Seasonal variations in sleep of free-ranging Arabian oryx (*Oryx leucoryx*) under natural hyperarid conditions FREE

Joshua G Davimes, Abdulaziz N Alagaili, Adhil Bhagwandin, Mads F Bertelsen, Osama B Mohammed, Nigel C Bennett, Paul R Manger, Nadine Gravett

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Abstract

Study Objectives

The Arabian oryx lives under hyperarid conditions in the Arabian Desert and exhibits temporal niche switching of activity patterns at a seasonal level. The objective of the current study was to provide a polysomnographic-based study of sleep in free-roaming Arabian oryx in their natural habitat to determine whether extreme seasonal climate variations resulted in changes in sleep patterns and physiology associated with the seasonal switching of temporal niches.

Methods

Electroencephalography, nuchal electromyography, actigraphy, and subcutaneous temperature were recorded in free-roaming Arabian oryx in the Mahazat as-Sayd Protected Area, Kingdom of Saudi Arabia during winter and summer.

Results:

Total daily sleep time in winter was 6.69 and 3.77 hr in summer. In winter, oryx exhibited nocturnal sleep typical of artiodactyls of around 60 kg body mass. In summer, oryx slept mostly during the day and subcutaneous temperature was seen to rise during sleep, but not as rapidly as the rises observed in ambient air temperature. Rapid eye movement sleep formed a very small percentage of total sleep time, especially so in the summer.

Conclusions

The unusual sleep patterns and physiology during summer appear to be related to high ambient air temperatures that affect both intrinsic and extrinsic factors necessary for survival. The Arabian oryx appears to use sleep physiology as an adaptive thermoregulatory mechanism in the hot summer months.

Statement of Significance

The current study provides electrophysiological sleep recordings in free-roaming Arabian oryx under natural conditions. Arabian oryx exhibit

typical artiodactyl nocturnal sleep patterns and physiology during the cooler winter months, but these patterns and physiology change dramatically during the hot summer months. These changes to sleep patterns and physiology in the summer months appear to be driven by the increased ambient air temperatures experienced, and the Arabian oryx appears to employ the standard physiology of mammalian sleep to derive a novel mechanism of thermoregulation.

Introduction

The Arabian oryx (*Oryx leucoryx*) is a medium-sized desert dwelling artiodactyl that was found throughout the hyperarid desert conditions of the Arabian Peninsula, but is now mostly restricted to protected areas of the region. Arabian oryx exhibit numerous behavioral and morphophysiological responses to high temperatures including enhanced selective brain cooling [1] and adaptive heterothermy [2–4]. Additionally, Arabian oryx undergo extensive seasonal changes in the amplitude of their daily body temperature rhythms [3–6] and have been shown to exhibit temporal niche switching of activity or inactivity patterns under natural conditions [5, 7–9]. The oryx change from a nocturnal inactivity pattern during the cooler winter months to a bimodal inactivity pattern during the hotter summer months [5]. The timing of the major inactive bouts shifts seasonally from the coolest periods of the winter nights to the hottest periods of the summer days. A full year study of free-roaming Arabian oryx in the deserts of Saudi Arabia confirmed that oryx exhibit a seasonal plasticity and switches between diurnal activity patterns during winter and nocturnal or crepuscular patterns during summer, with intermittent patterns during autumn and spring [9]. Significant inter- and intra-seasonal variations were noted in the temporal budgeting of 24 hr activity patterns in relation to changing weather patterns, photoperiod lengths, and possibly food and water availability. It appears that the temporal niche switching exhibited by the Arabian oryx is dictated by the availability of food and water, which in turn is primarily driven by seasonal shifts in ambient temperatures and rainfall [5, 9].

Comparative polysomnographic studies are mostly limited to captive or zoological species, apart from recent studies on wild sloths [10, 11], pectoral sandpipers [12], barn owls [13], ostriches (semiwild conditions) [14], and great frigatebirds [15]. Critical differences between captive and free-roaming animals include the following: (1) animals in captivity are often provided food and water ad libitum, thereby reducing or removing the need for foraging and (2) captive animals do not need to remain vigilant towards predators [16]. Thus, captive animals will have more time available for sleep and appear to sleep longer than their wild conspecifics [10, 16]. Polysomnographic studies on captive animals thus raise concerns that sleep durations and patterns reported do not truly reflect those found in wild, free-roaming animals [10, 17–19].

Descriptions of the activity-based phenomenon of temporal niche switching are rare (see reviews in Refs. 20 and 21), especially under natural conditions [5, 22–24]. No prior mammalian studies have examined temporal niche switching in terms of the physiological parameters of sleep; thus, the polysomnographic study of sleep in species that exhibit temporal niche switching (see Refs. 12 and 15 for examples in avians) may provide insights into how sleep patterns are influenced by hyperarid conditions (especially shifts in temperature) and determine the potential plasticity of sleep patterns. Thus, the aim of the current study was to provide a polysomnographic-based sleep study of the Arabian oryx to determine whether exposure to the hyperarid desert climate has led to any novelties regarding sleep architecture, patterns, or physiology in this species.

Materials and Methods

Animals used and experimental groups

In the current study, a total of six adult Arabian oryx (four males, two females—not pregnant, not lactating; mean body mass 62.7 ± 5.6 kg) were used. The animals were divided into two groups. Group 1 comprised three adult Arabian oryx (two males, one female; mean body mass 61.7 ± 8.5 kg) in which polysomnography (PSG) (electroencephalogram [EEG] and electromyogram [EMG]), subcutaneous temperature (Tsc), and fine-grain actigraphy (ACT) were recorded in the Mahazat as-Sayd Protected Area, northeast of Taif, Kingdom of Saudi Arabia (22°12′12″N, 41°49′36″E; 2200 km^2 area) during January 2016 (winter season). Group 2 consisted of three adult Arabian oryx (two males, one female; mean body mass 63.7 ± 1.5 kg) in which identical parameters, as those for group 1, were recorded during June 2016 (summer season). Due to PSG equipment malfunctioning, data could not be retrieved from all devices and as such the PSG data analysis was reduced to $n = 1$ (case #1: male, group 1) and $n = 2$ (cases #2 and #3: male, group 2). However, ACT and Tsc data were obtained from all six animals for the entire recording period and are presented (see limitations of the current study section). Ethical clearance for the current study was obtained from the University of the Witwatersrand Animal Ethics Screening Committee (clearance certificate number 2014/53/D), and all animals were treated according to the guidelines of this committee, which parallel those of the National Institutes of Health (NIH) for the care and use of animals in scientific experimentation.

Anesthesia protocol

The current study follows similar protocols for anesthesia and surgeries in the Arabian oryx as described previously [5, 6]. All animals were remotely injected using a Dan-Inject dart gun (Daninject, Børkop, Denmark) with etorphine hydrochloride (Captivon 98, Wildlife Pharmaceuticals Ltd., White River, South Africa; 19 μg/kg), ketamine (Ketaminol Vet., MDS Animal Health, Intervet International B. V., Boxmeer, The Netherlands; 0.3 mg/kg), midazolam (Midazolam, Wildlife Pharmaceuticals Ltd., White River, South Africa; 0.13 mg/kg), and medetomidine (Zalopine 10 mg/mL, Orion Pharma, Espoo, Finland; 5 μg/kg). All animals received oxytetracycline (Terramycin LA, Pfizer, Brazil; 20 mg/kg) and ketoprofen (Ketovet, Vetmedim Animal Health, Cantho City, Vietnam; 2 mg/kg). After the procedure, anaesthesia was reversed using naltrexone hydrochloride (Naltrexone, APL, Kungens Kurva, Sweden; 40 mg) and atipamezole hydrochloride (Antisedan, Orion Pharma; 2 mg). After the recording period, the animals were again immobilized using a similar drug combination, and the implants were removed. Again, oxytetracycline and ketoprofen were administered and the animals were allowed to recover in a shaded pen prior to release to their normal environment.

Neurologger and iButton implantation

Following recumbency after darting, the animals were moved to a shaded area for surgery. The implantation sites for the Neurologger (the left side of the neck and the scalp behind the horns) were shaved and washed with chlorhexidine disinfectant (CHX, 0.5% chlorhexidine digluconate in 75% alcohol, Kyron Laboratories Pty Ltd.). Sterile drapes were taped in place over the respective surgical sites to isolate the disinfected area. Under aseptic conditions, an incision (approximately 10 cm in length) was made at the left lateral aspect of the neck, and a subcutaneous pocket extending approximately 15 cm ventrally from the incision site was created for the implantation of the Neurologger unit (model: Neurologger 1, Evolocus LLC). The Neurologgers were fitted with two Lithium ion batteries (Lithium Primary Battery, SW-AA11, 3.6 V, Tekcell, Vitzrocell Co. Ltd.) and memory included an onboard 8GB micro SD card. The Neurologger had a mass of 78 g and approximate dimensions of $66 \times 36 \times 10$ mm (mass and dimensions include wax covering and batteries). A midsagittal incision was made over the skull and the skin reflected to expose the part of the skull overlying the cerebral cortex. A subcutaneous tunnel was made to join the pocket on the left side of the neck to the incision site on the skull in order to run the electrode wires from the Neurologger to the skull. Using a cordless Dremel drill, five 2-mm-diameter holes were made in the dorsal aspect of the cranium for electrode placement. The first hole was drilled posterior to the lambdoid suture, for the placement of the indifferent electrode, whereas two holes were drilled approximately 2 cm apart and 2 cm lateral to the sagittal suture over both the left and right cortices for the placement of the EEG electrodes (LiFY Colorflex Li-HF 0.06 mm^2; Conductor configuration: Cu $30 \times \varnothing0.05$mm; Insulation: PVC; electrode impedance approximately 1.1 Ω) The electrodes were placed in such a manner that the tips rested firmly on the surface of the dura mater and were secured in place with dental cement. The electrodes were presumably placed over the visual cortex based on the location of visual cortex in other artiodactyl species. For the EMG recordings, two electrodes (±2 cm apart) were sutured into the dorsal nuchal musculature. All skin incisions were sutured following implantation. Bioelectric signals from the cerebral cortex and nuchal musculature were recorded at 500 Hz (six channels including one EMG, two EEG, and three for accelerometer x, y, and z planes). The recording periods were approximately 10 days. All skin incisions were sutured following implantation.

One iButton data logger (DS1922L, Maxim Semiconductors, Dallas, USA) that measured Tsc (data acquisition rate set at 5-min intervals) was inserted within the same subcutaneous pocket used for the Neurologger (left lateral aspect of the neck) prior to the suturing of the sites. For recording Tsc, the device was calibrated against an accurate thermometer in an insulated water bath, providing an accuracy of ≤0.06°C.

The Neurologger and iButton units were coated in a biologically inert wax (SasolWax 1276, Sasol, Johannesburg, South Africa) and sterilized within a container with formalin pellets for 48 hr prior to implantation.

Actiwatch implantation

Following similar sterilization methods and aseptic techniques as described above, a subcutaneous pocket was created on the right lateral aspect of both the neck and hindleg for the implantation of the Actiwatches. The Actiwatch Spectrum (Philips Respironics) was used in the current study and had a mass of 25 g and approximate dimensions of $35 \times 35 \times 12$ mm (mass and dimensions include wax covering). Each Actiwatch, factory calibrated, was programmed (data acquisition rate set at 1 min intervals) with the Philips Respironics Actiware 5 software prior to implantation. The wristbands from the Actiwatches were removed, and the watches were insulated with standard electrical insulation tape and covered with two coats of biologically inert wax (SasolWax 1276, Sasol, Johannesburg, South Africa). An incision (<5 cm in length) was made at each of the respective implantation sites, and a subcutaneous pocket extending approximately 10 cm ventrally from the incision site was created. The Actiwatch, sterilized within a container with formalin pellets for 48 hr prior to implantation, was inserted into the respective pockets, and the incisions sutured and liberally sprayed with Necrospray (Bayer Animal Health). Following reversal of the anesthesia, the animals were monitored in holding pens for 2 days with access to food and water, before being released into a 1×2 km enclosure within the Mahazat as-Sayd Protected area for the 10 day recording period

(no further food or water provided; animals grouped together within enclosure). After the recording period, the implanted animals were reanesthetized, and all of the implanted devices were retrieved.

Recording of weather conditions

A permanent weather station within the Mahazat as-Sayd Protected Area (22.2° N, 41.9° E, altitude 1000 m) recorded weather parameters during the recording period (Table 1). This weather station provided a reading of ground temperature (Tg), air temperature (Ta), air pressure, relative humidity, wind speed, wind direction, rainfall, and solar radiation every 15 min throughout the recording period. Sunrise and sunset times were obtained from a freely accessible database (https://www.timeanddate.com/sun/saudi-arabia/riyadh) providing archival data for daily sunrise/sunset, day length, astronomical twilight, nautical twilight, and civil twilight times.

Table 1.

Weather parameters measured during the recording periods in January and June 2016 in the Mahazat as-Sayd Protected Area, Saudi Arabia
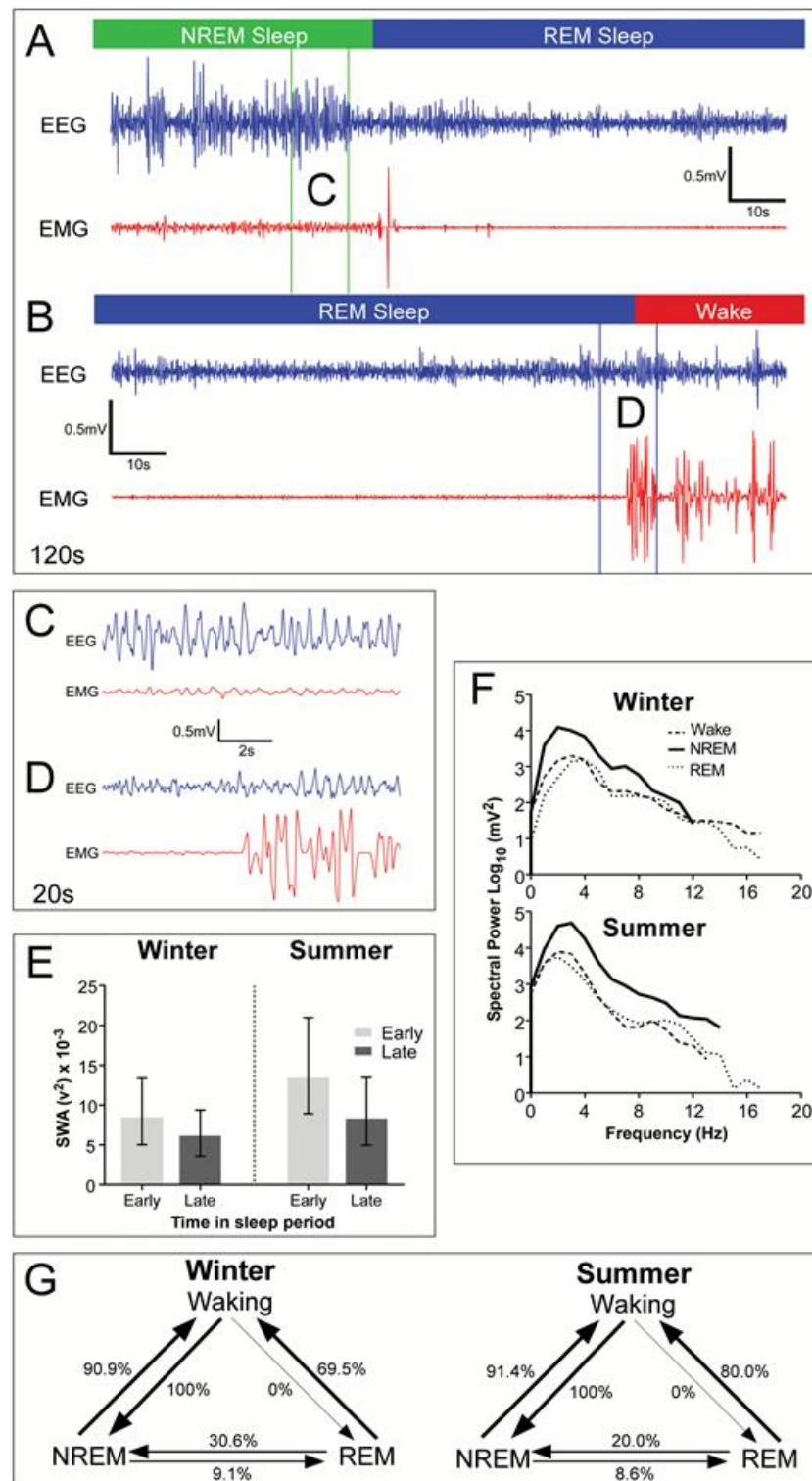
Mahazat as-Sayd Protected Area	Winter	Summer
	January (25th–31st) 2016	June (16th–22nd) 2016
24h air temperature (°C)		
Highest recorded	22.6	41.5
Maximum	18.6 ± 2.5	40.9 ± 0.6
Mean	12.5 ± 4.7	34.1 ± 5.1
Minimum	6.5 ± 4.0	25.3 ± 1.8
Lowest recorded	2.5	23.3
Light period mean	14.3 ± 4.7	35.9 ± 5.2
Dark period mean	11.0 ± 4.2	31.5 ± 3.5
24h ground temperature (°C)		
Highest recorded	27.6	50.9
Maximum	24.0 ± 2.8	49.6 ± 1.0
Mean	16.7 ± 5.0	38.4 ± 6.8
Minimum	11.1 ± 3.3	29.6 ± 1.3
Lowest recorded	8.4	28.5
Light period mean	18.9 ± 5.4	41.0 ± 7.4
Dark period mean	14.8 ± 3.7	34.9 ± 3.3
Rainfall (mm)	4.1	0.0
Time of sunrise	06h40	05h00
Time sunset	17h40	18h45

Light and dark period mean temperatures are according to sunrise and sunset times. All values are mean ± *SD*.

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Data analysis

The recorded data on the Neurologger micro SD were converted to float32 format and imported into Version 7.02a of the Spike 2 software (Cambridge Electronic Designs, UK) for visual scoring and analysis. Due to PSG device malfunctioning, only 48 hr of data was considered for each animal per season (ACT data were unaffected, see limitations of the current study section). The first 48 hr post-surgery was treated as habituation and data subsequently excluded. Prior to scoring, DC remove and smooth channel processes were applied to all channels. The PSG data were scored in 1 min epochs as follows: (1) wake, characterized by low-voltage, high-frequency EEG, and high-voltage EMG; (2) nonrapid eye movement (NREM), characterized by high-voltage, low-frequency EEG and EMG lower in voltage amplitude than waking; or (3) REM, characterized by low-voltage, high-frequency EEG and an almost atonic EMG (Figure 1A, B, C, and D). A state was only assigned to an epoch if the particular state occupied at least 50 per cent of the epoch. Adapted from the analysis undertaken by Voirin et al. [11] and for ease of comparison, the following variables were calculated and averaged across the recording period for each individual oryx: the percent time spent in each state (wake, NREM sleep, and REM sleep) per 24 hr, the percent of total sleep time (TST) in REM sleep, and the percent time spent in each state during the light period (sunrise to sunset) and during the dark period (sunset to sunrise). Additionally, the mean duration of episodes and the number of episodes per state for the 24 hr, light, and dark periods were calculated. Since the sample size of Arabian oryx for winter ($n = 1$) and summer ($n = 2$) was considered too small for statistical comparisons, only mean values for PSG data are reported. An episode was defined as a sequence of consecutive epochs of one state. From the 1 min scored data, the modal state for 5 min was calculated and used to determine the onset and duration of the major sleep bouts seasonally for all animals. Sleep bout duration frequencies for the 24 h, light, and dark periods were determined for winter and summer (Supplementary Figure S1). A sleep bout was defined as a period lasting at least 10 min (two consecutive 5 min sleep bouts without waking) and included both NREM and REM epochs. The number of REM sleep episodes and their occurrence relative to Tsc minimum (nadir) was determined for winter and summer.

Figure 1.

Polysomnographic recordings from Arabian oryx (*Oryx leucoryx*). (A) EEG recording (120 s) showing a period of NREM transitioning into REM sleep. NREM sleep was characterized by a low frequency, high amplitude EEG signal accompanied by a high frequency, low amplitude EMG signal. REM sleep was characterized by a high frequency, low amplitude EEG signal, resembling that of waking, accompanied by a near atonic EMG signal with irregular spikes. (B) Recording (120 s) showing a transition from REM sleep to wake characterized by an abrupt increase in EMG signal frequency and amplitude with no visible change in EEG signal to that of prior REM sleep. (C) Expanded views of 20 s recording from segment (A) showing NREM sleep, and (D) segment (B) showing the transition from REM sleep to wakefulness, at higher temporal resolutions. (E) NREM sleep EEG δ power (SWA; 0.5–4 Hz power) during the longest consolidated sleep bouts early and late in the sleep period for winter and summer oryx (median and quartiles for the median). (F) The spectral power and associated frequency band characteristics of waking, NREM, and REM sleep in the Arabian oryx during both the winter and summer periods. (G) State transition probabilities in the Arabian oryx during 24 hr based on the data from all animals studied for both the winter and summer periods. The format of this figure (A and B) is modeled on Figure 3 of Voirin et al. [11] for ease of comparison between studies.

The average NREM sleep EEG δ power (slow-wave activity [SWA], 0.5–4 Hz power density) was calculated from NREM sleep bouts early and late in the longest consolidated sleep periods for both seasons. Four second artifact-free epochs (REM epochs also excluded) were utilized and SWA was estimated using the Spike 2 software (total power of frequency in band, FFT number 512) (Figure 1E). The power spectrum for each of the defined states was calculated with the Spike 2 computer program (Figure 1F) (Hanning window, FFT number 512, sampling frequency 500 Hz, segment length 1.024 s; see Ref. 25). State transition probabilities per 24 hr were determined based on all animals studied for winter and summer (Figure 1G). All statistical analyses, wherever possible, were conducted using IBM SPSS Statistics software version 23, PAST 3 [26] and GraphPad Prism 6.

Maxim Integrated's 1-wire software tools were used to retrieve the temperature data recorded from the iButtons and then exported to Microsoft Excel for analysis. The animals from each group were analyzed individually and the data were then pooled by season. Tsc from each 5 min epoch was averaged across the recording period, and the data were then pooled to create an overall average Tsc per 24 hr per season. The subcutaneous and ambient temperature differentials (ΔTsc = Tsc at end of bout – Tsc at start of bout, ΔTa = Ta at end of bout – Ta at start of bout) between sleep bout onset and offset per season were determined for all sleep bouts lasting more than 20 min. Similarly, the temperature differentials were determined for wake bouts of 60 min following the major sleep bouts. The rate of change in Tsc and Ta per minute during major sleep and wake bouts was then determined for both seasons [Tsc rate of change = ΔTsc (°C)/bout length (minutes), Ta rate of change = ΔTa (°C)/bout length (minutes)].

Phillips Respironics Actiware 5 was used to retrieve the recorded data from each of the implanted actiwatches. The raw data were exported to Microsoft Excel where it was manually scored and analyzed. Data obtained from the neck and leg actigraphs were scored concurrently in 1 min epochs as either active or inactive. For an epoch to be scored as active, either the neck or leg actigraphs had to have an activity score greater than zero. Inactive epochs were scored when both the neck and the leg actigraphs had an activity score equal to zero. The percent time spent in each state (active and inactive) for the 24 hr, light (sunrise to sunset), and dark periods (sunset to sunrise) was calculated for all animals per season (winter: $n = 3$; summer: $n = 3$) over the same recording days used for PSG. Total time spent active/inactive was determined for the 24 hr, light, and dark periods per season for all animals. From the 1 min scored data, the modal state for 5 min was calculated and used to determine the onset and duration of the major inactive bouts seasonally for all animals.

Results

Actigraphy patterns seasonally

Significant differences were observed for time inactive per 24 hr, with winter oryx inactive 12.98 ± 1.66 hr (mean ± SEM) and summer oryx inactive 6.84 ± 1.42 hr (unpaired, two tailed t-test, $p < 0.001$). Time spent inactive during the light period was similar between winter and summer, with winter oryx inactive 4.33 ± 2.41 hr and summer oryx inactive 5.61 ± 1.74 hr (unpaired, two tailed t-test, $p > 0.05$). Time spent inactive during the dark period was significantly different between winter and summer with winter oryx inactive 8.65 ± 1.93 hr and summer oryx inactive 1.22 ± 1.74 hr (unpaired, two tailed t-test, $p < 0.001$) (see Table 2 for number and duration of ACT state episodes for winter and summer oryx over 24 hr and during the light and dark periods).

Table 2.

Mean number and duration of episodes of each defined state for the 24 hr, light, and dark periods using PSG and ACT

		Winter			Summer		
		24 hr	Light	Dark	24 hr	Light	Dark
Mean number of episodes							
PSG	Wake	113.5 ± 20.5	49.0 ± 15.0	65.5 ± 5.5	65.3 ± 9.8	53.8 ± 9.7	12.0 ± 4.5
	NREM	117.5 ± 19.5	49.0 ± 15.0	68.0 ± 4.0	66.0 ± 10.3	55.0 ± 10.4	11.0 ± 4.5
	REM	10.5 ± 1.5	3.5 ± 3.5	7.0 ± 2.0	4.3 ± 1.5	4.3 ± 1.5	0.0 ± 0.0
ACT	Active	19.2 ± 2.3	9.8 ± 2.2	9.3 ± 1.3	24.0 ± 1.7	19.3 ± 2.0	4.7 ± 1.3
	Inactive	20.0 ± 2.2	9.3 ± 2.3	10.7 ± 1.2	23.2 ± 1.8	19.2 ± 2.0	4.0 ± 1.5
Mean duration of episodes (min)							
PSG	Wake	9.6 ± 2.3	12.3 ± 5.0	7.8 ± 0.7	20.2 ± 3.6	13.9 ± 3.5	180.0 ± 140.2
	NREM	3.3 ± 0.1	2.5 ± 0.4	3.8 ± 0.2	3.4 ± 0.5	3.3 ± 0.6	3.1 ± 1.7
	REM	1.6 ± 0.2	0.7 ± 0.7	1.8 ± 0.4	0.8 ± 0.3	0.8 ± 0.3	0.0 ± 0.0
ACT	Active	35.2 ± 7.0	58.4 ± 20.3	24.5 ± 3.2	42.5 ± 2.5	25.2 ± 2.3	259.3 ± 112.8
	Inactive	44.0 ± 5.0	32.3 ± 4.2	55.3 ± 8.0	20.2 ± 3.7	20.2 ± 3.7	19.2 ± 9.5

Mean values are based on 1 min scoring for all animals per season. Subsequently light and dark mean values are according to sunrise and sunset times (winter: light–11 hr and dark–13 hr; summer: light–14 hr and dark–10 hr). All values are percentage mean ± SEM.
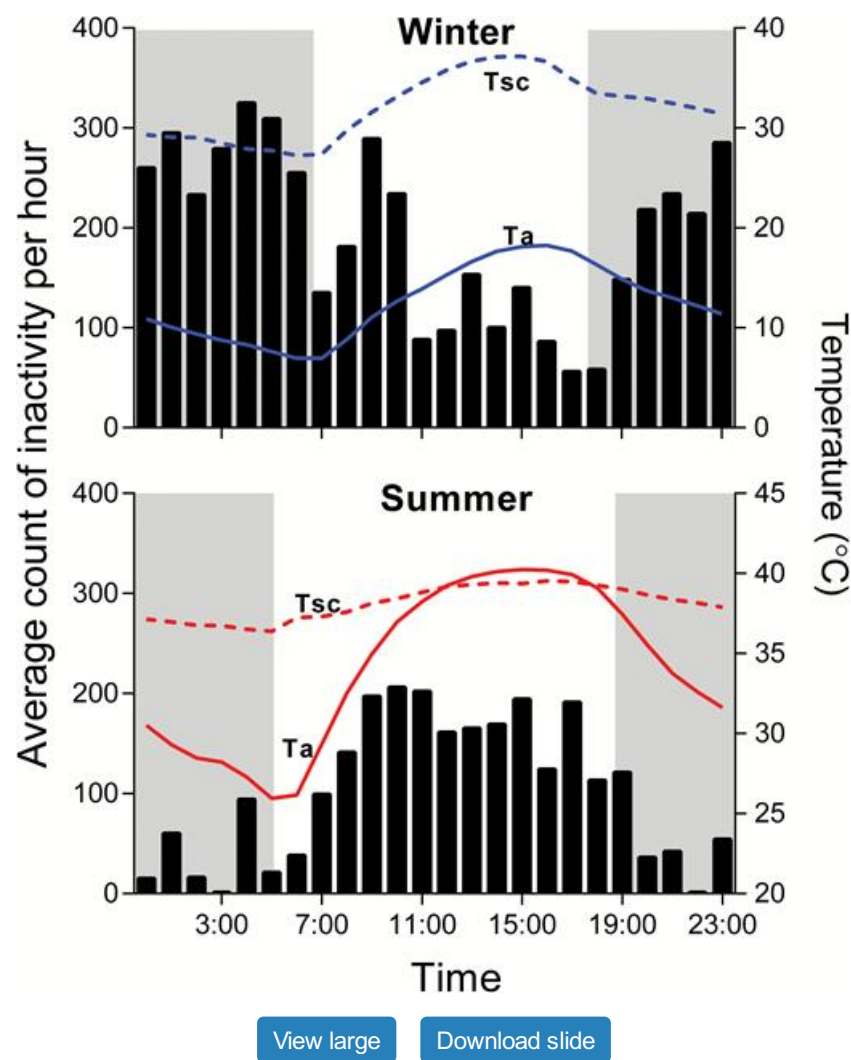
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When using 5 min modal times for all animals, the average daily onset of the main inactive bout (longest consecutive period of inactivity) occurred around 0300 hr during winter, whereas during summer the onsets occurred around 0940 hr or around 1225 hr. The average length of the main inactive bout was 127 ± 19 min during winter, whereas in summer it lasted 115 ± 50 min. Additionally in summer, oryx exhibited a third main inactive bout with an onset around 1500 hr and a length of 90 ± 37 min. Thus, during the winter recording period, 68.21% (±13.46%) of inactivity occurred during the dark period compared with 16.77% (±13.20%) during summer (unpaired, two tailed t-test, $p < 0.001$). During the light period, winter oryx were inactive 31.80% (±13.46%) compared with 83.23% (± 13.20%) during summer (unpaired, two tailed t-test, $p < 0.001$). Overall, the current findings of inactivity timing resemble previous reports [5], with winter oryx exhibiting a primarily nocturnal inactivity pattern (major inactive bout occurring during the cooler part of the night) and summer oryx exhibiting a primarily diurnal inactivity pattern (major inactive bouts occurring during the hottest parts of summer days) (Figure 2).

Temperature rhythms between seasons

Tsc rhythms between seasons exhibited similar daily timing patterns with an early morning trough at sunrise and a peak at 1500 hr followed by a dip at sunset across all animals. Winter mean Tsc was 32.92 ± 0.05°C and was significantly lower than the summer mean Tsc of 38.29 ± 0.02°C (unpaired, two tailed t-test, $p < 0.001$; Figure 2). The range of Tsc varied highly between seasons. Winter oryx exhibited an average daily variation of 8.93°C in Tsc, whereas summer oryx exhibited an average daily variation of 3.23°C in Tsc. Overall, Tsc rhythms exhibited no seasonal change in the timing, only amplitude, and thus resemble previous reports [3–5].

Figure 2.

Graphs illustrating the average count of inactivity per hour scored over 6 days using actigraphy in the winter month (upper graph, January 2016, Saudi Arabia, pooled from the three animals recorded) and the summer month (lower graph, June 2016, Saudi Arabia, pooled from the three animals recorded). The average ambient (Ta, solid lines) and subcutaneous (Tsc, dashed lines) temperatures, recorded every 15 (Ta) and 5 (Tsc) min, across the recording period are overlain on the activity graphs (blue for winter, red for summer). The gray regions represent the dark periods between sunset and sunrise.

Polysomnographic recordings of animal case #1: Winter

Twenty-four hour TST observed was 6.69 ± 1.21 hr (mean $\pm$ SEM) with 17.31 ± 1.93 hr spent in waking, 6.42 ± 1.84 hr in NREM sleep, and 0.28 ± 0.21 hr in REM sleep (Figure 3 and Table 3). TST observed during the light period was 2.18 ± 1.44 hr with 8.82 ± 2.42 hr spent in waking, 2.10 ± 2.31 hr in NREM sleep, and 0.08 ± 0.18 hr in REM sleep. TST observed during the dark period was 4.51 ± 1.84 hr with 8.49 ± 3.09 hr spent in waking, 4.32 ± 3.00 hr in NREM sleep, and 0.19 ± 0.32 hr in REM (for number and duration of state episodes over 24 hr, light, and dark periods, see Figure 3 and Table 2). REM sleep when expressed as a percentage of TST was $4.18 \pm 0.51\%$ over 24 hr, $3.67 \pm 3.68\%$ during the light period, and $4.21 \pm 0.25\%$ during the dark period (Figure 4) (see Figure 5 for total state times, episode numbers, and episode durations intraseasonally for winter during the light and dark periods). When using 5 min modal times, the average daily onset of the main sleep bout (longest consecutive period of NREM and REM sleep combined) occurred between 0330 and 0400 hr and lasted 110 ± 14 min. This oryx appeared to exhibit predominantly nocturnal sleep phasing, resembling previous inactivity timing reports [5], with the majority of NREM and REM sleep occurring during the dark period (coolest parts of the winter nights; dark period: $67.41 \pm 14.87\%$, light period: $32.58 \pm 14.87\%$, of 24 hr TST) (Figures 6 and 7).
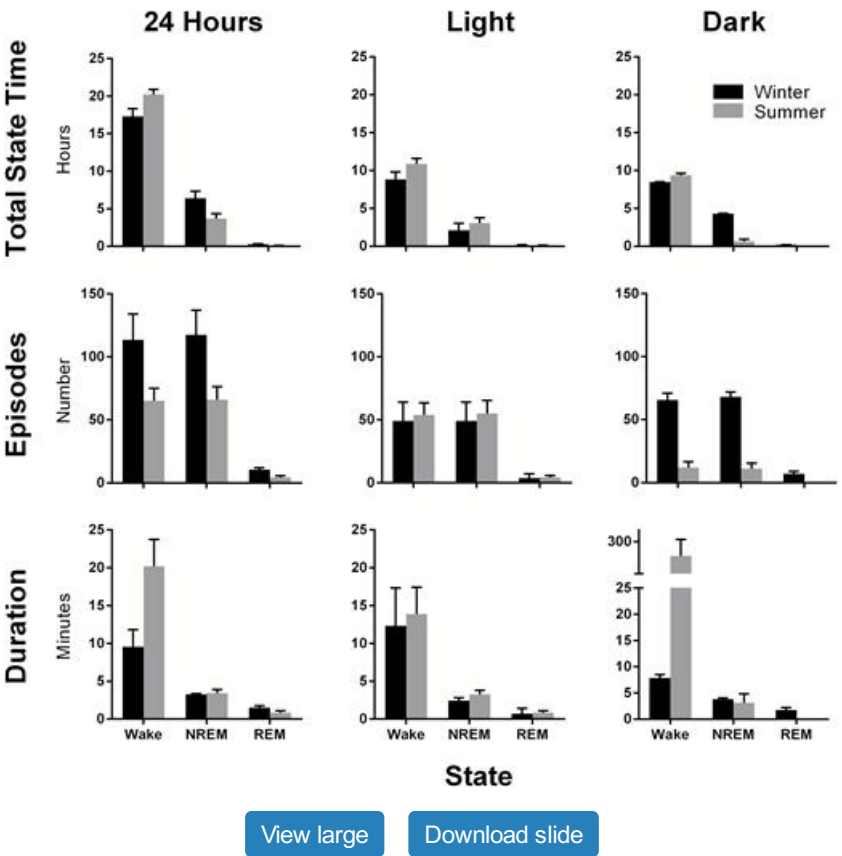
Table 3.

Total state times for the 24 hr, light, and dark periods

| 24 hr average | | | | | | | | Light | | | | Dark | | |
Season	Animal ID	Body mass (kg)	Sex	Total wake time†	Total sleep time†	Total Non-REM†	Total REM†	Total wake time†	Total sleep time†	Total Non-REM†	Total REM†	Total wake time†	Total sleep time†	
Winter	C	53.0	Male	72.1 ± 1.9	27.9	26.8 ± 1.8	1.2 ± 0.2	80.2 ± 2.5	19.8	19.1 ± 2.4	0.7 ± 0.2	65.3 ± 2.7	34.7	
Summer	A	65.0	Male	81.5 ± 2.4	18.5	18.2 ± 2.3	0.4 ± 0.1	71.9 ± 3.4	28.1	27.4 ± 3.3	0.6 ± 0.1	94.8 ± 2.1	5.2	
	C	62.0	Male	87.1 ± 1.7	12.9	12.6 ± 1.6	0.3 ± 0.1	83.4 ± 2.6	16.6	16.2 ± 2.5	0.5 ± 0.2	92.4 ± 1.6	7.6	
Summer Mean	-	63.5	-	84.3 ± 1.5	15.7	15.4 ± 1.4	0.3 ± 0.1	77.6 ± 2.2	22.4	21.8 ± 2.1	0.6 ± 0.1	93.6 ± 1.3	6.4	

†Values are based on 1 min scoring and are percentages of 24 hr for each animal as well as the species mean. Subsequently light and dark values are percentages of light and dark hours according to sunrise and sunset times (winter: light–11 hr and dark–13 hr; summer: light–14 hr and dark–10 hr). All values are percentage mean ± SEM.

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Figure 3.

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The average number of hours, average number of episodes, and average episode duration per state for the 24 hr (first column), light (second column), and dark (third column) periods for winter (black bars) and summer (grey bars). The results represented are the grouped averages for all animals studied. Error bars show standard error of the mean. The format of this figure is modeled on Figure 4A of Voirin et al. [11] for ease of comparison between studies.
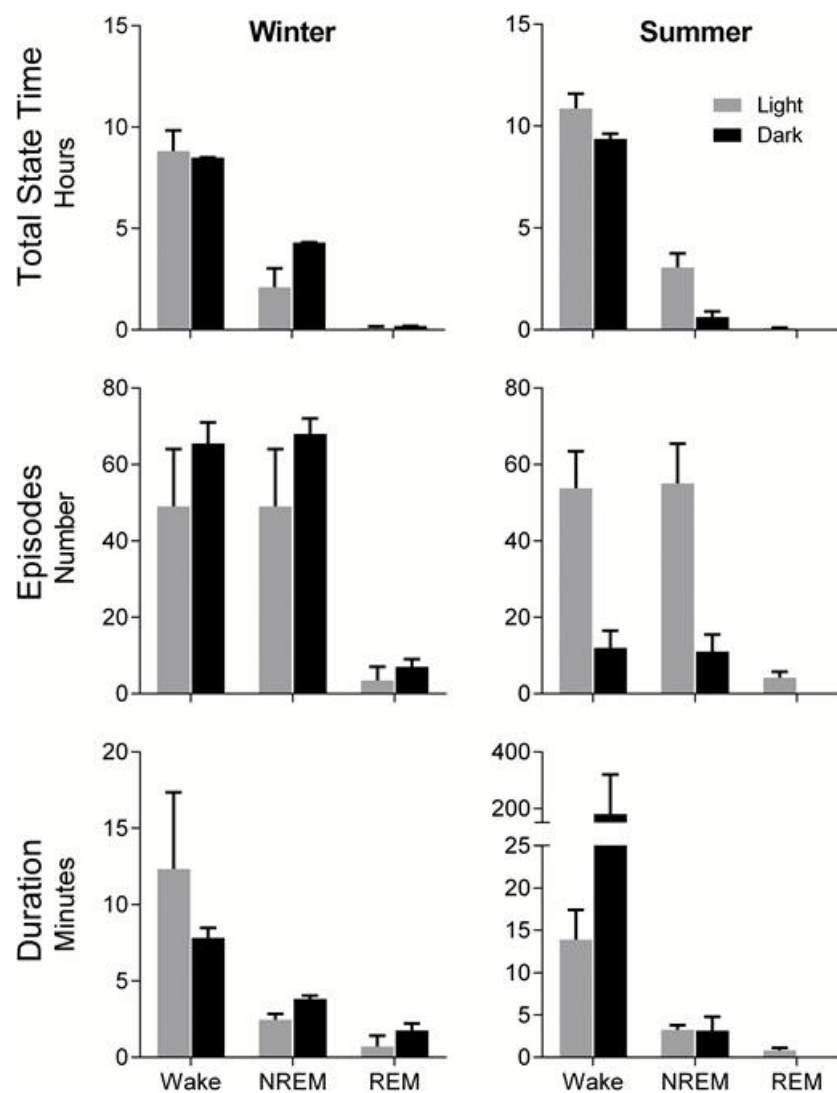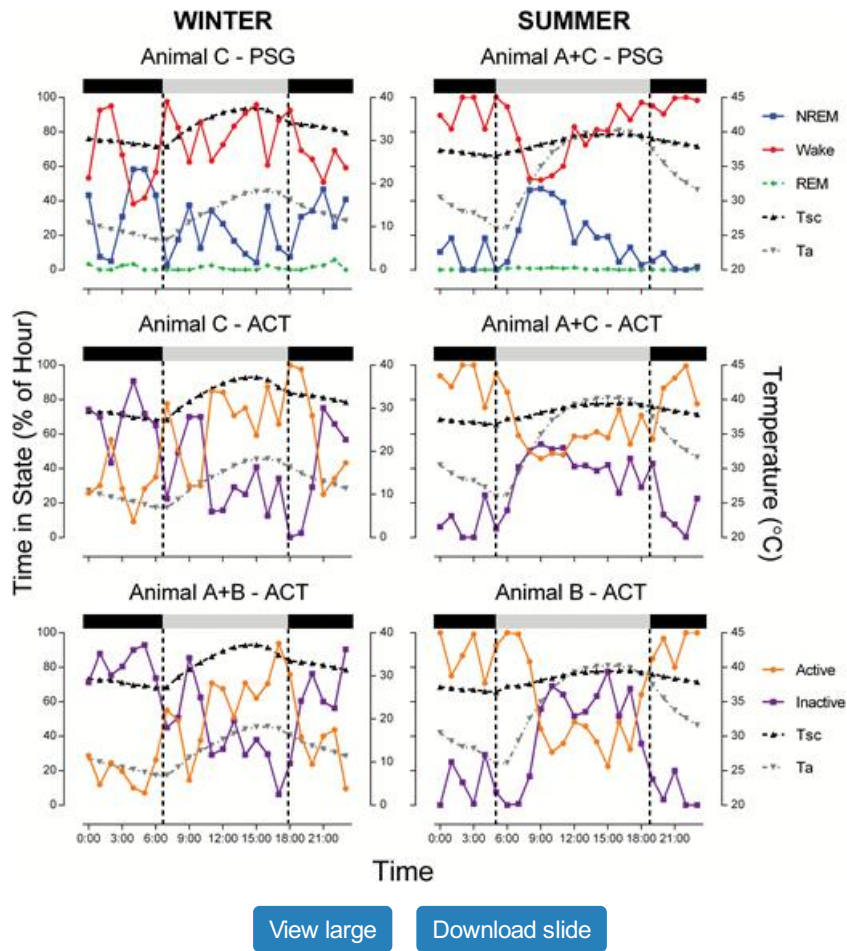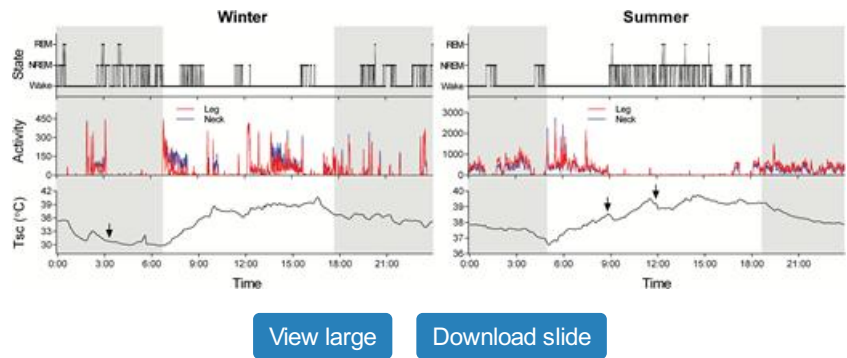
Figure 4.

REM sleep as a percentage of total sleep time for the 24 hr, light, and dark periods for winter (black bars) and summer (grey bars). The results represented are the grouped averages for all animals studied. Error bars show standard error of the mean. The format of this figure is modeled on Figure 4B of Voirin et al. [11] for ease of comparison between studies.

Figure 5.

The average number of hours, average number of episodes, and average episode duration in each state intraseasonally for winter (left column) and summer (right column) for the light (grey bars) and dark periods (black bars). The results represented are the grouped averages for all animals studied. Error bars show standard error of the mean. The format of this figure is modeled on Figure 6 of Voirin et al. [11] for ease of comparison between studies.

Figure 6.

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Time spent per hour (%) in wake (red line, circle markers), NREM sleep (blue line, square markers), and REM sleep (green dashed line, diamond markers), recorded with PSG (upper graphs), for winter (left) and summer (right) Arabian oryx. The corresponding time spent per hour (%) active (orange line, circle markers) and inactive (purple line, square markers), recorded with ACT, for the same oryx as recorded for PSG (middle graphs), and the oryx only recorded using ACT (lower graphs) during winter (left column) and summer (right column). Horizontal bars above graphs represent light (grey, sunrise to sunset) and dark (black, sunset to sunrise) periods. Dashed vertical lines represent sunrise and sunset per recording period. Data reflect all 2 days for each Arabian oryx. Subcutaneous temperature (Tsc—black dashed line, triangle markers) and ambient temperature (Ta—grey dashed lines, inverted triangles) is plotted on the secondary y-axis and reflects averages for all Arabian oryx for all days per recording period. The format of this figure is modeled on Figure 5 of Voirin et al. [11] for ease of comparison between studies.

Figure 7.

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Individual hypnograms (upper graphs) illustrating wake, NREM, and REM sleep states across 24 hr and corresponding raw activity (middle graphs; leg activity—red line, neck activity—blue line) and Tsc (lower graphs) traces for winter (left column, case #1 oryx) and summer (right column, case #2 oryx) periods. The gray regions represent the dark periods between sunset and sunrise. The black

arrows in the lower graphs indicate the time of the major sleep bouts per season as described.

Polysomnographic recordings of animal cases #2 and #3: Summer

Twenty-four hour TST observed was 3.77 ± 0.78 hr (mean ± SEM) with 20.23 ± 1.45 hr spent in waking, 3.69 ± 1.41 hr in NREM sleep, and 0.08 ± 0.07 hr in REM sleep (values are averages of both oryx; Figure 3 and Table 3). TST observed during the light period was 3.13 ± 1.21 hr with 10.87 ± 2.16 hr spent in waking, 3.05 ± 2.10 hr in NREM sleep, and 0.08 ± 0.11 hr in REM sleep. TST observed during the dark period was 0.64 ± 0.70 hr, with 9.36 ± 1.32 hr spent in waking and 0.64 ± 1.32 hr in NREM sleep. No REM sleep was observed during the dark period for either oryx (for number and duration of state episodes over 24 hr, light, and dark periods, see Figure 3 and Table 2). REM sleep when expressed as a percentage of TST was 2.12 ± 0.70% over 24 hr and 2.56 ± 1.53% during the light period (Figure 4) (see Figure 5 for total state times, episode numbers, and episode durations intraseasonally for summer during the light and dark periods). When using 5 min modal times, the average daily onset of the main sleep bout occurred either around 0800 or 1230 hr and lasted 135 ± 21 min. Summer oryx appear to exhibit predominantly diurnal sleep phasing, resembling previous inactivity reports [5], with the majority of NREM and all of REM sleep occurring during the light period (sunrise until early afternoon; dark period: 16.98 ± 22.53%, light period: 83.02 ± 22.53%, of 24 hr TST) (Figures 6 and 7).
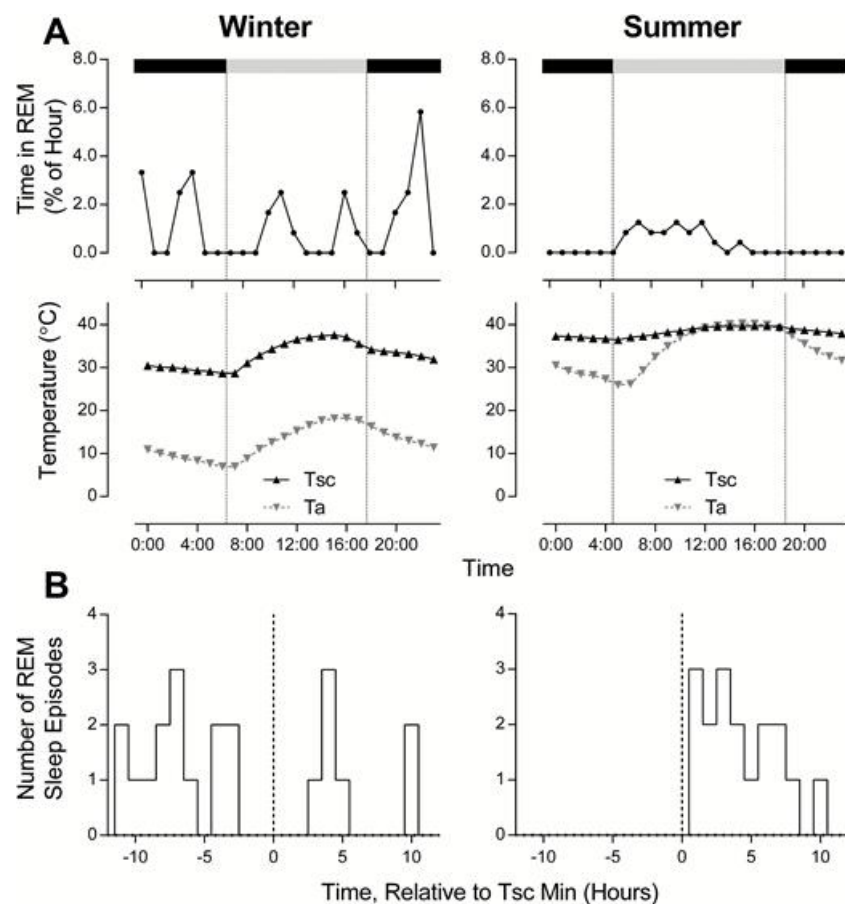
Variations between winter and summer sleep

The number of sleep bouts and the duration of these bouts were similar between winter and summer for the 24 hr, light, and dark periods and overall appears polyphasic (Supplementary Figure S1). Sleep bouts with longer durations were more frequent during summer, particularly during light hours, whereas shorter sleep bouts were more frequent during winter especially during dark hours. NREM sleep-related SWA examined early (between 1900 and 2100 hr in winter; between 0600 and 0900 hr in summer) and late (between 0300 and 0500 hr in winter; between 1000 and 1400 hr in summer) into the longest consolidated sleep periods for both seasons exhibited differences. During winter and summer, SWA was higher early compared with late into the longest sleep periods [winter median SWA ($v^2 \times 10^{-3}$): early—8.50, late—6.16; summer median SWA: early—13.45, late—8.33; Figure 1E]. SWA during summer exhibited higher median power compared with winter during both early and late into the longest sleep periods (Figure 1E). Between winter and summer, oryx exhibited variation in vigilance state transition probabilities, namely, NREM–REM and REM–wake transitions. The probability of REM–NREM transitions was 30.6 per cent of the time during winter and 20 per cent during summer. The probability of REM–wake transitions was 69.5 per cent of the time during winter and 80 per cent during summer (Figure 1G).

When comparing PSG and ACT data over the same recording days for time spent in state (% of the hour), both methods show similarity during winter and summer periods (Pearson correlation, $p < 0.001$; Supplementary Figure S2). PSG and ACT data show similar patterns per season and between individual oryx (Figures 6 and 7). Overall, similar patterns of nocturnal inactivity or sleep during winter and diurnal inactivity or sleep during summer can be observed for all animals (including oryx for which PSG data could not be retrieved) and thus resemble a previous report [5].

Relationship between sleep and temperature

During winter, 67 per cent (14/21 episodes) of the time spent in REM sleep occurred during the night (2000–0100 hr) and prior (0200–0500 hr) to Tsc min (28.7 ± 0.2°C at 0600 hr) (Figure 8A and B). During summer, 88 per cent (15/17 episodes) of REM sleep occurred after Tsc min (36.5 ± 0.1°C at 0500 hr) and ended around noon (0500–1230 hr) when Ta reached peak values (40.2 ± 0.1°C). During winter, Tsc at the onset and offset of the main sleep bout was 33.2°C and 32.0°C (0330 hr), respectively (Ta start: 5.4°C, Ta end: 3.9°C). During summer, the Tsc at the onset and offset of the main sleep bout was 36.5°C and 37.2°C (0800 hr) and 38.5°C and 39.1°C (1230 hr), respectively (0800 hr: Ta start: 31.9°C, Ta end: 35.7°C; 1230 hr: Ta start: 39.6°C, Ta end: 40.5°C).

Figure 8.

(A) Time spent per hour (%) in REM sleep (upper graphs) and the corresponding ambient (Ta—grey dashed lines, inverted triangles) and subcutaneous (Tsc—black dashed line, triangle markers) temperature rhythms (lower graphs) for winter (left column) and summer (right column) Arabian oryx. Horizontal bars above graphs represent light (grey, sunrise to sunset) and dark (black, sunset to sunrise) periods. Dashed vertical lines represent sunrise and sunset times. Data reflect 2 days for each Arabian oryx. (B) The number of REM sleep episodes shown as a function of their time of occurrence relative to the time of the minimum subcutaneous temperature (Tsc Min) within the cycle during winter (left graph) and summer (right graph).

When examining the rate of change of Tsc and Ta during sleep bouts greater than 20 min, seasonal differences were noted (Figure 9, Table 4). During winter sleep bouts of greater than 20 min during the dark period, when most sleep in winter occurred (67.41% of TST, see above), Tsc was observed to decrease at a rate of −0.0125°C/min, whereas Ta decreased at a similar rate of −0.0110°C/min. During summer sleep bouts of greater than 20 min during the light period, when most sleep in summer occurred (83.02% of TST, see above), Tsc was observed to increase at a rate of 0.0023°C/min, whereas Ta increased at a much faster rate of 0.0178°C/min (Table 4). Thus, during sleep in the light period in summer, Tsc increased at a rate almost 8 times slower than Ta while the oryx were asleep. In contrast, in 1 hr following a light period sleep bout in summer, when the oryx were awake, Tsc increased at a rate of 0.0076°C/min, whereas Ta increased at a rate of 0.0016°C/min (Table 4), indicating that following sleep, Tsc increased at a rate of 4.75 times faster than Ta. Thus, during the light period sleep bouts in summer, the rate of increase in Tsc was substantially lower than the rate of increase of Ta, but when awake, the rate of increase in Tsc was substantially higher than the rate of increase of Ta (Figure 9). This indicates that sleep bouts during the light period in summer slow the overall rate of increase of body temperature (Figure 9).
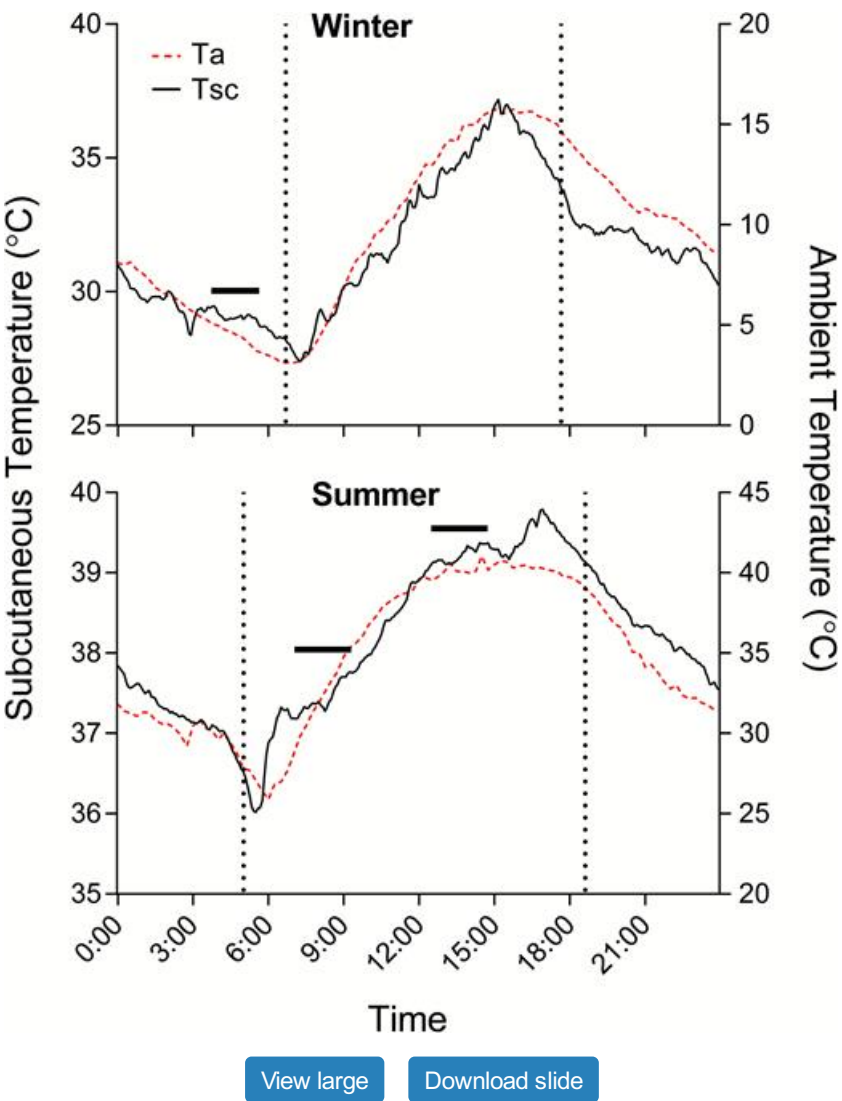
Table 4.

Rates of change in subcutaneous (Tsc) and ambient air (Ta) temperatures during sleep and wake bouts for the 24 hr, light, and dark periods during summer and winter

Winter				Summer	
	Period	Tsc rate (Δ°C/min)	Ta rate (Δ°C/min)	Tsc rate (Δ°C/min)	Ta rate (Δ°C/min)
Sleep bouts > 20 min	24 hr	−0.0035	−0.0037	−0.0004	0.0079
	Light	0.0213	0.0161	0.0023	0.0178
	Dark	−0.0125	−0.0110	−0.0083	−0.0221
Wake bouts (60 min)	Post sleep bouts > 20 min	0.0172	0.0213	0.0076	0.0016

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Figure 9.

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The average ambient (Ta, red dashed lines) and subcutaneous (Tsc, black solid lines) temperatures, recorded every 15 (Ta) and 5 (Tsc) min, across the recording period for winter and summer. Ta is plotted on the secondary y-axis. The results represented are the grouped averages for all animals studied per season over the 2 day recording period. The horizontal black bars represent the time of the major sleep bouts per season as described. Dashed vertical lines represent sunrise and sunset in each recording period. Tsc for winter and summer are shown on different y-axis scales so as to best represent the data shown and reinforce the shifts observed in temperature related to the major sleep bouts.

Discussion

The current study documents polysomnographic and associated recordings in a freely roaming artiodactyl species that inhabits very harsh, hyperarid, desert conditions. The recordings revealed that the Arabian oryx exhibits typical mammalian sleep–wake states [27] that can be readily defined as wakefulness, NREM, and REM sleep. In addition, the Arabian oryx exhibits sleep patterns that vary seasonally confirming previous reports of seasonal temporal niche switching and varying activity or inactivity patterns [5, 7–9]. The temporal variation of electrophysiologically defined sleep patterns between seasons exhibited by Arabian oryx appears to be related to thermoregulation in response to the challenges faced with high ambient temperatures during the summer.

Limitations of the current study

Arabian oryx were brought to the edge of extinction through excessive hunting, the last naturally occurring populations being eliminated in the Nafud and the Rub al Khali deserts in the Kingdom of Saudi Arabia during the 1970s [28]. Since then, Arabian oryx numbers have been restored through captive breeding programs and they are now assigned "vulnerable" status on the IUCN Red List (June 2011) [29]. This vulnerable status is reflected in the primary limitation of the current study, which is the small sample size of oryx from which we obtained comprehensive PSG recordings, with an n of 1 in winter and an n of 2 in summer. Although we attempted to have an n of 3 for each season, equipment failure resulted in a smaller sample size than intended. Although the sample size for the PSG data is small, it does correlate significantly with the timing patterns of the ACT data for all six animals. In the case of ACT data, an underestimation of wakefulness compared with PSG will always be present as quiet waking can be scored and interpreted as inactivity. Moreover, the combination of ACT and PSG data in the current study is very similar to the seasonally defined patterns of activity and inactivity described in previous studies of the Arabian oryx [5, 7–9]. In the case of any potential effects of rumination on sleep and EEG patterns, no prior information exists for Arabian oryx and no examination was conducted within the current study. In other artiodactyl species, no specific EEG pattern was associated for the onset or offset of rumination during sleep states and no correlations between EEG and rumination were reported [30]. Due to the invasive nature of the current study, the vulnerable conservation status of the Arabian oryx, and ethical and governmental approval limitations due to the conservation status of the oryx, the experimental procedures unfortunately could not be repeated to increase the sample size. This will obviously reduce the interpretive strength of the results obtained; thus, in the ensuing discussion, although we generalize our data, we are cognizant of the fact that the results we are discussing should be considered as case studies and we temper our conclusions appropriately.

Arabian oryx sleep in winter

Our analysis indicates that during the winter, the Arabian oryx obtains the majority of its sleep (~67%) during the coolest hours of the early morning prior to sunrise. During winter, the oryx recorded had a TST of 6.69 hr, with REM occupying 4.18 per cent of TST, the remainder of sleep being NREM. This total amount of sleep, the timing of sleep, the polyphasic nature of sleep, the observation that sleep consists of readily identifiable NREM and REM states, with no unusual sleep states being observed, all indicate that the Arabian oryx, being a herbivorous mammal with a body mass of around 60 kg, sleeps, in the winter, similarly to what might be predicted from previous studies of mammalian species, albeit captive studies, of similar size, diet, and phylogenetic affinities [18, 27, 31, 32]. In addition, during sleep in the winter, the subcutaneous temperature of the oryx was seen to decrease at a rate similar to the decrease in ambient air temperature, and this is also a typical feature of mammalian sleep [33–35]. The one specific difference is that in the Arabian oryx REM occupies only 4.18 per cent of TST, which is substantially less than ~13%–30% of TST being REM reported in other artiodactyl species [32].

Arabian oryx sleep in summer

In contrast to what might be described as a typical sleep pattern for an artiodactyl in the winter, in the hot summer months, sleep in the Arabian oryx was substantially different. Although the typical sleep states of NREM and REM were observed, rather than sleeping during the dark period, the majority of this polyphasic sleep (~83%) occurred during the light period. During the summer, we observed that the Arabian oryx slept an average of 3.77 hr per day, with REM occupying 2.12 per cent of TST. Thus, in the summer, the oryx slept mostly during the light period and had substantially less sleep than in the winter (around 2.92 hr/day less), and the percentage of TST occupied by REM was approximately half, whereas the actual amount of REM decreased from 16.8 min/day in winter to 4.8 min/day in summer. In addition, during the sleep bouts in the summer, the subcutaneous temperature was observed to rise, although not as rapidly as the ambient temperature rose. Thus, similar to many other mammals, the TST in summer was less than that observed in winter [36]; however, the timing of sleep in the light period, the substantially lowered amount of REM sleep, and the increase in body temperature during sleep are not features that can be described as typical of artiodactyl sleep physiology.

Why is summer sleep so unusual in the Arabian oryx?

As outlined above, there are several features of the patterns and physiology of sleep that change in the summer when compared with the winter in the Arabian oryx. Although it is typical for mammals to reduce daily TST in summer, the Arabian oryx has approximately half the amount of sleep per day in summer compared with winter (3.77 hr/day compared with 6.69 hr/day), which is a far larger reduction in daily TST than generally observed in other species [36, 37]. This dramatic reduction in TST may be related to the decline in seasonal biomass quality and quantity during the summer as a result of markedly reduced precipitation, and the relative contribution of certain flora species, like perennial grasses, to the oryx diet. Thus, more time must be allocated for active foraging and grazing in the summer, and less time is available for sleep [2, 9, 38].

A second major variation is the allocation of the majority of sleep to the light period in summer compared with the dark period in winter. Thus, the Arabian oryx appear to be actively foraging at night, which may help mitigate the effects of exposure to the hot sun during the day. However, in addition, nighttime humidity is higher during the summer than in the winter, providing plants with a higher water content and thus allowing the oryx to gain access to necessary hydration from metabolic water in their diet [9, 39–42].

The third major variation observed in summer sleep for the oryx is the reduction in the amount of time spent in REM sleep, from 16.8 min/day in winter to 4.8 min/day in summer. Indeed, it is clear that, irrespective of the season, the amount of time spent in REM sleep per day by the Arabian oryx is substantially less than that observed in other artiodactyls [32]. It is well documented that during mammalian REM sleep the temperature of the core CNS increases (e.g. Ref. 34); however, Arabian oryx are always exposed to high ambient air temperatures compared with many other mammals, even in the winter (Table 1). Given that the Arabian oryx possesses enhanced selective brain cooling compared to close relatives [1], and their exposure to consistently warm conditions, it is possible that REM sleep times are reduced in this species, especially so in the summer, to avoid overheating, or unnecessary heating, of the brain.

The last major variation observed in the summer sleep physiology of the Arabian oryx compared with the winter is the rise in subcutaneous temperature during summer sleep. When sleeping in the winter, the subcutaneous temperature of the oryx decreases, which is typical for mammals, but winter sleep occurs during the dark period when ambient air temperatures are also dropping at a similar rate. In contrast, summer sleep occurs during the light period when ambient temperatures are rising; however, during this daytime summer sleep, the rate of increase in subcutaneous temperature is approximately eight times slower than the rate of increase in ambient air temperatures. Immediately following a daytime summer sleep bout, when the oryx are awake, the rate of increase in subcutaneous temperature is approximately 4.75 faster than the rate of increase in ambient air temperature. Thus, overall body temperature in the awake oryx is strongly influenced by ambient air temperature, but while sleeping, the body temperature of the oryx appears to be substantially less influenced by ambient air temperatures. Thus, the oryx may be making use of the normal physiology of mammalian NREM sleep, where body temperature normally drops, to mitigate, or delay, increases in body temperature (Figure 9). By mitigating or delaying the inevitable rise in body temperature in the summer by sleeping, the Arabian oryx may be using daytime summer sleep as a novel mechanism for thermoregulation, preventing their body temperatures rising beyond levels that their physiology can accommodate.

As core body temperature begins to decrease in the daily phase, the occurrence of sleep is most probable; however, it is rather uncommon for sleep to transpire during the rising phase [35, 43–45] or under extreme ambient heat and heat stress [46–48], and this is most likely when ambient temperature supersedes body temperature in oryx during the summer. Through an underlying circadian rhythm, core body temperature decreases during normal sleep onset and the sleep that follows further promotes this effect [49, 50]. Changes in peripheral skin temperature are the primary driver of this effect [51] and have been subsequently associated with the timing of melatonin secretion and thus the timing of sleep [52]. The extreme ambient temperature cycle in the desert would strongly affect both peripheral skin and core temperature (both possibly under different regulation) and has been suggested to advance circadian core body temperature and REM sleep [50]. Such phase advancing effects of temperature on internal circadian mechanisms may dictate or drive the seasonal timing of sleep in the Arabian oryx.

During both seasons, SWA appears to decrease as the sleep period progresses (early vs. late into the longest sleep periods), indicating that sleep may be homeostatically regulated in the oryx [53]. Additionally, during summer, SWA is higher overall compared with during winter, as was similarly observed for the spectral power of all vigilance states (Figure 1, E and F). Previous studies have shown that active cooling of brain temperature in rats, cats, and humans can lead to decreased EEG wave amplitude and frequency [35, 54–57]; however, whether active warming of the brain leads to an increased amplitude in EEG patterns, like that observed during summer, is not well described or understood and no further comments can be made. The high ambient temperatures, and associated body, brain, and core temperatures in the oryx, during summer may restrict NREM and REM sleep to the point of reducing sleep quality, i.e. manifesting as sleep deprivation, and thus leading to the increased SWA observed. As both sample size and recordings were limited (see limitations of the current study section), our conclusions, in all instances, are speculative at best and further investigations are warranted.

Conclusion

The Arabian oryx, which inhabits the hyperarid desert environment of the Arabian Peninsula, shows an unusual seasonal variation in sleep. Although sleep in the cooler winter months can readily be described as typical for an artiodactyl of around 60 kg body mass, sleep in the hotter summer months shows significant variations. It would appear that all the variations noted in these summer sleep patterns and physiology are directly related to the increased ambient air temperatures, which not only affect the individual animal's thermoregulatory physiology, but the time of the day, when nocturnal activity is most likely to be beneficial to survival through the ingestion of plants that have more water due to higher nocturnal humidity levels. Lastly, the Arabian oryx appears to be using the standard physiology of sleep to mitigate or delay increases in body temperature as a novel thermoregulatory mechanism to prevent overheating. Thus, the Arabian oryx presents an interesting case of using the physiology of sleep in an adaptive way to ensure survival in an environment where most large mammals would rapidly perish.

Supplementary Material

Supplementary material is available at *SLEEP* online.

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Notes

Conflict of interest statement. None declared.

Acknowledgments

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