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Characteristics of Sleep–Wakefulness Cycle and Circadian Activity in the Lesser Mouse-Deer (*Tragulus kanchil*)

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Abstract

The pattern of sleep and circadian activity of the lesser mouse-deer (*Tragulus kanchil*) that is the smallest (body mass between 1.5 and 2.2 kg) representative of the basal group (Tragulidae) of even-toed ungulates which evolved 40–50 Ma were studied. In naturalistic conditions, a total of 30 days of full-day video of the animal behavior and 15 days of 24-h polysomnographic data were collected in 6 animals. The mouse-deer were active less than 20% of 24 h and were quiescent during 60–80% of the remaining time. Slow wave sleep (SWS) accounted for on average 49.7 ± 3.7% of 24 h and paradoxical (rapid eye movement, REM) sleep accounted for 1.7 ± 0.3% of 24 h. During the majority of SWS (87.0 ± 4.4%) the eyes were open. The most of SWS and REM sleep occurred during the daytime hours (9 a.m. to 4 p.m.) and in the first half of the night (8 p.m. to 2 a.m.); the animals were most active during twilight hours (4–6 a.m. and 6–7 p.m.). We suggest that the main features of sleep in the mouse-deer are largely determined by ecological factors, including environmental temperature and predation, as well as the size and physiology of the mouse-deer.

Keywords

sleep; REM sleep; slow wave sleep; circadian activity; ecology; evolution; the lesser mouse-deer; *Tragulus kanchil* ; Tragulidae; ungulates

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COMPLIANCE WITH ETHICAL STANDARDS

The research plan was approved by the Bioethics Commission of the Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences and the Joint Russian–Vietnam Tropical Research and Technological Center.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

INTRODUCTION

Ungulates are one of the most interesting groups for comparative studies of sleep patterns in animals. These mammals live in different habitats and lead a predominantly gregarious life. There are many domesticated species among them. Most of the electrophysiological studies of sleep were performed on domestic animals [1, 2], and only three studies investigated the sleep of wild even-toed ungulates [3–5]. The total duration of sleep in the studied species varies in the range from 12 to 43% of 24 h, while the amount of paradoxical sleep (REM sleep, abbreviation from *rapid eye movement*) in all ungulates is relatively small: from 1.2 to 7.2% of 24 h [1–5].

Lesser mouse-deer (Tragulidae, Artiodactyla) are the smallest among ungulate mammals. They live in the tropical forests of South Asia and Africa. Lesser mouse-deer appeared 40–50 Ma and almost have not changed during this time [6]. This is the only surviving basal group of even-toed ungulates. Tragulidae, which are called “living fossils”, have are a number of morphophysiological and behavioral traits that are considered “archaic” for even-toed ungulates [7]. Considering the phylogenetic position, characteristics and size of animals, as well as their distribution, lesser mouse-deer are of particular interest for comparative studies of sleep, especially understanding the role of environmental and evolutionary factors in the formation of sleep parameters and testing a number of hypotheses about sleep function.

The goal of this work was to study sleep and circadian rhythm in the lesser mouse-deer (*Tragulus kanchil*).

MATERIALS AND METHODS

Two series of experiments were performed on 6 adult female lesser mouse-deer (weight of 1.7–2.2 kg, body length of 42–48 cm) in the Buzyamap National Park (Vietnam). In the first series, the behavior of lesser mouse-deer was investigated by video filming (a total of 14 days in 3 animals). In the second series, polysomnographic studies were carried out using telemetry (15 days of recording in 4 animals). All animals were implanted under general anesthesia with electrodes for recording an electroencephalogram (EEG) of the cerebral cortex, electromyogram of the cervical muscles, and electrooculogram. During the experiments, the animals were kept one at a time in an open-air enclosure of 3.5 × 3.5 m with natural vegetation; the enclosure had a house (shelter) of 0.9 × 0.7 × 0.7 m, in which the animals spent most of the daytime. The lighting mode (dawn at 6 a.m., sunset at 6 p.m.) and noise were natural. The animals were fed twice a day with leaves of shrubs (at 6–7 p.m. and at 3–4 p.m.). In addition, ripe cashews fell from trees into the enclosure. Electropolygrams and video recordings of behavior were processed in 20-s epochs.

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RESULTS AND DISCUSSION

The lesser mouse-deer were in the shelter for most of the daytime and stayed in the enclosure at night. Two-thirds of 24-h (on average 64.0 ± 2.1% in series 1 and 66.7 ± 4.7% in series 2), the animals were quiescent in a characteristic posture that resembled the posture of the sphinx: the lesser mouse-deer lay leaning on the sternum, limbs were bent under the body, neck was held vertically, the head was directed forward (Fig. 1). Approximately 16% of the time (18.3 ± 3.2% in series 1 and 14.0 ± 3.4% in series 2), the lesser mouse-deer were standing. Less than 2% of the time (2.0 ± 0.9% and 1.3 ± 0.3%), lesser the mouse-deer lay with their heads stretched forward and laid on the ground. The periods of high activity (moving around the enclosure and feeding) accounted for 15.7 ± 4.1% of the time in series 1 and 18.0 ± 2.6% in series 2. Thus, the duration of the main forms of behavior in intact and implanted lesser mouse-deer was the same, and the animals were inactive more than 80% of the time.

Electropolygrams of active and quiet wakefulness (AW and QW), slow-wave sleep (SWS), and REM sleep in the lesser mouse-deer did not differ from those in other ungulates (Fig. 1b). Wakefulness accounted for 46.2 ± 2.9% of 24 h, i.e., less than half of the whole day. Almost 60% of this time was occupied by QW, during which bursts with a frequency of 5 to 14 Hz were recorded in the EEG against the background of low-amplitude activity (typical for AW and QW).

At night, the lesser mouse-deer slept mainly in the open space of the enclosure; during the day, they usually slept in the house. SWS was characterized by high-amplitude slow waves in the EEG with a frequency below 6 Hz and decreased muscle tone (Fig. 1). SWS accounted for 49.7 ± 3.7% 24-h. Almost the entire SWS (96.2 ± 2.2%) was recorded in the sphinx position, and only a small amount was recorded in the standing position (3.7 ± 2.2%). The eyes of the lesser mouse-deer were open during most of the SWS. The state of one or two eyes was determined for 47.6 ± 13.4% of SWS epochs. The eyes were open on average during 87.0 ± 4.4% of this time. In the daytime, SWS was accompanied by frequent (3–5 times/s) shallow breathing panting and profuse salivation.

REM sleep was characterized by almost continuous eye movements and even lower muscle tone in comparison with SWS (up to atony) and low-amplitude EEG that is characteristic of the state of wakefulness (Fig. 1b). All lesser mouse-deer showed increased activity in the EEG in the range of theta rhythm (frequency of 6–7 Hz). In REM sleep, the eyes could be closed or open. The eyelids were often closed and opened in parallel with eye trembles. The duration of REM sleep in different animals varied from 1.2 to 2.4% of 24 h and averaged 1.7 ± 0.3% or 3.2% of the total amount of sleep. A total of 35.3 ± 6.4% of REM sleep was recorded in the sphinx position and 64.7 ± 6.4% was recorded in the lying position (head on the ground). The duration of the episodes was 2.0 ± 0.2 min and varied from 20 s to 8 min; 12.3 ± 1.5 episodes of REM sleep were recorded per day.

Chewing (Ch, rhythmic chewing of food) was recorded in the lesser mouse-deer in QW and SWS. In total, Ch accounted for 17.0 ± 3.7% of 24 h: 68.3 ± 9.1% of all Ch was recorded

during SWS, and 26.8 ± 7.1% was recorded in QW. Similar to other undulates [1, 2], Ch of lesser mouse-deer never coincided in time with REM sleep.

Episodes of wakefulness and sleep were recorded in the lesser mouse-deer throughout the day (Fig. 2). In both series, the animals were the most active before dawn (4–6 a.m., up to 60% of time) and immediately after sunset (6–7 p.m., 36%) and the least active in the morning (7–9 a.m., 10%) and in the second half of the day (1–5 p.m., 8%). The greatest amount of time was spent by the animals in SWS in the morning hours (7–9 a.m., up to 71%) and the least amount of time was spent in SWS before dawn (5–6 a.m., 15% of time). In the period from 9 a.m. to 5 a.m. of the next day, the average hour amount of SWS gradually decreased. The hour amount of AW and SWS in the lesser mouse-deer significantly depended on the time of day (ANOVA with replications, $p < 0.001$ and $p = 0.008$, respectively). The episodes of REM sleep coincided with the periods of the greatest amount of SWS (8 a.m. to 4 p.m. and 7 p.m. to 2 a.m.).

We have established that the stages of SWS and REM sleep in the lesser mouse-deer well differentiated, like in other placental mammals. At the same time, the total amount of SWS (49.7% of 24 h or almost 12 h) in the smallest animal among undulates turned out to be the greatest among all the studied undulates, and the amount of REM sleep (1.7% of 24 h or 25%) was comparable with values in other species [1–5, 8] (Fig. 3). The record amount of SWS in lesser mouse-deer agrees with the general trend of increase in the duration of sleep in undulates in proportion to a decrease in weight (Fig. 3a). It is believed that larger herbivorous animals must spend more time on searching and eating food, which reduces the time for sleep. The versatile diet of lesser mouse-deer (leaves, fruits, mushrooms, and sometimes insects) leaves them more time for sleep. On the other hand, the low level of activity and the large amount of SWS also make lesser mouse-deer less noticeable for wild cats, for which small undulates account for a significant portion of prey. Therefore, the main strategy of counteracting predators in lesser mouse-deer is hiding [6, 7]. Finally, the high daily air temperature in the tropical forest (more than 30°C) and the narrow thermally neutral zone in lesser mouse-deer (15–30°C) may also cause a large amount of SWS and QW. The intense motion activity of lesser mouse-deer under such conditions leads to hyperthermia [9]. Consequently, the large duration of SWS in lesser mouse-deer agrees with the idea about sleep as the state of adaptive immobility, which decreases or excludes the activity of animals, when it is inexpedient.

A small amount of REM sleep in ungulates is also often associated with the fact that they are prey for wild cats [6]. REM sleep is accompanied by atony or decreased muscle tone and high arousal thresholds for awakening [8, 11, 12]. Both factors can slow down the response of animals to danger. The duration of REM sleep in lesser mouse-deer as well as in two other wild species studied under naturalistic conditions was the lowest among ungulates (Fig. 3b). On the other hand, the largest amount of REM sleep was recorded in domestic animals, namely, ponies and pigs [2], for which one of the main breeding principles was the formation of a calm attitude towards humans. Consequently, the small amount of REM sleep in lesser mouse-deer is consistent with the data on the relationship between the duration of REM sleep and the protection of animals, as well as the level of alertness during sleep.

It is believed that Tragulidae are guided primarily by sense of smell and hearing, while herd ungulates use vision and collective alertness to detect predators [6, 7, 13]. We found that the lesser mouse-deer slept in an open space with their eyes open most of the time. Therefore, there is reason to believe that the lesser mouse-deer are able to process visual information during SWS, which may also contribute to higher alertness. It is interesting that ponies and pigs that have a record duration of REM sleep for ungulates kept the eyes closed during SWS [1, 2]. Taken together, these data support the idea that SWS with open eyes and a small amount of REM sleep are features of a more alert state in animals.

A small amount of REM sleep in the lesser mouse-deer may also be associated with the high temperature of the air and the peculiarities of thermoregulation in the animals. Unlike SWS, REM sleep is characterized by impaired thermoregulation. Thus, rapid breathing in the lesser mouse-deer (one of the ways to lower body temperature) was recorded during QW and SWS, but it stopped some time before the onset of a REM sleep episode and was restored after awakening. During REM sleep, the brain temperature also rises in the animals [14]. Although we found no differences in the number and duration of episodes of daytime and nocturnal REM sleep in the lesser mouse-deer, all the most prolonged episodes of REM sleep (4–8 min) were recorded in them before 9 a.m. or after 4 p.m., i.e., the outside the hottest time of day. In addition, Tragulidae do not have a system of flow cooling for the blood flowing to the brain, which is found in other species of even-toed ungulates (the so-called miraculous net [15]). Thus, a reduced amount of REM sleep may not only increase the alertness of animals, but also reduce the risk of brain overheating.

Considering that predators in a tropical forest can be active at different times of day [6, 13], the twilight (crepuscular) activity of lesser mouse-deer can be a strategy to maximize activity during periods of the most comfortable (in terms of temperature) time of day. At the same time, polyphasic sleep as well as a decrease in the degree of cyclicity in the form of alternating episodes of SWS and REM sleep make the behavior of lesser mouse-deer plastic, changing depending on external conditions (for example, the mode of activity of predators).

Thus, our study of the peculiarities of sleep and circadian rhythm of the lesser mouse deer under naturalistic conditions has shown that these smallest ungulates are at rest and SWS during most of the day, and SWS is accompanied mainly by the open state of the eyes. In total, SWS in the lesser mouse-deer accounts for about half of the time of day (the largest amount among the studied ungulates), and REM sleep is very short (as in wild species). Other important features of the lesser mouse-deer are the twilight nature of activity, polyphasic sleep, and reduced cyclicity of sleep stages. We have not found any signs of a relationship between sleep parameters in the lesser mouse-deer and their phylogenetic status. Our data suggest that the features of the sleep–wakefulness cycle in the lesser mouse-deer are primarily determined by environmental factors, such as the nature of feeding, temperature conditions, and the impact of predators, as well as body size and physiological features of the lesser mouse-deer.

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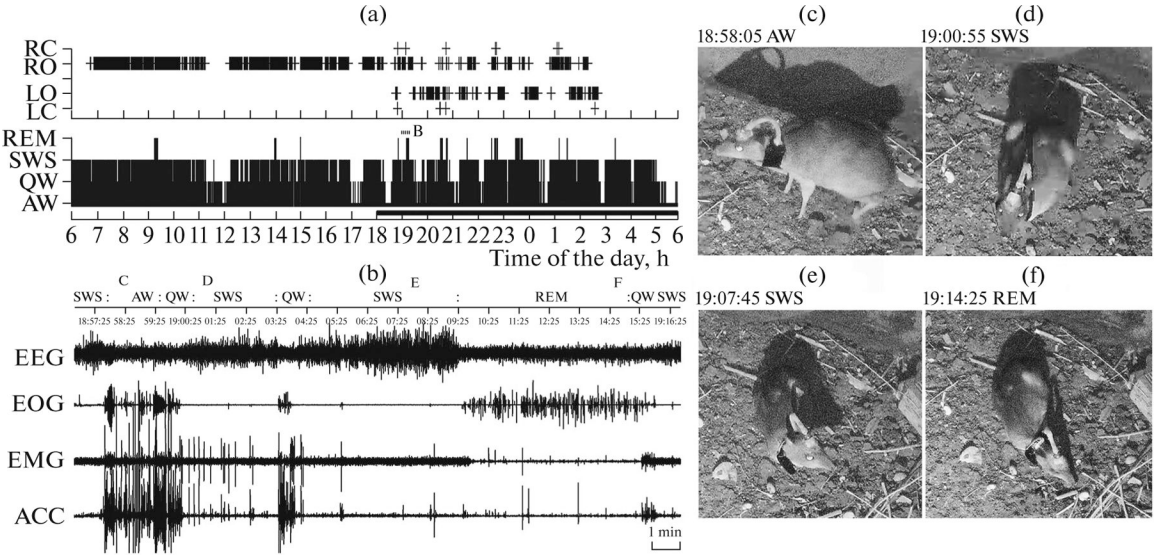

Fig. 1.

(a) Dynamics of the sleep and wakefulness stages and the state of the eyes in the lesser mouse-deer during one day. The state of the right (R) and left (L) eyes: O, open; C, closed. (b) Electropolygram of AW, QW, SWS, and REM sleep with a duration of 20 min. Electroencephalogram (EEG), electrooculogram (EOG), electromyogram (EMG), and acceleration (ACC) during the episode indicated by the dotted line in (a). The arrows above the timeline mark the time of photographing. (c–f) Photos: AW (c), SWS in the sphinx position (eyes are opened, reflect IR light) (d, e), REM sleep in the lying position (head on the ground, the eye directed towards the camera is closed) (f). Dark time of the day from 6 p.m. to 6 a.m.

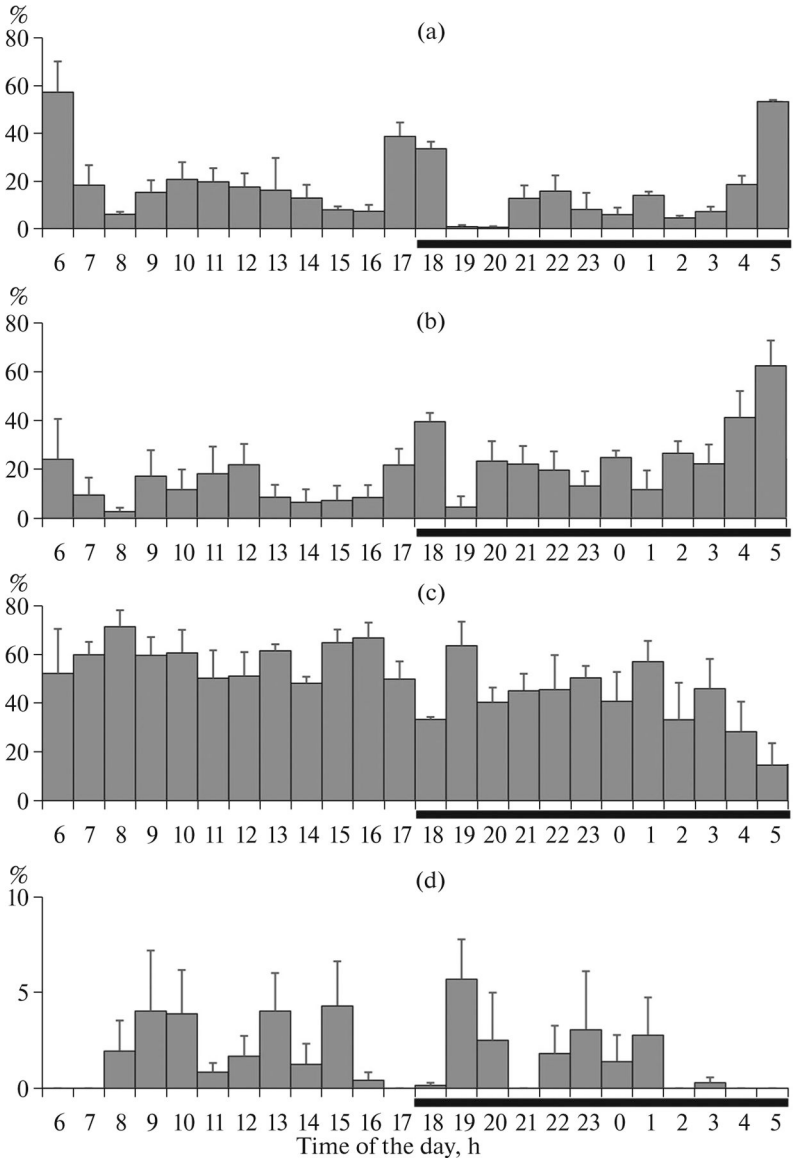

Fig. 2.

Average hourly amount of AW, SWS and REM sleep in lesser mouse-deer (mean ± S.E.M.). (a) Series 1, behavioral studies (3 animals, 4–5 days in each), AW. (b–d) Series 2, electrophysiological studies (4 animals, 1 day in each): (b) AW; (c) SWS; (d) REM sleep. Dark time of the day from 6 p.m. to 6 a.m.

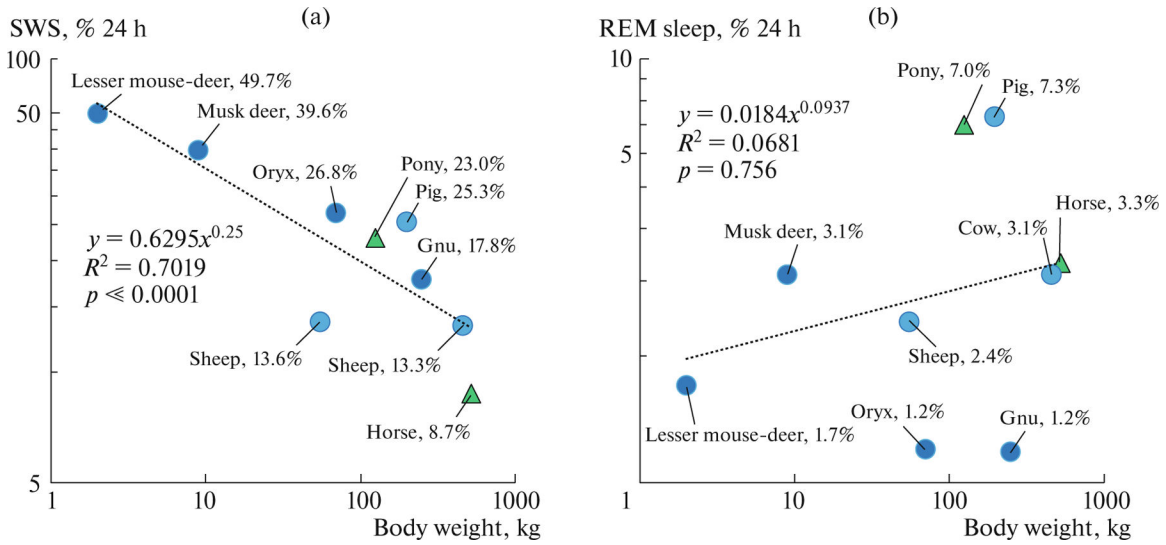

Fig. 3.

The correlation between the (a) amount of SWS and (b) REM sleep and body weight in ungulates. The dark and light blue circles represent wild and domestic even-toed ungulates (Artiodactyla), respectively. Triangles mark odd-toed ungulates (Perisso-dactyla). Data on the amount of sleep were taken from the studies [1–5, 8]. R^2 is the correlation coefficient, p is the significance level.