portable equipment. The PSG results showed that the camel exhibited different vigilance states that rapidly shift from one to another, consisting of wakefulness, drowsiness, NREM and REM sleep, and rumination. Clearly, camels exhibit polyphasic sleep. Moreover, behavioral postures were correlated with PSG vigilance states, thereby allowing us to reliably evaluate the duration spent in REM and NREM states.

Nocturnal resting postures in the camel

Resting behavior is important for physical and physiological recovery, which can be achieved by relaxing both the musculoskeletal system (awake rest) and the central nervous system (sleep rest) [27–29]. The results of this study showed that the camel exhibits nocturnal rest behavior by positioning itself in SR with the head and neck raised upright, in motion (Moved Head up-SR; i.e. chewing, ruminating, shaking the ear, moving the head), a rest–awake state, or motionless (Motionless Head up-SR), most probably reflecting a state of drowsiness. Camel nocturnal rest also includes a specific sleep-like behavior: an SR position with the head and neck lying on the ground here called the Head Lying Down-SR posture, which has previously been described as the major rest posture in camels [30, 31]. Approximate descriptions of similar postures can be found in earlier reports and illustrations from naturalists and explorers of the Orient from the last century. However, the present study offers the first description of the whole spectrum of these behavioral postures in the camel and their correlations to polysomnographic recordings of sleep.

In several species, including giraffes, horses, cattle, sheep, and piglets, paradoxical sleep has been associated with the

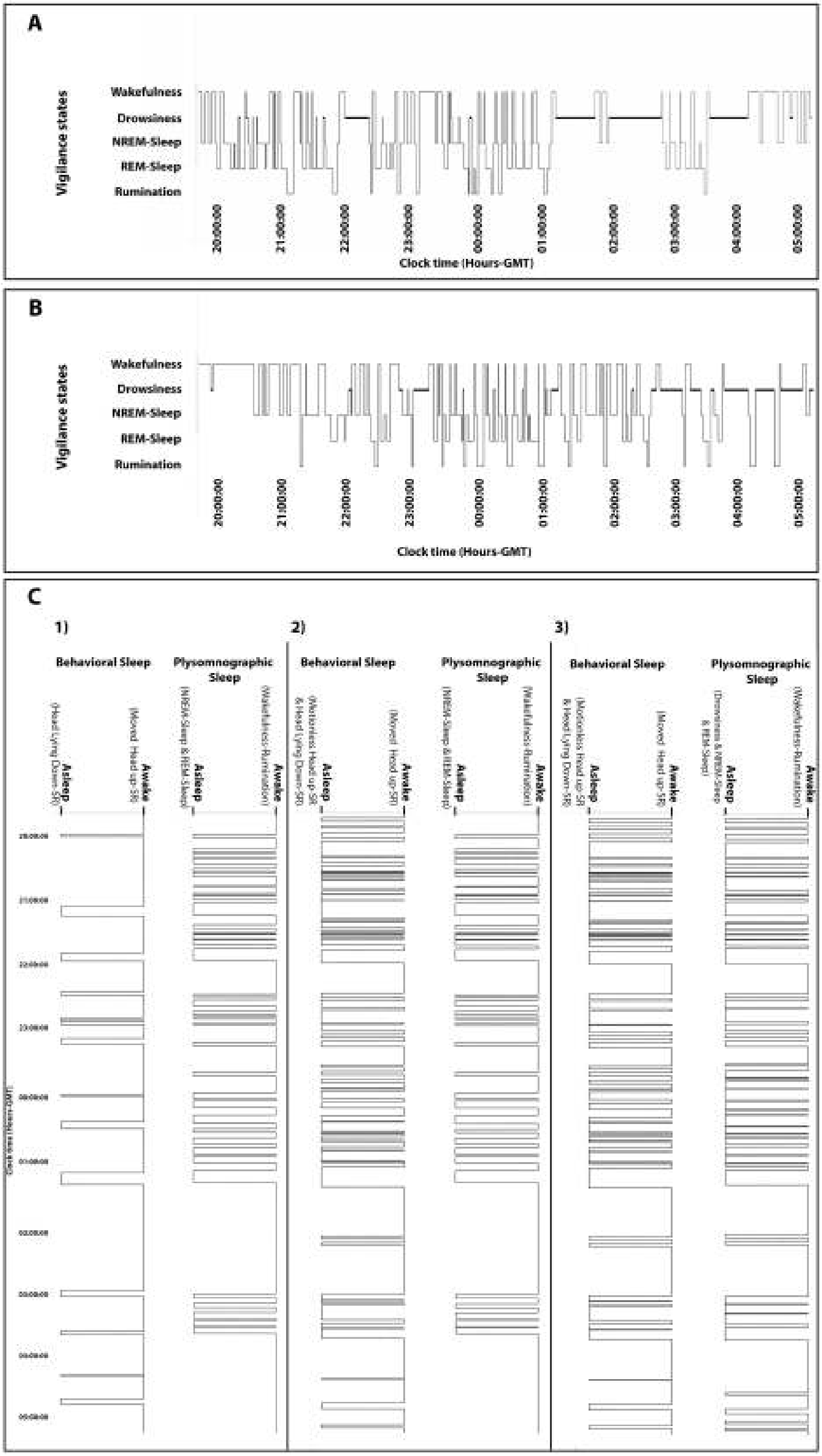

Figure 10. Hypnograms illustrating the sequential nature of vigilance states (wakefulness, drowsiness, NREM sleep, REM sleep, and rumination) in two camels during a 9.5-hour period of darkness (07:41 pm to 5:16 am) (A and B). Panel C shows hypnograms comparing polysomnographic and behavioral sleep: (1) behavioral sleep was limited to the Head Lying Down-SR posture, while polysomnographic sleep corresponds to NREM and REM sleeps. In (2), behavioral sleep was estimated from Motionless Head up-SR and Head Lying Down-SR, while polysomnographic sleep was maintained as in (1): NREM sleep and REM sleep, and finally in (3), behavioral sleep was estimated as in (2): Motionless Head up-SR and Head Lying Down-SR, while in polysomnographic sleep, drowsiness was included with the NREM and REM sleeps.

Table 4. Percentages of transitions between the different vigilance states calculated from the polysomnographic recordings of all camels

		Wakefulness	Drowsiness	NREM sleep	REM sleep	Rumination	Total
Wakefulness	Mean number of transitions		26.0	3.0	1.3	3.3	33.7
	% of transitions		77%	9%	4%	10%	100%
Drowsiness	Mean number of transitions	18.7		14.7	3.7	2.3	39.3
	% of transitions	48%		37%	9%	6%	100%
NREM sleep	Mean number of transitions	7.7	6.7		3.7	3.0	21.0
	% of transitions	37%	32%		17%	14%	100%
REM sleep	Mean number of transitions	4.7	3.0	0.7		1	9.3
	% of transitions	50%	32%	7%		11%	100%
Rumination	Mean number of transitions	1.7	4.3	2.3	0.7		9.0
	% of transitions	19%	48%	26%	7%		100%

Table 5. Correspondence between the polysomnographic vigilance states and the nocturnal rest behavior exhibited by camels

(A) Vigilance states determined by PSG analysis as a percentage of video-recorded behavioral postures

Behavioral postures Polysomnographic vigilance states	Moved Head up-SR	Motionless Head up-SR	Head Lying Down-SR
Wakefulness	79.1%	8.5%	12.4%
Drowsiness	5.7%	83.2%	11.1%
NREM sleep	0.8%	60%	39.2%
REM sleep	0%	0%	100%
Rumination	89.3%	8.4%	2.3%

(B) Video-recorded behavioral postures as a percentage of PSG vigilance states

Behavioral postures Polysomnographic vigilance states	REM sleep	NREM sleep	Drowsiness	Rumination	Wakefulness
Head Lying Down-SR	60.6%	23.7%	6.7%	7.5%	1.4%
Motionless Head up-SR	0%	37.4%	51.9%	5.2%	5.3%
Moved Head up-SR	0%	0.45%	3.25%	51%	45.22%

recumbency posture together with the head resting in a specific position [32, 33]. Based on these previous results, we considered that, in the camel, REM sleep corresponds to the state of Head Lying Down-SR. Importantly, this was further confirmed by the polysomnographic recordings showing that 100% of camel REM sleep occurred in this posture. Nevertheless, only 60.6% of the head reclining-SR posture corresponded to REM sleep, the remainder being associated with NREM sleep (23.7%), drowsiness (6.7%), rumination (7.5%), and wakefulness (1.4%).

Vigilance states in the camel

Wakefulness. Polysomnographic signals in calves and adult cows have shown similar recordings to those of camels, with fast, low-amplitude EEG signals [11, 19]. However, in the camel, we characterized three major patterns of arousal based on the occurrence of eye blinking and horizontal eye movements, voluntary movements of the head and ears, and chewing.

The camels spent approximately 2.3 hours of the total night duration (27.6% of total nighttime) in frequently repeated bouts of awake states lasting approximately 4 minutes each. Cows showed almost the same wakefulness time, but some Perissodactyla such as horses spend more than 50% of the night awake [10]. For 79.1% of the total awake time, the camels were in an SR position with the head and neck erect and moving (Moved Head up-SR posture). The same posture has been observed during the awake state in cows [34] and goats [17], whereas other herbivores, such as horses [10] and elephants [35], lay down to sleep for a while, but they spend a significant part of their nighttime awake and standing.

In most cases, wakefulness switched toward drowsiness (77%), a pattern that has also been observed in cows (47% of cases). In contrast, direct shifts from wakefulness to sleep were found in camels (9% for NREM sleep and 4% for REM sleep), while such direct transitions are absent in cows [34] and, to the best of our knowledge, in other ruminants including goats and sheep.

Drowsiness. According to Tobler [36], the criteria used to distinguish drowsiness from sleep are arbitrary. Hänninen et al. [19] also noted that it was difficult to distinguish drowsiness from NREM in calves. In contrast, it was relatively easy to define drowsiness in the camel, particularly when using a combined interpretation of different PSG recordings. In the EEG signal, drowsiness was highlighted by lower amplitude but higher frequency signals than in NREM sleep and by the presence of some K-complex waves. Additionally, EMG muscle tonic activity was weaker than in wakefulness. The EOG pattern was low in frequency and amplitude, with slow-wave depolarization linked to eye-rolling movements. This particular feature is commonly observed in NREM sleep in humans [37]. In the camel, drowsiness is expressed as short bouts repeated overnight with a total duration of approximately 2 hours per night. Unlike Ruckebusch et al. [38], who considered rumination as typically associated with drowsiness in ruminants, rumination was considered as a separate vigilance state in the present study. Consequently, drowsiness was of a relatively short total duration (only 23.5% of the polysomnographic recordings).

NREM sleep. As reported in most vertebrates, the NREM sleep EEG signal in the camel predominantly showed high-voltage slow (delta-type) wave sleep (SWS) without myogenic artifacts and EMG traces characterized by lower muscle tonic activity and the absence of muscle movements. Additionally, eye blinking and eye movements were absent except for some occasional low-voltage depolarization in the EOG. EEG activity in NREM sleep was 34–76 μV in amplitude, occasionally larger (100 μV) at the frontal electrode. Similar amplitudes have been reported in some ruminant species, such as calves (< 100 μV) [19] and adult cattle (> 100 μV) [39]. Unlike higher primates, in whom NREM sleep is divided into four stages, and carnivores who show two NREM categories (i.e. light and deep SWS), the other mammalian species do not show any subdivision of NREM sleep [36]. Herein, the camel was found to spend 14.4% of the total recording time in NREM sleep (equivalent to 1.2 h per night of successive bouts mixed with other vigilances states). This NREM sleep duration is lower than that observed in other ruminants, such as cows (25%) [34] and sheep (22%) [40]. In the latter species, the slow waves of rumination were often considered the SWS of NREM sleep, which strongly suggests that these animals can ruminate while sleeping [18, 33, 34]. However, when rumination is considered as a separate state, the NREM sleep state is shorter, thereby avoiding overestimation.

NREM sleep takes place when the camel is in the SR position with the head and neck either raised but motionless or stretched on the ground. NREM sleep in cows only occurs when they are in the SR position with their head raised and motionless [34], In the horse, NREM sleep is typically observed not only in SR but also in a standing position when the environment is unfamiliar and when the animal possibly feels insecure [10, 41]. Interestingly, NREM sleep in camels turns into REM sleep in only 17% of the cases. This is in line with the hypothesis that deep sleep in the camel, whose average bout duration does not exceed 3.40 minutes, has to switch immediately to a nonsleep state (wakefulness in 37%, drowsiness in 32%, and rumination in 14% of the cases) to maintain vigilance, alertness, and digestion by rumination. This also seems to be common in other herbivores. However, NREM sleep in calves turns more likely into the REM or awake state rather than into rumination or drowsiness (the switch from these last two states to NREM is only observed in adult cows) [19, 34].

REM sleep. In general, camel REM sleep features were quite similar to those reported in ruminants [19, 39], and their characterization was quite easy. In the camel, REM sleep was characterized by the presence of clear rapid eye movements on the EOG channels. The tonic muscular activity was lower than in other stages, and occasional muscle twitches were observed. Brain activity was similar to that observed in the state of arousal, with cortical waves showing regular low-voltage and fast patterns [36]. The camel spent an average of 5.6% of the night in REM, which is much shorter than that recorded in other herbivore species, including horses with a percentage of 7.8%, cows with 6.3%, and sheep with 4.8% [40]. During all REM sleep episodes (100%), the camel's head and neck remained on the ground because of cervical muscle atonia. In fact, muscle relaxation during REM sleep is a common feature in most species, albeit to variable extents [42]. For example, REM sleep is usually observed in the horse when lying down in lateral recumbency with relaxed muscles [41], whereas in the case of an uncomfortable environment, it can occur in a standing position [10]. The duration of REM sleep episodes in the camel was stable, averaging 3 minutes, a duration quite similar to that reported in many mammals, including adult dairy cows (3 minutes) [11], young calves (2 minutes) [19], and pigs (3 minutes) [43].

REM sleep in several mammalian and bird species is typically initiated after an NREM sleep state [42]. In contrast, the camel can enter into REM sleep directly from drowsiness (9% of the time) or from direct wakefulness (4% of the time). This finding seems to be exceptional among taxa, being only observed in young participants such as newborn humans [44] or calves [19]. As our camels were all adults, with complete brain development, such a transition seems to be a specific feature of REM sleep in this species.

Rumination. The polyphasic pattern of sleep in ruminants appears to be driven by the frequent occurrence of rumination overnight. EEG recordings in different ruminant species showed that cud chewing occurs not only during wakefulness and drowsiness but also during NREM sleep [11–19, 33, 38]. In the present study, cud-chewing episodes during rumination were difficult to disentangle from chewing occurring during other vigilance states, specifically NREM sleep, drowsiness, or even wakefulness. No specific change in either the behavioral postures or the EMG traces allowed such dissociation. Although an SWS-like EEG with low-frequency and high-amplitude oscillations was always present during rumination, it was entirely different from the typical SWS EEG of NREM sleep in terms of shape, amplitude, and presence of regular myogenic artifacts and spike-like waves. Although it has been reported that ruminants can sleep during rumination, this hypothesis is still debated. In 1970, Ruckebusch et al [38] raised the question of whether it was reasonable to consider rumination as NREM sleep or rather as a different state with some electrocorticographic aspects in common with NREM sleep. Additionally, Tobler [36] considered rumination as a state of dissociation between behavior and EEG. Finally, another argument in favor of rumination being considered as an induvial aspect in PSG tracings is that, in contrast to other vigilance states (including NREM sleep), EEG during rumination is similar across ruminant species.

For camels, rumination time, as defined from polysomnographic recordings, was 2.4 hours (28.9% of total nighttime). Rumination bouts were shorter in camels (mean duration: 7.8 minutes, with some individual bouts lasting only 2 minutes) than in cows and calves (approximately 30 minutes for each bout) [11, 45]. Rumination in the camel occurred during the last half or last third of the night when the animal was in a resting SR position with the head and neck erected (Moved Head up-SR: 89%). This position has previously been described as a preferred position for rumination in this species [30–46] as well as in other ruminants [33, 47–49].

Short sleep duration in the camel

As discussed above, the dromedary camel and other ruminants exhibit a fragmented sleep pattern, possibly reflecting an evolutionary adaptation to the risk of predation to remain vigilant.

Some vulnerable prey species have adopted a reduction in sleep time, particularly in REM sleep [50]. According to Allison and Cicchetti [51], larger herbivorous mammals sleep little and hence exhibit less REM sleep than predators and small animals with a low predation index (e.g. rodents). Camels sleep 1.7 hours per night with only 30 minutes of REM sleep. Other phylogenetically close species, such as other herbivores/ruminants, seem to sleep longer. For instance, total sleep time and REM sleep in different species are, respectively, 3 hours 30 minutes/24 hours in the horse [40], 4.6 hours 13 minutes/24 hours in the giraffe [32], 3 hours 45 minutes/24 hours in the cow [40], 5 hours 3–7.5 minutes/24 hours in sheep [40, 52], and 3.7–6.7 hours 4.8–16.8 minutes/24 hours in the oryx [53]. Differences in sleep duration between camels and these close species are possibly associated with the total duration of the recording. In the listed species, sleep was calculated in most cases over 24 hours, while, in the present study, sleep recording was limited to nighttime only. Furthermore, our study was carried out during summertime with a short night duration and this possibly also affected sleep duration [53]. The short duration of camel sleep in the present study is also possibly linked to rumination, which, in contrast to other studies, was considered a separate vigilance state and not associated with NREM sleep.

The total sleep time is known to be negatively correlated with body mass and brain weight [19] and to show large differences within the Mammalia class, possibly reflecting genetic, health state, environmental, and ecological pressure. In addition, Balch [47] suggested that ruminants, including the camel, cannot adopt the normal sleep posture of lateral recumbency due to the anatomical layout of the ruminant stomach and the continuous activity of the reticulum.

Sleep is essential for several functions, including cognition and maintaining a healthy body and mind balance [54–56]. Moreover, sleep is necessary for learning and memory consolidation [57, 58], for brain development (see review in [27]), and for the regulation of synaptic strength [59]. It modulates the secretion of gonadotropin growth hormones [60] and is critical for the maintenance of metabolic and thermal balances and immune competence [61, 62]. However, the short sleep duration in the camel does not necessarily preclude its involvement and control of such functions. Cognitive, immune, metabolic, hormonal, and other physiological functions in response to sleep deprivation could help better understand sleep function in the camel. The role of sleep and its architecture may differ depending on the species and their specific ecological and biotope conditions. For example, the REM sleep stage is known to facilitate memory consolidation and learning in humans [58]. Therefore, enhanced capacity for learning may be expected in animals with the highest REM sleep duration. Results of comparative studies, however, showed that this is not the case. For instance, opossums and platypus, characterized by a high amount of daily REM sleep (approximately 5 hours, up to 8 hours/24 hours), nevertheless do not show cognitive abilities as developed as primates (see review in [42]). Describing in detail the role of sleep in each species requires considering adaptive strategies to cope with the environment. Furthermore, evolutionary adaptation to specific ecological niches is an important factor that can help reach a better understanding of the differences in the quality and quantity of sleep. Cetaceans, in which REM sleep has not yet been detected, sleep partially with only one hemisphere to keep their bodies moving (see review in [63]). In ruminant species, rumination is a major component of nocturnal time partitioning. Most of these animals are diurnal species that graze and feed rapidly during the day and then hide to limit their exposure to predators [64, 65]. Ruminants, including camels, also show a predominance of drowsiness, which may be a compromise between sleep and alertness to predatory threats.

Conclusion

The results of the present study showed that camels exhibit polyphasic sleep during the night. Five different vigilance states were distinguished: wakefulness, drowsiness, REM sleep, NREM sleep, and rumination. The sleep architecture in the camel showed that these states rapidly shifted from one to another. Importantly, behavioral postures were correlated with PSG vigilance states, thereby allowing us to predict sleep by observing two postures in SR, either with the head erected but completely motionless or with both the head and neck lying down on the ground. Interestingly, 100% of REM sleep was found in this last posture. Although the overall pattern of sleep displays some similarities with that of other close Cetartiodactyla and Perissodactyla herbivores, the behavioral and EEG characteristics of REM and NREM sleep were shown to be different in the camel.

Finally, it is important to note that while behavioral sleep and PSG sleep were monitored during the night in the present study, it remains possible that sleep and drowsiness may occur during the daytime, even in a standing position. Future studies are required to obtain a comprehensive understanding of sleep in the camel.

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Disclosure Statement

None declared.

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