Nocturnal behavioral patterns of African ungulates in zoos

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Abstract

Since the analysis of animal behavior is a central element of ethology and ecology, it is not surprising that a great deal of research has been conducted describing the behavior of various ungulates. Most studies were conducted during the daylight hours, thus much less is known about nocturnal behavior. Detailed analyses of nocturnal behavior have only been conducted for very prominent ungulates such as giraffes, elephants, or livestock, and the nocturnal rhythms exhibited by many ungulates remain unknown. In the present study, the nocturnal rhythms of 192 individuals of 18 ungulate species from 20 European zoos are studied with respect to the behavioral positions standing, lying - head up, and lying - head down (the typical REM sleep position). Differences between species of the orders Perissodactyla and Cetartiodactyla, as well as between individuals of different age were found. However, no differences with respect to the sex were seen. Most species showed a significant increase in the proportion of lying during the night. In addition, the time between two events of “lying down” was studied in detail. A high degree of rhythmicity with respect to this quantity was found in all species. The proportion of lying in such a period was greater in Cetartidactyla than in Perissodactyla, and greater in juveniles than in adults.

NOCTURNAL BEHAVIORAL PATTERNS OF AFRICAN UNGULATES IN ZOOS

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1. Introduction

The description and analysis of animal behavior is a central element of ethology and ecology. There is extensive knowledge about the behavior and especially the rhythms displayed during the daylight hours of various ungulates (Caboń-Raczyńska et al., 1983; Leuthold & Leuthold, 1978; Manjrekar et al., 2017; Packard et al., 2014; Reta & Solomon, 2014; Zhang, 2000). The categories of "activity" and "rest" are the most prominent behavioral stages measured to study rhythms (Merrow et al., 2005). There are four main temporal partitioning strategies that differentiate activity patterns: nocturnal, diurnal, cathemeral and crepuscular. Most ungulates of the orders Perissodactyla and Cetartiodactyla are diurnal or crepuscular (Bennie et al., 2014), i.e. behavior patterns during daylight and during night differ (Davimes et al., 2018; Gravett et al., 2017; Wu et al., 2018). In particular, sleeping patterns are shifted into the night or dusk in many ungulates (Bennie et al., 2014; Gravett et al., 2017; Wu et al., 2018), and, for instance, Arabian Oryx shift their sleeping patterns even further into the night during the colder months (Davimes et al., 2018). Therefore, to fully understand the behavior of a species, it is necessary to also analyze its nocturnal behavior. Of course, nocturnal behavior is well studied for some very prominent species, such as giraffes (Burger et al., 2020; Sicks, 2016; Tobler & Schwierin, 1996) and elephants (Gravett et al., 2017), or for various farm animals (Greening & McBride, 2022; Ruckebusch, 1972; Ternman et al., 2014). However, to the best of our knowledge, the nocturnal behavior of many other ungulates is much worse explored.

Many challenges arise in the analysis of nocturnal behavior when animals are observed in their natural habitat. It is much more accessible to observe the nocturnal behavior of zoo animals (Ryder & Feistner, 1995). Observations in zoos provide an excellent opportunity to generate vast knowledge about animal behavior (Hollén & Manser, 2007; Melfi & Feistner, 2002; Rees, 2023), as zoos provide consistent and better access to animals and easier conditions for data collection (Ryder & Feistner, 1995). The latter is a requirement for understanding animal behavior on much more data than could be recorded in the wild. However, the ecology of zoo animals differs from the ecology of the wild living conspecifics. Thus, certain aspects of the activity budgets vary. Nevertheless, it is well known that a variety of characteristics of zoo animals and their wild conspecifics equal (Burger et al., 2020). Therefore, studies conducted with zoo animals help us to learn about the species' behavior in the wild (Rees, 2023). Especially in zoos, video recordings are a good tool to study nocturnal behavior because the observation method is non-invasive and does not cause behavioral changes by disturbing the observed animals.

The current study is based on video recordings of 192 individuals of 18 ungulate species in 20 European zoos. It builds on the results of a recent study investigating the basic characteristics of nocturnal behavior in ungulates (Gübert et al., 2023). The previous contribution examined the factors that influence the behavioral poses standing, lying - head up, and lying - head down. More specifically, the previous study identified the main factors influencing the activity budget and the number of phases per night of these behaviors. Age, body-size, and the feeding type were found to have a strong influence (Gübert et al., 2023). However, the activity budget and the number of phases of a behavior during night give a fundamental, though very basic, description of behavior. The current study takes a much finer look at behavior patterns, also distinguishing the behavioral poses standing, lying - head up and lying - head down. Lying - head down is the typical REM (rapid eye movement) sleep posture which can be used to estimate REM sleep non-invasively (El Allali et al., 2022; Greening & McBride, 2022; Lyamin et al., 2021; Ternman et al., 2014). The duration of REM sleep in ungulates is supposed to be associated with a factor related to predation risk, and long REM phases are detrimental to ungulates in the wild (Allison & Cicchetti, 1976). Therefore, a focus of this study is the timing of lying cycles and the occurrence and duration of phases spent in the REM sleep position.

2. Material and Methods

2.1. **Ethogram.** The ethogram is defined as in the study by Gübert et al. (2023) and can be found in Table 1 in the supplementary material. The two main behaviors are standing and lying. Lying is further divided into lying - head up (LHU) and lying - head down (LHD). LHD describes the typical REM (rapid eye movement) sleep posture and can be used to estimate REM sleep. Although measuring LHD yields only an approximation to REM sleep, previous studies prove that LHD is a reliable indicator. Its validity increases, in particular, if the REM sleep phases become longer (El Allali et al., 2022; Greening & McBride, 2022; Seeber et al., 2012; Ternman et al., 2014; Zizkova et al., 2013). If no animal is present on the recording, the category out of view (Out) is assigned.

To study rhythms in the described behavioral poses, lying cycles and the lying fraction were used. Lying cycles (LC) are defined as the periods starting at the first lying phase observed after a standing phase to the next lying phase observed after the following standing phase (Figure 1 A and B), where only LCs without Out in this period were used in the analysis. For every LC, the fraction of lying (LF) in this cycle was calculated and denoted by LF (Figure 1 C). In order to compare different species, we also used a species standardized LF, standardizing the LF with the mean and standard deviation of LFs of all individuals of the respective species.

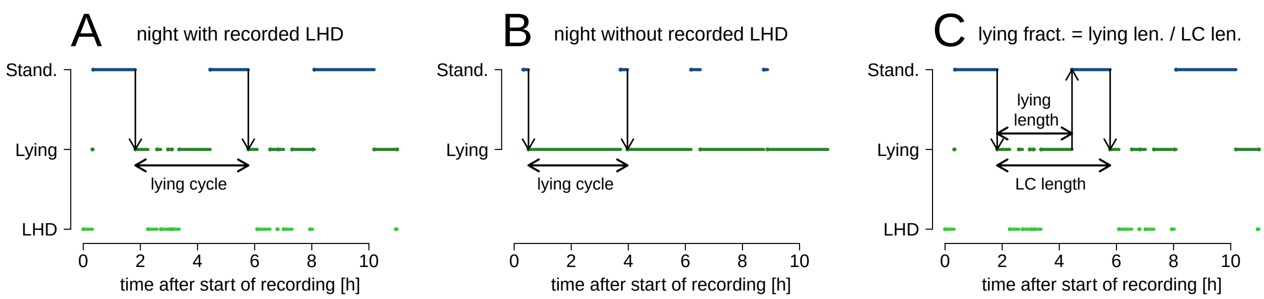

FIGURE 1. The definition of lying cycles (LC) in nights with recorded lying - head down (LHD) (A) and without recorded LHD (B). (C) visualizes the definition of the lying fraction (LF).

2.2. **Data recording and data processing.** In this study, the nocturnal behavior of 192 individuals from 18 species is investigated. The following species are included: Greater Kudu (*Tragelaphus strepsiceros*), Sitatunga (*Tragelaphus spekii*), Bongo (*Tragelaphus eurycerus*), Common Eland (*Tragelaphus oryx*), African Buffalo (*Syncerus caffer*), distinguished into the subspecies African Forest Buffalo (*Syncerus caffer nanus*) and African Savannah Buffalo (*Syncerus caffer caffer*), Blesbok (*Damaliscus pygargus*), Common Wildebeest (*Connochaetes taurinus*), Roan Antelope (*Hippotragus equinus*), Sable Antelope (*Hippotragus niger*), Scimitar-horned Oryx (*Oryx dammah*), Addax (*Addax nasomaculatus*), Waterbuck (*Kobus ellipsiprymnus*), Mountain Reedbuck (*Redunca fulvorufula*), Okapi (*Okapia johnstoni*), Plains Zebra (*Equus quagga*), Grevy's Zebra (*Equus grevyi*) and Mountain Zebra (*Equus zebra*).

The data was collected by video recordings with night vision cameras with built-in infrared emitters (Lupus LE139HD or Lupus LE338HD with the recording device LUPUSTEC LE800HD or TECHNAXX PRO HD 720P). The frame rate is 1 fps and the resolution ranges from 704x576 px to 1920x1080 px. The cameras were installed in the stables of animals in 20 EAZA zoos in Germany (Zoologische Gärten Berlin (Tierpark and Zoo), Zoo Vivarium Darmstadt, Zoo Dortmund, Zoo Duisburg, Zoo Frankfurt, Zoom Erlebniswelt Gelsenkirchen, Erlebnis-Zoo Hannover, Zoo Heidelberg, Kölner Zoo, Zoo Krefeld, Opel-Zoo Kronberg, Zoo Landau in der Pfalz, Zoo Leipzig, Allwetterzoo Münster, Zoo Neuwied, Zoo Osnabrück, Zoologischer Garten Schwerin, Der Grüne Zoo Wuppertal) and the Netherlands (Königlicher Burgers Zoo Arnheim). Data was collected during the colder season (September to May) between 2017 and 2021 during night, with a "night" being defined as the time from 7 p.m. to 6 a.m.. A part of the recorded nights was evaluated manually with the open source software BORIS (Behavioral Observation Research Interactive Software), version 7.7.3 (Friard & Gamba, 2016). Therefore, a continuous sampling was used with an exact time span for each behavioral sequence (Martin & Bateson, 2015).

All other nights were annotated using the software package BOVIDS (Behavioral Observations by Videos and Images using Deep-Learning Software) (Gübert et al., 2022). This software package is based on machine learning techniques and the manually annotated videos were partly used as test and training sets. BOVIDS achieved average f-scores of 0.992 ± 0.003 (lying), and 0.956 ± 0.006 (LHD) on the unseen test data. Detailed information on the performance per individual on the testing set is given in the supplementary material. The software package BOVIDS applies a set of post-processing rules to achieve high classification accuracy (Gübert et al., 2022; Hahn-Klimroth et al., 2021). Most importantly, standing and lying sequences shorter than 5 minutes and LHD sequences shorter than 35 seconds are discarded. In addition, on the analyzed nights, recordings where an animal is not present for at least 20% of the time and recordings with at least three occurrences of Out are discarded. A total of 9,156 nights with 100,716 hours were evaluated for standing and lying discrimination, with an average of 48 nights per individual. On a subset of the data, lying was further distinguished into LHU and LHD. This reduced dataset consisted of 6,226 nights from 129 individuals. Detailed information about the sample sizes are provided in the supplementary material.

After discarding nights as described above, 733 nights out of 9,156 nights contained sequences of Out. To study lying cycles, i.e. periods between two consecutive events of lying after standing, and the lying fraction (see Section 2.1), the following pre-processing was performed. This pre-processing was not performed for the description of standing and lying during night in Section 3.1. First, Out periods occurring at the beginning (or the end) of a night were simply discarded by starting (ending) the night at its first (or last) classifiable event. Second, a sequence of 'standing - Out - standing' in which the out period was shorter than 30 minutes was merged into a standing period. Third, in a sequence of 'lying - Out - standing' or 'standing - Out - lying' in which the Out period was shorter than 30 minutes, the out period was considered as standing and thus merged with the standing period. This pre-processing reduced the number of nights with Out periods to only 297 out of a total of 9,156 nights. For the analysis of lying cycles we then included only cycles without remaining Out periods.

2.3. **Statistical Methods.** For statistical comparisons, we use standard nonparametric procedures as the Wilcoxon-, and Kruskal-Wallis tests. Those tests were conducted in R (R Core Team, 2022). The three levels of significance 5%, 1%, and 0.1% are distinguished and indicated by *, **, and ***. For data preparation the Python programming language and the pandas library (Pandas Team, 2022) were used. Visualizations were done in R and matplotlib (Hunter, 2007).

To classify the increase and decrease of the lying proportion during the night for each species, we considered all adult individuals of each species separately. For each individual, we then estimated the trend in the lying proportion in the first (from 19:00 to 00:30) and in the second half (from 00:30 to 06:00) of the nights using standard linear regression. As a simple classification heuristic, we tested the slopes of all individuals per species for systematic deviations from zero in each part of the night, as well as for differences between the first and second part of the night using t-tests for all species with at least three adult individuals. Species with, e.g., non-significant ($p > 0.05$) results for the first part of the night, and positive slopes with $p < 0.05$ in the second part of the night also showed significant differences in slopes between first and second part of the night and were classified in the same class. For the other classes, we proceeded analogously.

In order to investigate the relation between the total LHD duration within a lying phase and the lying duration, we applied censored linear regression in the classical Tobit model using the R package censReg (Henningsen, 2010, 2017) in order to take into account that the total LHD duration cannot be negative. Analogously, the relation between the lying duration and the number of phases LHD per lying phase was also investigated with censored linear regression.

3. Results

3.1. **Distribution of the behavioral poses.** The first set of results is a description of the behavioral poses' distribution. Figure 2 (A and B) reports each species' mean of the proportion per behavioral pose over a night. The figure visualizes the change in the proportion of behavioral poses as the night progresses. The three zebra species have a much higher proportion of standing compared to all Cetartiodactyla. In the following, the change of the proportion lying over night is analyzed in more detail. More precisely, it is possible to cluster the single species into two clusters with respect to the change in the proportion lying in the first and the second part of the night (see Figure 2 C). Details of this clustering are given in Section 2.3. In the first cluster, the lying proportion shows no particular change in the first part of the night, but a significant increase in the second part of the night. This cluster consists of 12 species (Addax, African Savannah Buffalo, Arabian Oryx, Blesbok, Bongo, Greater Kudu, Mountain Reedbuck (†), Roan Antelope, Sable Antelope (†), Scimitar-horned Oryx, Sitatunga (†), and Waterbuck). The species marked with a † could not be tested for statistical

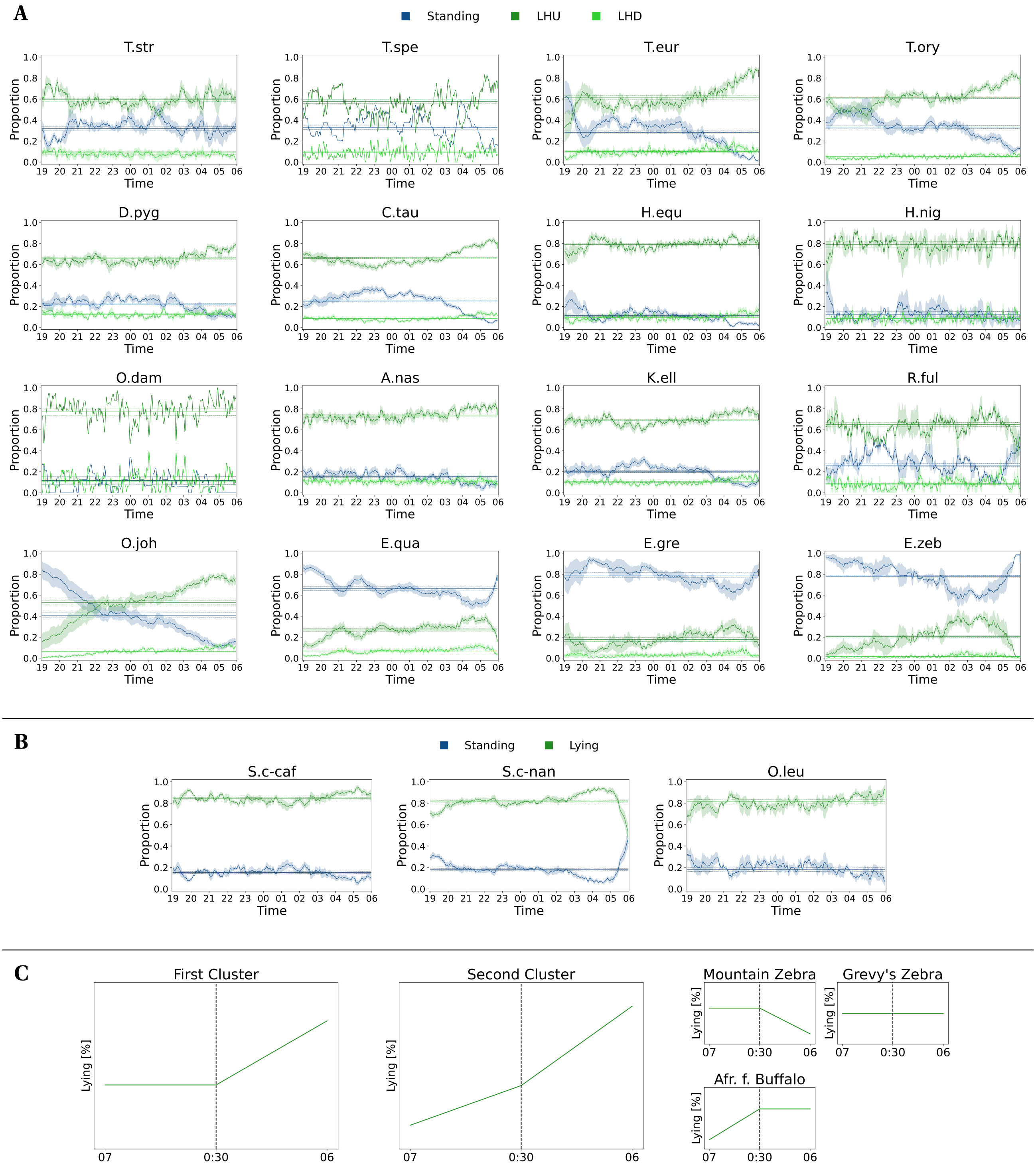

FIGURE 2. Distribution of the mean nocturnal behavior of the adult individuals per species. (A) contains those species on whose recordings lying was distinguished into lying - head up (LHU) and lying - head down (LHD) whereas (B) shows the three species in which LHD was not evaluated. The $y-$axis reports the proportion of the behavioral pose and the area around the curve visualizes the SEM over all individuals of a species. The horizontal lines mark the mean (solid) and the standard deviation (dotted) of the behavior in a complete night. (C) gives a schematic visualization of two clusters (and three exceptions) of the change in the proportion lying during the night. The exact sample sizes for (A) and (B) are given in the supplementary material.

significance in the trend due to low sample sizes, but they show a highly similar pattern. The species in the second cluster exhibit an increase in the lying proportion in both parts of the night, this cluster consists of four species (Okapi, Plains Zebra, Common Eland and Common Wildebeest). Finally, three species show a different trend and do not fit into one of the two clusters. Mountain Zebras show no particular change in the first part of the night, but the lying fraction decreases in the second part. Grevy's Zebras show no change in either part, and the African Forest Buffaloes show an increase in the first part, but no increase in the second part. Note that, also for the three species that do not fit into the clusters, an increase in the second part of the night is visible until the last 1-2 hours. This means, that up to the last two hours of the recording, Grevy's Zebras could be sorted into the first cluster and African Forest Buffaloes might be part of the second cluster.

Regarding the more fine-grained view on LHD it can be observed in Figure 2 that LHD is shown throughout the night in every species. This indicates that LHD is shown regularly in any sufficiently long lying phase. This will be presented in detail in Section 3.3.

While it is beyond the scope of the current study to present the behavior of every single individual, Figure 3 exemplarily reports the nocturnal behavior of four adult individuals in detail. Those examples underline that there are no severe changes in the analyzed behavioral poses in different nights of one individual. In particular, the examples show that the number and the length of the standing and lying phases of one individual do not seem to change largely in their pattern, and their typical length does not vary strongly between different nights. A male Addax and a female Bongo are chosen as representatives of the family Bovidae, a female Okapi as a representative of the family Giraffidae and, finally, a male Grevy's Zebra represents the order Perissodactyla. In particular, the trends described above of the proportion lying are visible in these representatives for the corresponding species.

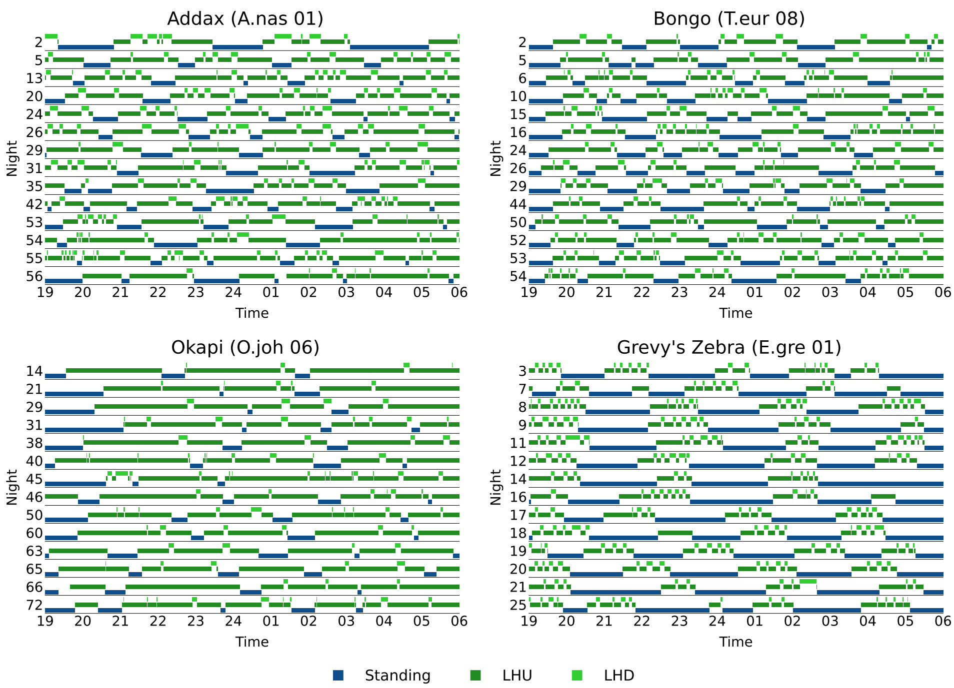

FIGURE 3. Exemplary representation of the nocturnal behavior of four adult individuals of the species Addax, Bongo, Okapi, and Grevy's Zebra. The behavioral poses standing (blue), lying - head up (dark green), and lying - head down (light green) are shown. For each individual, 14 randomly chosen nights are displayed.

3.2. **Lying cycles (LC) and lying fraction (LF).** In the previous subsection, the basic trends of the proportion lying were presented. In the following, a more detailed view on rhythms occurring over the night is given by studying lying cycles (LC). Around 86% of the analyzed individuals show a regular distribution of LC durations, which could be described approximately by a normal distribution. An example of an adult Common Eland is given in Figure 4 A. Accordingly, this regularity was often reflected in a certain rhythmic change of lying and standing periods when aligning the behavior at the start of the first lying cycle (Figure 4 B). The mean LC duration per individual is reported in Figure 4 C. The average mean LC duration over all species is 2.14 hours and the standard deviation amounts to 0.24 hours. Not only is the standard deviation comparably small, but the average mean LC duration is indeed similar between all species. It ranges from 1.8 hours (Greater Kudu) to 2.6 hours (Okapi). However, in some species, like all zebras, Okapis and Common Wildebeest, there are much higher variations between the individuals as can be seen in Figure 4 C. Moreover, no considerable difference was observed as a function of sex or age.

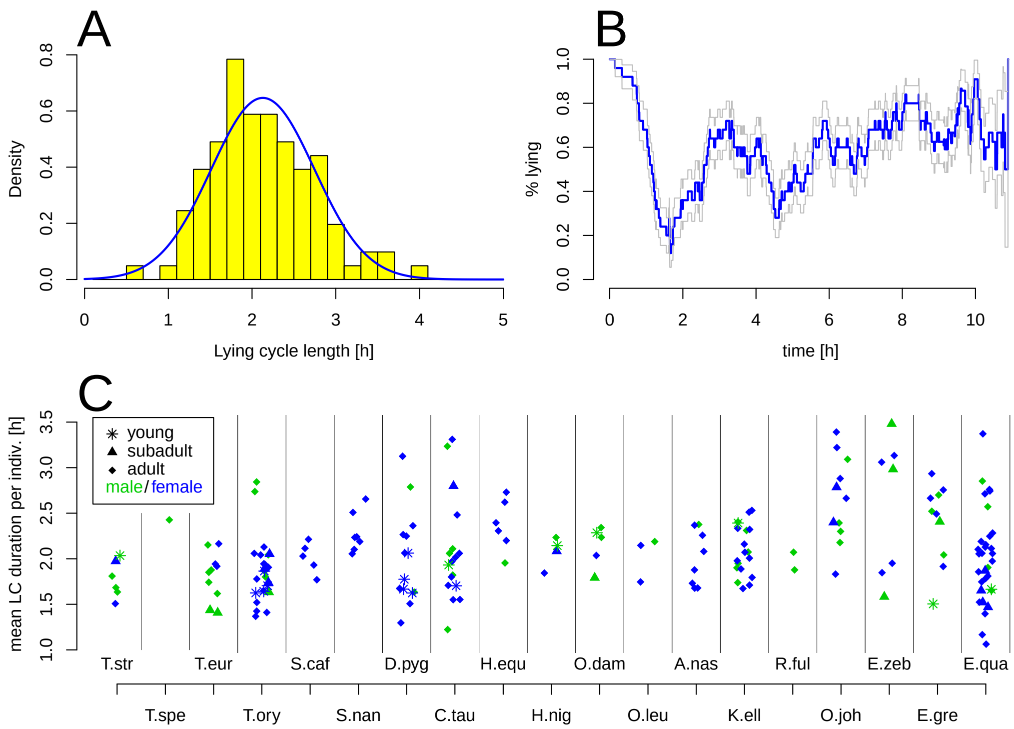

FIGURE 4. Lying cycles (LC) can occur rhythmically. (A) Distribution of LC lengths are typically symmetric. Here: LC distribution of a female adult Common Eland. (B) Average percentage of lying and standing during all nights of this individual, aligned at the start of the first fully observed lying cycle (blue: proportion, grey: 95%-confidence band). C. Mean LC duration for each animal.

In around 14% of the analyzed individuals severe deviations of LC lengths from a symmetric distribution could be observed (see Figure 5 A; example of a young Common Wildebeest). In such cases, animals showed a high degree of very short LCs as compared to the typical LC lengths in the respective species, and such distributions could typically be observed in younger animals. Indeed, 62.5% of the juvenile individuals show a large proportion of such short LC lengths while this is only the case for 20% of the subadult and 7.7% of the adult individuals. In order to quantify this effect, we calculated the 1% quantile of the LC distribution for all adult individuals being stalled as the only individual in a box, and then used the medians of these 1% quantiles across each species as references. As the normalization is performed for each species, no species specific differences can be observed. This normalization allows us to compare the proportion of short phases of young, subadult and adult individuals for different species. A visualization is given in Figure 5 B. Differences between age groups in the percentage of short LCs were statistically significant ($p < 0.01$ for young vs. subadult, $p < 0.03$ for subadult vs. adult, $p < 0.0001$ for young vs. adult, Wilcoxon rank sum tests). Interestingly, these differences were not reflected in systematic age differences in the mean LC duration (see Figure 4 C). Figure 5 C shows for each individual the percentage of LCs shorter than this reference. The individuals are distinguished by their species, their sex and their age. Adult individuals range around the 1% quantile (horizontal line), while some strong deviations up to more than 20% of short LCs can be observed, particularly in young and subadult individuals which are indicated by stars and triangles, respectively.

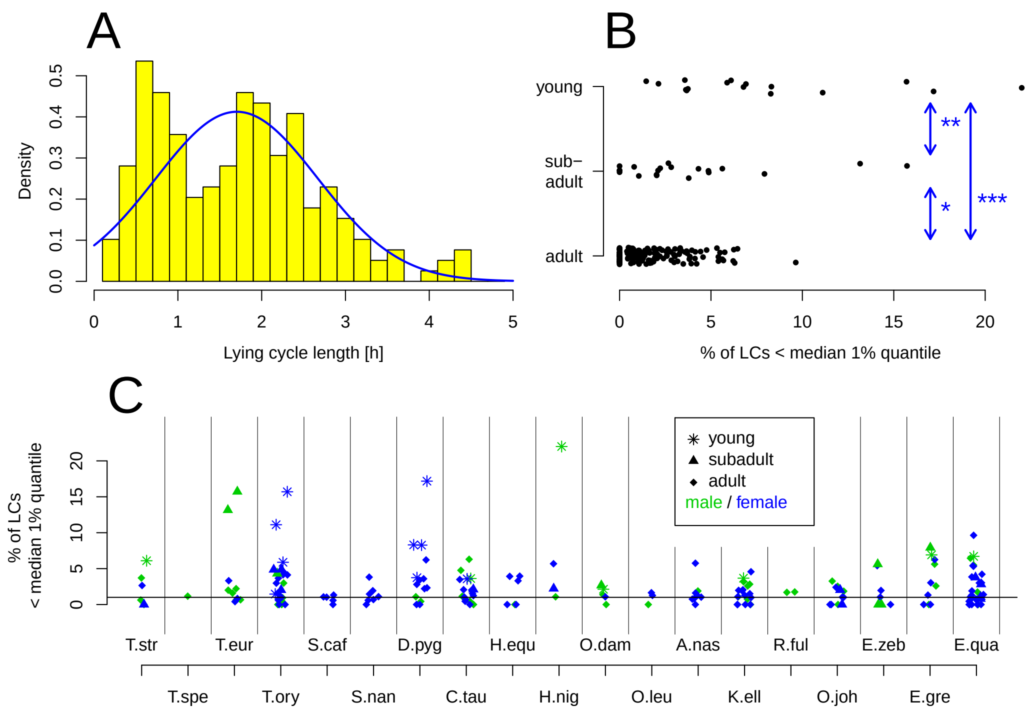

FIGURE 5. The durations of lying cycles (LC) are less regular in young animals, showing a high degree of short LCs. (A) Distribution of LC lengths in a female young Common Wildebeest. (B) and (C) Percentage of LCs per individual shorter than median 1% quantile in single adults in the respective species, as a function of age (B) and species and age (C). Stars indicate statistical significance on the 5% (*), 1% (**) and 0.1% (***)-level.

The fraction of lying (LF, see Figure 1 C for definition) during an LC differed considerably across species, ranging between a mean of about 31% in Grevy's Zebras up to a mean of about 85% in Roan Antelopes (Figure 6 A). Visual inspection of the figure leads to two clusters of species. On the one hand, there are the three Perissodactyla (35.8% ± 3.8%) and on the other hand, the studied Cetartiodactyla (74.6% ± 6.1%). The mean lying fractions of Perissodactyla and Cetartiodactyla were highly separated: While only 6.2% of all Perissodactyla showed a mean lying fraction above 60%, less than 7% of all Cetartiodactyla showed a mean lying fraction below 60% (Figure 6 A). Furthermore, young animals showed a longer relative duration of lying than older ones (Figure 6 B), $p < 0.05$ for young vs. sub-adult, $p < 0.01$ for subadult vs. adult, $p < 0.0001$ for young vs. adult, Wilcoxontest).

3.3. **Lying - head down.** In order to investigate the duration and structure of LHD phases, thus the time animals spend in the REM sleep position, we investigated the number of LHD phases per lying phase, the total duration of LHD during a lying phase, respectively its proportion, as well as the typical duration of a LHD phase.

Figure 7 A and B show examples of LHD length distributions of a female Common Eland and a female Plains Zebra. Most distributions did not tend to be symmetric. We therefore used the medians (blue vertical lines) as a measure of location. Figure 7 C shows the median LHD durations for all individuals for which nights with LHD could be recorded. The mean median LHD duration per species ranged from about 2.2 minutes in adult Mountain Zebras to about 7.6 minutes in adult Blesboks.

In order to investigate differences between sex and age groups, we again applied species standardization, using the mean and standard deviation of median LHD durations of all adult individuals per species for standardization. Figure 7 D and E show the results as a function of sex and age, respectively. Females tended to show slightly smaller median LHD durations than males, where this difference was not significant at the 5% level. The group of young and

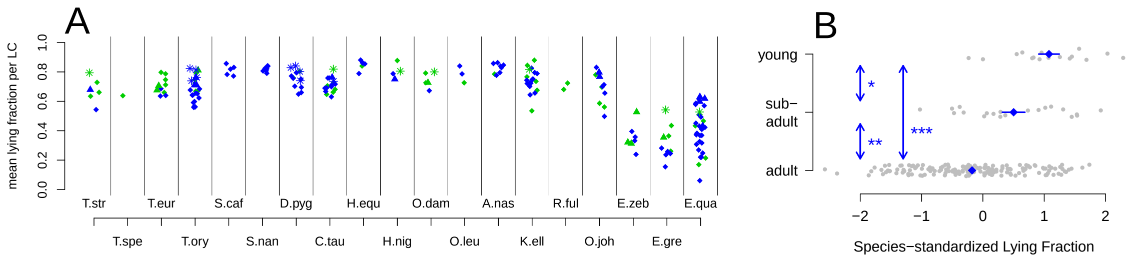

FIGURE 6. Length of lying relative to the lying cycle (LC) duration tends to be longer in young animals. (A) LF as a function of the age group, standardized with the mean and standard deviation of the LF in each respective species. Blue diamonds and lines indicate mean ± SEM. (B) Mean LFs per animal as a function of the species, age and sex. Point characters and colors as in Figure 4

subadult animals showed a slightly larger median LHD duration as compared to the adult individuals of the same species ($0.05 < p < 0.1$, Wilcoxontest).

The number of LHD phases and its total duration seemed to increase linearly with the duration of the lying phase (Figure 8 A and B show an example of a female adult Waterbuck), suggesting a certain regularity in the LHD structure with a roughly constant degree of LHD throughout the lying phase. Blue lines indicate censored regression lines where points are assumed to be censored at zero, as the number of LHD phases and the total time spent in LHD cannot be negative. Across all animals, no systematic differences in the intersection of the censored regression line (Figure 8 A) with the x-axis could be observed, indicating no systematic differences in the minimal lying duration that is required for LHD. The median minimal lying duration such that LHD was observed was 36.7 minutes. Noteably, the increase in LHD duration per lying duration (slope in Figure 8 A) showed no systematic age differences. Slopes tended to be higher in zebras (Figure 8 E) than in other species, suggesting a higher increase in LHD duration per lying duration. However, zebras showed more lying phases without LHD (Figure 8 F, $p < 0.1\%$, Wilcoxontest between adult zebras and adult individuals of the order Cetartiodactyla). No further systematic differences in the fraction of lying cycles with LHD could be observed as a function of sex or age.

Concerning the proportion of LHD during a lying phase, i.e. total LHD duration per phase divided by length of lying phase, we observed no systematic differences across species (Figure 8 C). However, the proportion LHD per lying phase tended to be larger in young animals (Figure 8 D, LHD fraction standardized per species, Kruskal-Wallis-Test $p < 0.1\%$ for all three age groups, $p < 1\%$ for young vs. subadult, and $p < 0.1\%$ for young vs. adult animals, subadult vs. adult not significant). In particular, adult individuals (across all species), spend 9.9% of a lying phase in the LHD position while this value is 19.4% for juvenile and 10.3% for subadult individuals.

4. DISCUSSION

4.1. **Summary.** In this contribution, rhythms in the nocturnal behavior of ungulates have been studied. Most of the analyzed species showed a significant increase in the proportion of lying during the second phase of a night, some species even showed a monotonous increase over the whole night. The duration of the LC was approximately Gaussian for most individuals, and differences in the mean duration were only visible with respect to species, not with respect to age or sex. The lying fraction LF varied between all age groups and was found to be greater in younger animals. In general, zebras showed a lower LF than Cetartiodactyla. No differences were found in the proportion of LC without LHD as a function of age or sex, but zebras had a lower proportion of such LC than the studied Cetartiodactyla. The minimum duration of a lying phase before LHD occurred did not vary systematically with age, sex or species. Although the fraction of LHD per LC was greater in young animals and the increase in time spent with LHD per lying phase was greater in Perissodactyla than in Cetartiodactyla, no species specific differences were found with respect to the proportion of a typical lying phase spent in LHD between adult individuals. More precisely, adult individuals spent, in

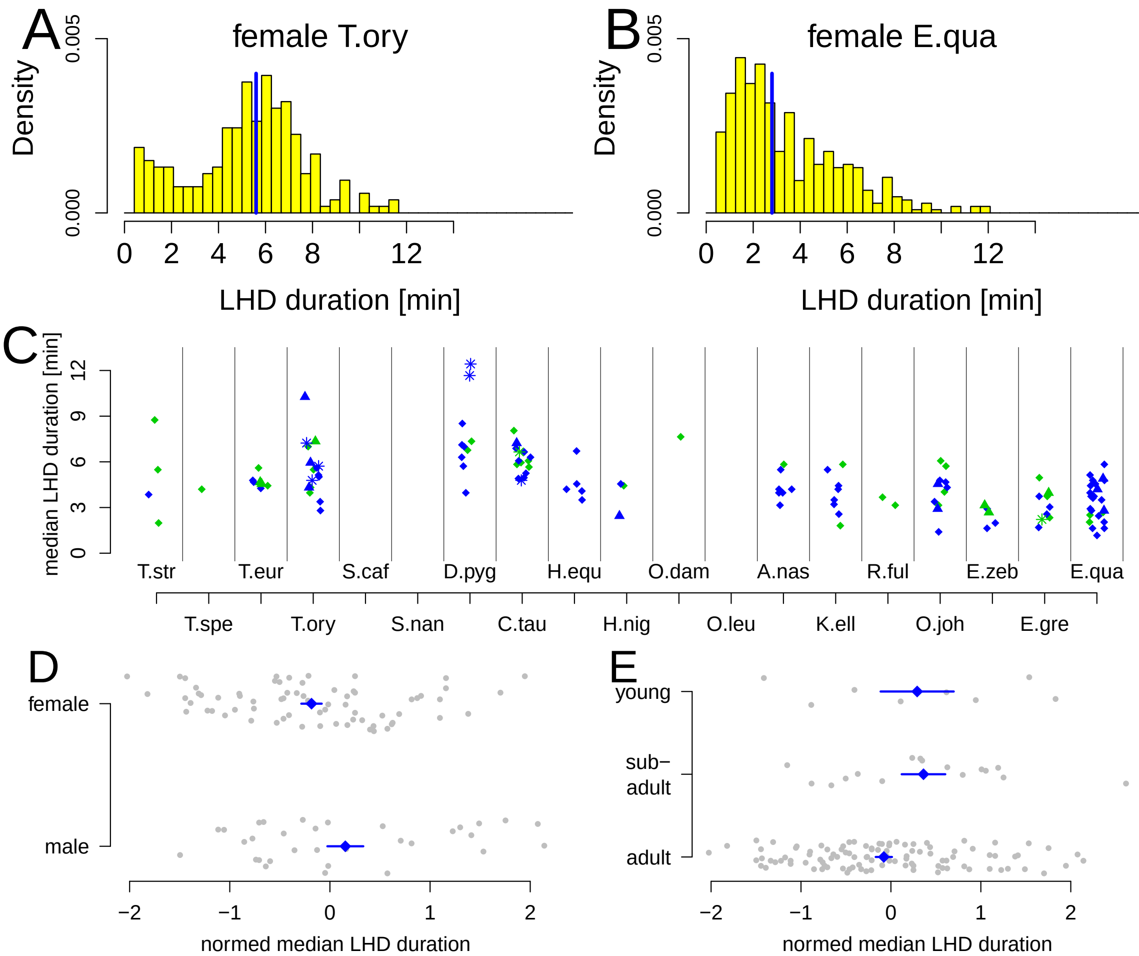

FIGURE 7. Duration of LHD during lying phase. (A and B) Examples of two distributions of LHD durations for a female T.ory (A) and a female E.qua (B). The distributions are non symmetric. (C) Median LHD duration as a function of the species. Point characters and colors as in Figure 4. (D) Species-standardized LHD duration as a function of sex. (E) Species-standardized LHD duration as a function of age group. Blue points and lines in (D) and (E) indicate mean and standard error, respectively.

the mean, 9.1% of a typical lying phase in LHD. Finally, the average median LHD duration ranged between 2.2 minutes in Mountain Zebras to about 7.6 minutes in Blesboks. Moreover, male individuals were found to have slightly longer LHD phases than females.

4.2. **Differences between sex and age groups.** We analyzed differences in the lying cycles, the lying fraction and the time spent in the REM sleep position (LHD) as a function of the age and sex of the individual, and graphically investigated species differences.

Differences between age groups were most prominent. In particular, younger animals showed a high proportion of extremely short lying cycles. The lying fraction, i.e., the proportion of lying in a lying cycle, of younger individuals was greater than the lying fraction of adult individuals. This is not surprising as previous studies have shown that activity/rest cycles may vary as a function of age (Ruckstuhl & Neuhaus, 2009; Siegel, 2005; Steinmeyer et al., 2010). In addition, the current data show that the time spent in the REM sleep position varied systematically with the age of the individual, i.e., young and subadult animals tended to spend more time in the REM sleep position during a typical lying phase than adult individuals. This extends the results of a previous study on the same dataset (Gübert et al., 2023), which already showed systematic differences of REM sleep for different age groups, while the total time per night spent

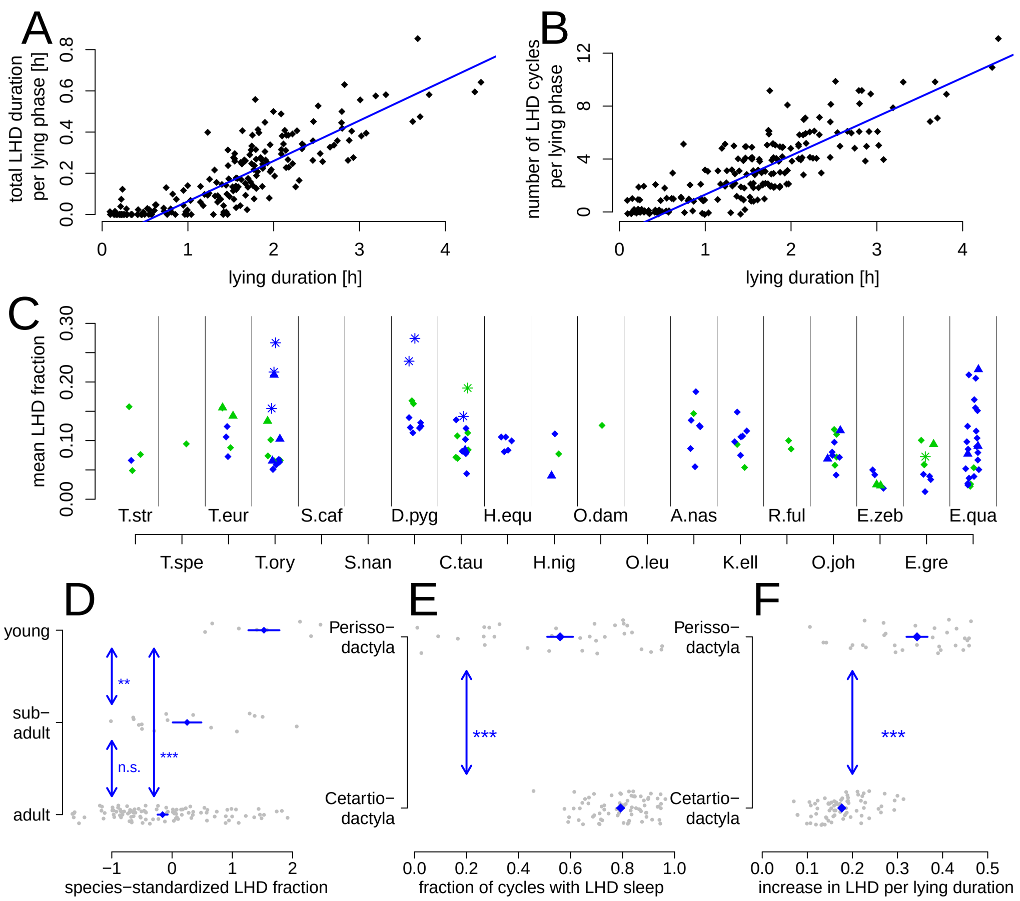

FIGURE 8. Relative duration of LHD during lying phase. (A) The LHD duration increases linearly with the length of the lying phase. Example of a female adult Waterbuck. Blue line indicates censored linear regression line, censored at zero because negative LHD durations cannot be observed. (B) The number of LHD cycles per lying cycle increases linearly with the length of the lying phase. Example of the same female adult Waterbuck. Blue line indicates censored regression line, censored at zero. (C) Mean LHD fraction (LHD duration divided by duration of lying phase) as a function of the species. Point characters and colors as in Figure 4. (D) Species-standardized LHD fraction as a function of age group. (E) Increase in LHD duration per Lying duration (slope of (A)) for Zebras and animals of other species (only adult animals). (F) Fraction of observed cycles with LHD sleep for Zebras and animals of other species (only adult animals). Stars indicate statistical significance on the 5% (*), 1% (**) and 0.1% (***)-level.

in LHD decreased with age. However, no significant age difference was found with respect to the median duration of a REM sleep phase. Nevertheless, in some species, our results suggest that younger animals actually have longer REM sleep phases (see Figure 7), but observations of more individuals would be necessary to verify this conjecture statistically. Finally, the fact that the REM sleep pattern of mammals and birds vary as a function of the age of the individual is also well known for various species (Cajochen et al., 2006; Rattenborg et al., 2017; Ruckstuhl & Kokko, 2002; Steinmeyer et al., 2010).

We could replicate sex specific differences in the median length of a phase spent in the REM sleep position, although these differences were statistically not significant in the present data set. However, similar to other reports, males tended to stay longer in this position. A case study on Common Eland behavior found small differences in the amount of time spent in the REM sleep position between males and females Gübert et al., 2022, and this difference was also found in studies of other mammals and birds Cajochen et al., 2006; Rattenborg et al., 2017; Steinmeyer et al., 2010. However, there are also studies indicating that sex differences occur only in dissimilar-sized species (Ruckstuhl & Kokko, 2002), or that do not consider sex as a possible influencing factor at all Tobler and Schwierin, 1996, or that do not find sex as a significant factor (Burger et al., 2021; Zhang, 2000). Finally, the previously mentioned study, which analyzed the most important factors regarding basic nocturnal behavior on this dataset, assigned a low importance to the sex of the individual (Gübert et al., 2023). It is important to mention that this study did not consider phase lengths which indicates that the very basic quantities (number of phases per night and the proportion of the shown behavior) do not vary as a function of sex, but phase lengths do. This is also supported by the fact that no significant sex differences with respect to the lying fraction were found in the current study.

Moreover, we observed several differences between the three zebra species as Perissodactyla and all other species as Cetartiodactyla. In particular, the Perissodactyla showed a much lower proportion of lying per lying cycle. This fits well with previous findings, e.g. a study on farm animals, that the total time spent lying is much lower in Equidae than in Bovidae (Ruckebusch, 1972), and also observed in the previous study on this dataset (Gübert et al., 2023). The reason behind this observation might be found in the different digestion types. Zebras, which are hind-gut fermenters, require a larger food intake than ruminants (Owen–Smith & Goodall, 2014). In particular, this leads to more foraging behavior. Ruminants, on the other hand, spend more time in a lying position because ruminating occurs often while resting (Janis, 1976). The current results extend the previous findings, as they do not only refer to the proportion spent with a specific behavior during night, but they show that the time spent lying is well distributed over the night. Furthermore, the increase in time spent in the REM sleep position per time spent lying is greater within the Perissodactyla, which, together with the overall lower lying fraction, suggests that they also have more periods of lying without being in the REM sleep position at all. Finally, the mean duration of an LHD phase in adult zebras tended to be smaller, ranging from 2.2 minutes in Mountain Zebras to about 7.6 minutes in Blesboks. These durations fit well with the literature. Lesser mouse-deers (*Tragulus kanchil*) were observed to spend 2.0 ± 0.2 min in the REM sleep position (Lyamin et al., 2021), adult Common Elands (*Tragelaphus oryx*) have a median REM duration of 4.4-4.6 min (Gübert et al., 2022), and male Arabian oryx (*Oryx leucoryx*) spend 7 ± 2 min in the REM sleep position in the dark in winter (Davimes et al., 2018). Moreover, the longest phases per night spent in the REM sleep position were observed to be 6.6 ± 4.0 minutes for horses (*Equus* sp.) (Pedersen et al., 2004) and the corresponding average phase length was found to be 3.9 minutes (Ruckebusch, 1972).

4.3. **Trends and Rhythms.** Despite all the differences discussed above, many similarities could be observed between all individuals, regardless of species, age, or sex. All individuals showed a consistent behavior during most nights, see Figure 3 for an example. Furthermore, there was an increase in the proportion of lying during the second half of a night found in all but three species. Similar observations have been made for some species such as Arabian Oryx (*Oryx leucoryx*), Common Elands (*Tragelaphus oryx*), Blue Wildebeests (*Connochaetes taurinus*) or African Elephants (*Loxodonta africana*), where inactivity increases during the night (Clauss et al., 2021; Davimes et al., 2018; Gravett et al., 2017; Gübert et al., 2022; Malungo et al., 2021). Okapi, Plains Zebra, Common Eland and Common Wildebeest also showed an increase in the first part of the night. Those species have in common that they are larger and more fortified than most other analyzed species. The three exceptions that did not show a significant increase in the second part of the night also have a visual increase until the last 1-2 hours. A possible explanation is that the behavior is just shifted by a few hours, and over a 24-hour cycle these species could fit well into one of the two clusters.

In addition, all species show a similar mean lying cycle duration of about 2.14 hours, i.e. typically an individual lies down every 2.14 hours. Lying cycle duration follows a Gaussian distribution for most individuals and is well concentrated. This implies that there is a high degree of rhythmicity in the nocturnal behavior of the studied ungulates. Deviations from this rhythmicity could therefore be a good indicator of reduced animal welfare, but further studies would be needed to examine the influence of disturbing events on this rhythmicity.

4.4. **Implications with regard to REM sleep.** One focus of the current study was to describe and analyze periods spent in the REM sleep position. We found the average length of such a period to range from 2.2 minutes (Mountain Zebra) to 7.6 minutes (Blesbok). This fits well into the sparse existing literature, as in general, ungulates spend only short periods of time in the REM sleep position (Davimes et al., 2018; Ruckebusch, 1972). It is to notice that REM sleep plays an important role in several physiological processes (Blumberg et al., 2020). Therefore, events that reduce the duration of REM sleep could have a negative impact on an animal's well-being (Mellman et al., 2002; Sicks, 2016; Siegel, 2001; Suchecki et al., 2012). Such events could be perturbations that reduce the duration of REM sleep in the long term, or stress events that have only a short impact. Field studies show that environmental conditions can strongly influence the timing of sleep. For example, seasonal variation affects REM sleep in free-ranging Arabian oryx (*Oryx leucoryx*) (Davimes et al., 2018). Also, extreme weather events prevent Giraffes (*Giraffa camelopardalis*) from lying down, which shortens the total duration of sleep (Burger et al., 2020). In addition, some studies suggest an influence of predation risk on the length and timing of REM sleep (Allison & Cicchetti, 1976; Lima et al., 2005). One reason may be that large terrestrial animals, such as many ungulates, must lie down during REM sleep due to loss of muscle tone, which increases their vulnerability to predation (Lima et al., 2005; Ternman et al., 2014). Our results suggest that a minimum amount of lying time is usually required for an animal to be in the REM sleep position at all, and that the time spent in the REM sleep position, as well as the number of such phases during a lying phase, increases linearly with the length of the lying event (see Figure 8). Therefore, it is natural to ask whether the aforementioned external factors may affect animals in such a way that they cannot lie down long enough to show REM sleep. Future comparative studies of zoo and wild animals could, for example, focus on whether the environment of zoos, without the risk of predation, is associated with changes in REM sleep patterns.

Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

JG: Conceptualization (lead); Data curation (lead); Formal analysis (supporting); Investigation; Methodology; Visualization (supporting); Writing – original draft (equal). **GS**: Data curation (supporting); Formal analysis (lead); Funding acquisition; Visualization (lead); Writing – original draft (equal). **MH**: Data curation (supporting); Formal analysis (supporting); Visualization (supporting); Writing – original draft (equal). **PD**: Conceptualization (supporting); Funding acquisition; Resources (lead); Supervision (lead); Writing – original draft (equal). All authors approved the submitted version.

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Data Availability Statement

The original contributions presented in the study are included in the article/supplementary files, further inquiries can be directed to the corresponding author/s.

SUPPLEMENTAL DATA

Ethogram. In this paragraph, the three behavioral poses standing, lying - head up, and lying - head down are defined. The ethogram was originally used by Gübert et al. (2023). Notice that lying - head down is the typical REM (rapid eye movement) sleep position. The REM sleep position can be used to estimate REM sleep (El Allali et al., 2022; Greening & McBride, 2022; Seeber et al., 2012; Ternman et al., 2014; Zizkova et al., 2013).

TABLE 1. Ethogram used in the study as defined by Gübert et al. (2023).

	Behavior	**Description**
Standing	Standing	The animal stands in an upright position. Other behaviors like feeding, resting, walking, or ruminating can occur simultaneously.
Lying	Lying - head up (LHU)	The animal is in a sternal recumbency with the trunk touching the ground. Its head is lifted.
	Lying - head down (LHD)	Cetartiodactyla: The animal is in a sternal recumbency with the trunk touching the ground (like in Lying - head up) but its head is resting on the ground. Perissodactyla: The animal is lying in a lateral recumbency.

Supplementary tables. Details of the dataset are given in *Supplementary Table.xlsx*, sheet *Overview*. For each observed individual, the corresponding species, age, and number of nights evaluated are reported. Moreover, The performance of the used deep learning-based software package is also given in *Supplementary Table.xlsx*, sheet *Performance BOVIDS*. The size of the test set per individual, the f_1-score for lying and LHD, the proportion of lying and LHD, and the median length of the standing, lying, and LHD phases are reported per individual. The proportion lying implies the proportion standing completely. In addition, the same supplementary file, contains the values to produce the contribution's figures. Sheet *LHD Regression* contains a summary of the x-axis intercept and regression coefficients for all individuals in the censored regression models (Figure 8). Sheet *LyingCycles* reports the data basis of Figures 4 – 6, and sheet *LHD Duration* reports the data basis of Figure 7.

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