RESEARCH ARTICLE

Biological and environmental factors as sources of variation in nocturnal behavior of giraffe

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Abstract

Upon a drastic decline of the giraffe population in the wild, conservation efforts and therefore the role of zoos have become more important than ever. With their unique opportunities, zoos provide excellent conditions to study animal behavior, expanding the knowledge about the giraffe's behavior repertoire and their ability to adapt. This study therefore examined the nocturnal behavior of 63 giraffe living in 13 different EAZA zoos across Germany and the Netherlands. Giraffe were observed and videos recorded via infrared sensitive cameras during the winter seasons 2015–2018. The observation period spanned nightly from 17:00 to 7:00. Thus, 198 nights, with a total of 2772 h were recorded and analyzed. Linear mixed models were then used to assess potential biological and environmental factors influencing behavior during the dark phase. Results show that individual variables such as age, subspecies and motherhood determined nocturnal activity and sleep behavior most. Among the variables studied, husbandry conditions and environmental factors complying with EAZA standards had no influence on the giraffe's nocturnal behavior. By combining nocturnal activity analyses and an assessment of potential influencing factors, our findings present a holistic approach to a better understanding of captive giraffe behavior and allow for management implications.

KEYWORDS
biological variables, giraffe behavior, housing conditions, nocturnal activity, sleep

1 | INTRODUCTION

Behavioral observation is a common tool in zoological research to provide important information on how zoo animals allocate their time, and to analyze implications for management issues and welfare. Hence, numerous behavioral studies have been conducted in zoos, most of them in mammals. Most studies focus on daily activity, while only a few concentrate on nocturnal behavior or even 24 h periods (giraffe: Baxter & Plowman, 2001; Duggan et al., 2016; Tobler & Schwierin, 1996; Veasey et al., 1996; African elephants: Rothwell et al., 2011; Schiffmann

et al., 2018; Wilson et al., 2006). While zoos provide good conditions for observing and collecting data on nocturnal behavior, greater difficulties arise in the field (e.g., lack of information regarding age, biography and social relationships of the observed animals, unpredictability of encountering animals, high costs, etc.). Nevertheless, there are initial studies that have taken up these challenges and are using state-of-the-art technology and innovative approaches to gain knowledge of the nocturnal behavior of wild large herbivores (e.g., Burger,Fennessy, et al., 2020; Davimes et al., 2018; Gravett et al., 2017; Pellew, 1984; Santymire et al., 2012). Among species, nocturnal activity budgets are

quite diverse. Especially the sleep behavior may vary tremendously (Campbell & Tobler, 1984; Favreau et al., 2009; Tobler, 1995). The distribution of activity and sleep over a 24 h cycle mainly depends on whether a species is mostly active during the day (diurnal) or night (nocturnal), during twilight (crepuscular) or during hours of daylight and darkness (cathemeral). While the majority of mammals are nocturnal, large herbivores mostly show diurnal activity patterns, with sleep mostly occurring during darkness (Bennie et al., 2014; Wu et al., 2018). According to the definition of Siegel (2009), sleep is a rapidly reversible state of reduced responsiveness, reduced motor activity and reduced metabolism. In mammals and birds this can be divided into rapid eye movement (REM) and non-REM states. While the definite function of sleep still remains unclear, some theories suggest that sleep keeps species from being active at inopportune times and that it is an energy saving state (Acerbi & Nunn, 2011; Capellini, Barton, et al., 2008; Capellini, Nunn, et al., 2008; Cirelli & Tononi, 2008; Fenn & MacDonald, 1995; Siegel, 2005). In particular, carnivorous and herbivorous mammals show different sleep behavior patterns. Herbivorous mammals sleep significantly less per day than carnivores, whereby in herbivorous mammals sleep time correlates inversely with body mass (Gonfalone & Jha, 2015; Siegel, 2005). Besides body mass, an animal's digestive physiology has a crucial impact on body posture (Pucora et al., 2019). Against this background, the sleep behavior of ruminants with their unique digestive system is of particular interest, since it is mainly characterized by short REM sleep phases. Typically, giraffe (*Giraffa camelopardalis*) show polyphasic sleep behaviors with various short sleep events which alternate cyclically with stages of foraging, moving and suckling events during the night (Burger, Hartig, et al., 2020; Razal et al., 2017; Saito et al., 2020; Sicks, 2012; Tobler & Schwierin, 1996; Zoelzer et al., 2020). These cyclical behavioral sequences settle in a 24 h rhythm, which is generated by endogenous biological clocks (Mistlberger & Rusak 2005). Circadian rhythms are normally synchronized by environmental stimuli, so called "zeitgebers" of which light is known to be the most powerful one (Aschoff, 1998; Mistlberger & Rusak, 2005; Reppert & Wearver, 2002). Other nonphotoic stimuli such as environmental conditions, food availability or social cues can also cause shifting in circadian rhythms in giraffe (Bashaw et al., 2001; Orban et al., 2016; Razal et al., 2017; Takagi et al., 2019).

Obviously, zoo-living animals have to face different challenges than their counterparts living in the wild. While zoo animals do not have to care about food or predators, they have to deal with limited space, social structures, and management time schedules (Price & Stoinski, 2007). To investigate the effect of social and environmental stimuli on nocturnal activity and sleep, zoos offer great opportunities by providing information about an animal's demographic background, social patterns, enclosure conditions, and management schedules (Hutchins et al., 2019; Watters et al., 2009).

Across phylogeny, there are *individual characteristics* which impact an animal's behavior. Several zoo studies on large herbivores reported an effect of age on activity and sleep, with older animals tending to be more active and sleep less than juveniles or subadults (Holdgate et al., 2016; Ruckstuhl & Neuhaus, 2009; Sicks, 2012; Tobler & Schwierin, 1996). In contrast, the data about impact of sex on nocturnal activity

patterns are equivocal (Ruckstuhl & Neuhaus, 2009; Santymire et al., 2012; Shannon et al., 2008; Sicks, 2012; Tobler & Schwierin, 1996). Correlations between subspecies and stereotypic behavior were reported for captive giraffe (Bashaw et al., 2001) and significant differences were found between African (*Loxodonta africana*) an Asian (*Elephas maximus*) elephants regarding the amount of recumbent rest as well as the factors affecting recumbence (Holdgate et al., 2016). Besides the immutable endogenous factors, various exogenous factors determine an animal's behavior. The *environmental conditions* under which an animal lives and their role in circadian rhythms are therefore of current interest (Croft et al., 2016; Wey et al., 2007). Favreau et al. (2009) summarized that the activity of social or family partners can affect an individual's activity rhythm. Circadian rhythm synchronization can be found in mother-offspring relationship in herbivores (Green, 1992; Pluhacek et al., 2010; Ralls et al., 1986), in social species living in a constraining environment (Bashaw, 2011), in hierarchical relationships (Correa et al., 2013; Horova et al., 2015; Thompson, 1993) as well as between competitors or sexual partners (Bercovitch et al., 2006; Curren et al., 2015; Favreau et al., 2009). Even if giraffe in the wild live in so called fission-fusion societies, they exhibit structured social patterns. Females choose with whom they stay (Carter, Seddon, et al., 2013; Carter, Brand, et al., 2013). Bashaw et al. (2007) and Horova et al. (2015) describe an adaptation to a herd structure in zoos where giraffe developed affiliative social bonds and dominance hierarchies. Furthermore, studies on African large herbivores showed a great variance in activity depending on season, temperature, habitat, vegetation, and food availability (Berger et al., 2003; Burger, Fennessy, et al., 2020; Deacon & Smit, 2017; Gravett et al., 2017). Understanding how various endogenous and exogenous factors affect the nocturnal activity and sleep behavior of captive giraffe was the aim of our research project.

Although giraffe are one of the most iconic animals in the world and kept in nearly every zoo, they are still a rarely studied species and their nocturnal behavior remains poorly understood. Since 2016, the giraffe has been assessed as vulnerable, with a decreasing trend in population size by the IUCN Red List of Threatened Species (Muller, Bercovitch, et al., 2018). This highlights the importance of successful management and conservation breeding in zoos. The purpose of this study is therefore to add a piece of knowledge about how giraffe allocate their time during the night and which factors may influence their behavior by assessing the influence of both individual and environmental conditions. This article presents a holistic observational behavioral study, analyzing the nocturnal activity budgets of 13 multi-aged groups of giraffe living in European zoos, with special focus on the variation in standing activities and REM sleep behavior between individuals and zoos.

2 | METHODS

2.1 | Ethics statement

This study was approved by the European Association of Zoos and Aquaria Giraffe EEP (EAZA Ex situ Program) and each participating zoo. To avoid possible disturbances from observers during the night,

we only videotaped giraffe behavior. This study was noninvasive as it was observational in nature and caused no undue harm to the giraffe.

2.2 | Behavior states

To analyze the nocturnal activity budget of giraffe, the overall observed behaviors were divided into five main behavior states, namely *feeding*, *walking*, *standing*, *lying*, and *REM sleep*. Behaviors occurring while the animal was on its four legs such as feeding, walking or standing were defined as *standing activities*. An animal resting on the ground was considered lying or in REM sleep position. A *feeding* animal was observed to be standing while browsing and ingesting concentrates or while drinking. A *standing* animal was recorded when the giraffe stood on its four legs without moving forward, in contrast to a *walking* giraffe which was observed when the animal was moving in one direction (Seeber et al., 2012). Rumination could be observed while a giraffe was walking, standing or lying. Nevertheless, continuous observation of rumination was not possible due to the quality of the video footage. The same applies to stereotypical behavior, which is why these behavior patterns were not included in the analyses. A *lying* animal was observed to be sitting on the ground with the abdomen or flank folded under and slightly displaced to the side, and the neck and head erect or slightly bent (Seeber et al., 2012). *REM sleep* was recorded when an animal lay on the ground, bent its neck backwards and rested the head on the flank/ground (Burger, Hartig, et al., 2020; Seeber et al., 2012; Sicks, 2012; Takagi et al., 2019; Tobler & Schwierin, 1996).

2.3 | Data collection and observation period

The study was carried out in 13 EAZA zoos in Germany and the Netherlands during winter seasons 2015–2018. Participating zoos were: Burger's-Zoo Arnhem, Cologne Zoo, Duisburg Zoo, Erlebniszoo Hannover, Frankfurt Zoo, Münster Zoo, Opel-Zoo Kronberg, Osnabrück Zoo, Schwerin Zoo, Tierpark Berlin, Tierpark Hagenbeck Hamburg, Tiergarten Nuremberg, and Zoom Erlebniswelt Gelsenkirchen. Behavioral data were collected from 63 giraffe (*Giraffa camelopardalis rothschildi* and *Giraffa camelopardalis reticulata*) of all ages from seven months to 29 years. To obtain information about the nocturnal behavior of giraffe, infrared-sensitive cameras (Mobotix AllRound Dual M15) were mounted at each stable to capture the whole enclosure. The recording period spanned 10–14 nights for each zoo. Thus, 198 nights, with a total of 2772 h, were recorded and analyzed. Observations were conducted by using an all-occurrence sampling for the five behavior states described previously (Martin & Bateson, 2007). Video data were analyzed with the software BORIS 2.1.5 (Friard & Gamba, 2016). To assess influencing factors on behavior, zoo curators and keepers completed a comprehensive questionnaire, answering questions about husbandry and management (e.g., demographic data and relationship, enclosure size and design, types of food and feeding routines, temperature regulation, and observed abnormal behavior patterns). In addition, keepers filled out

a detailed daily protocol to record the daily routine and special events. Using the provided information, the biological background of an animal was considered, including subspecies, sex, age, motherhood (a nursing cow), and use of contraceptives. Furthermore, the following environmental and social conditions were assessed: group size, the presence of a bull in a herd, the way animals were stalled during the night, material used for sleep sites, material of enclosure walls and enclosure size. During the whole observation time, food and water were available ad libitum, but the exact amount of food consumed was not evaluated. As we wanted to show comprehensive overall activity budgets of captive giraffe during night and twilight, total observation period nightly spanned 14 h, starting from 17:00 to 7:00. This time frame was also chosen to ensure for better comparison with existing behavioral studies on giraffe (Duggan et al., 2016; Sicks, 2012; Tobler & Schwierin, 1996). Due to housing conditions and the use of artificial light, the length of the dark phase varied between 9 and 14 h among zoos. To account for this great variance, the detailed analysis of influencing variables based solely on the dark phase of the night. For better distinguishability, the term *nocturnal* from now on defines the period of darkness while *nightly* covers the 14 h observation period.

2.4 | Preparation and analysis of the nocturnal data set

In this study, effects of potential factors influencing the giraffe's nocturnal activity were estimated with linear mixed models (e.g., Cleasby et al., 2015; Harrison et al., 2018). To fit the model, behavioral observation data was aggregated for each individual per night. First, univariate correlations between the dependent variables *standing activities* and *REM sleep* and various independent variables in zoo giraffe were analyzed. To avoid collinearity, we excluded the variables "*material of sleep sites*" and "*material of enclosure separation walls*" from analysis, due to high correlation with most of the other predictor variables. Afterwards, predictors were fitted into an Individual Characteristics Model (IC model) and an Environmental Conditions Model (EC model). Individual characteristics, such as age, sex, subspecies, motherhood, and contraception were unique for each giraffe and were combined in one model. Environmental and social influences such as enclosure size (m²), presence of a bull, group size and the way the animals were stalled (together or separately) were zoo dependent variables and fitted into a second model. Moreover, data on the type and amount of food was collected, but due to the great diversity of feeding management across zoos, it was not possible to categorize this information reasonably for model analyses. The presented two models were then fitted for both *standing activities* and *REM sleep* as responsible variables. In total, four models were used to analyze the effects of the presented explanatory variables on standing activities and REM sleep behavior. *Individual identity* (ID) and *zoo* were used as random factors. For better understanding, results will be presented in % per dark phase of the night. The estimate's mathematical unit is presented in % aggregated per individual and night. Null models and reduced models

were respectively fitted for standing activities and REM sleep behavior. Afterwards, likelihood ratio tests using the analysis of variance (ANOVA) function were done to identify whether the two random effects ID and zoo were significant. Finally, all predictors were combined in one model, and automatic backward elimination of nonsignificant random and fixed effects was used to determine the most parsimonious prediction models using all available explanatory variables. All analyses were conducted in R (version 3.6.0) using lmer function from the lmer4 package for mixed models (Bates et al., 2015). To overcome convergence problems occurring with some of the models, the BOBYQA optimizer (Bound Optimization BY Quadratic Approximation; Powell, 2009) was used to estimate the model parameters. Otherwise, default settings of the lmer function were applied.

3 | RESULTS

3.1 | Nightly activity budgets (17:00–7:00)

During the 14 h observation period standing activities correlated strongly negatively to light (Pearson r = −.514). Captive giraffe spent on average half of the 14 h observation period lying and in REM sleep position, whereas the other half was dominated by standing activities such as standing, walking and feeding. The detailed nightly activity budget per zoo is shown in Figure 1. Results show that the percentage of standing activities varies widely between zoos (30%–71%). Furthermore, results indicate great variance across zoos in terms of specific behavior states. Within standing activities, feeding varied between 19% and 39% and standing time spanned 6%–48%. Interestingly, giraffe walked with
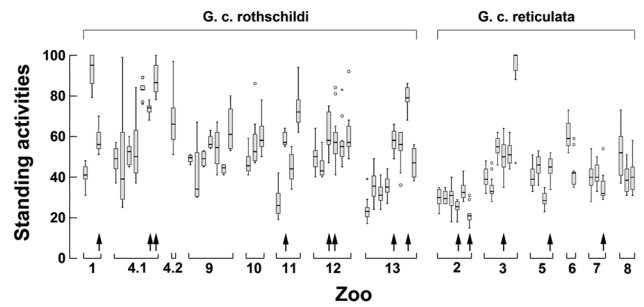

FIGURE 2 Individual variation in time spent on standing activities (%) depending on giraffe subspecies. Observation period spanned from 17:00 to 7:00. Individuals within one zoo are presented by ascending age. Nursing cows are marked by black arrows

1%–12% very little during the 14 h observation period. Giraffe were lying between 28% and 67% across zoos, while REM sleep only accounted for 1%–3%.

Moreover, results show a high interindividual variation across zoos and even within the same zoo (Figure 2). Results further reveal that activity budgets varied widely between the two observed subspecies Rothschild's giraffe and reticulated giraffe. The two subspecies thereby did not differ in age (Rothschild's 8.9 ± 6.7 years; reticulated giraffe 9.1 ± 7.0 years). Rothschild's giraffe spent more time on standing activities (58%) than reticulated giraffe (42%). Rothschild's giraffe spent 5% on walking, 25% on standing and only 41% on lying, whereas reticulated giraffe were observed walking 1%, standing 15%, and lying 56%. Interestingly, feeding and REM sleep behavior did no vary much between the two subspecies. Rothschild's giraffe spent 27% on feeding and 2% on REM sleep, while reticulated giraffe spent 26% on feeding and 2% on REM sleep.
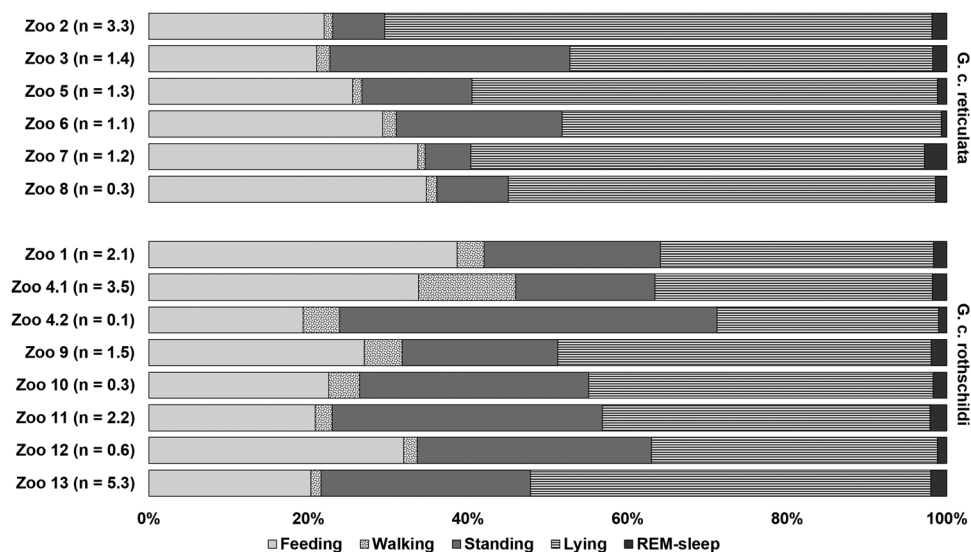

FIGURE 1 Nightly activity budget across zoos: Mean nightly activity budget per zoo from 17:00 to 7:00. Herd size per zoo is given on the left; first number indicates the number of males, second number the number of females. Upper block shows the zoos keeping reticulated giraffe; lower block shows Rothschild's giraffe. Zoo 4 is subdivided into two groups due to completely separated enclosures

TABLE 1 Linear mixed models of factors influencing nocturnal standing activities and REM sleep behavior in captive giraffe

Model	Estimate	Std. Error	df	t value	Pr (>| t |)
Standing Activities					
IC model					
Intercept	60.1452	8.3461	24.2990	7.206	1.77e−07***
Age	0.6538	0.2486	53.3249	2.630	**0.01113***
Sex	−2.5812	3.5778	56.0975	−0.721	0.47364
Motherhood	11.6389	4.0415	54.3636	2.880	**0.00568**
Contraception	−0.3065	4.1878	55.0077	−0.073	0.94192
Subspecies	−14.5752	3.9959	9.4538	−3.648	**0.00492**
EC model					
Intercept	60.8093	13.5313	11.1918	4.494	0.000872***
Age	0.6359	**0.2486**	**53.9406**	**2.558**	**0.013363***
Subspecies	12.4547	**6.4034**	**8.7978**	−2.683	**0.001510**
Motherhood	−17.1775	**3.7034**	**48.6026**	3.363	**0.025593***
Bull present	1.5014	7.0132	8.1082	0.214	0.835767
Stable (individually)	1.8716	4.9264	45.6071	0.380	0.705768
Stable (all together)	−7.0773	7.9424	31.6813	−0.891	0.379606
Group size	0.5947	0.9106	7.8953	0.653	0.532206
Enclosure size	−3.4951	1.7667	25.2545	−1.978	0.058902
REM sleep					
IC model					
Intercept	3.00105	0.51596	58.74475	5.816	2.63e−07***
Age	−0.06776	**0.01674**	**55.99191**	**−4.048**	**0.00016***
Sex	0.06070	0.25059	57.94381	0.242	0.80946
Motherhood	−0.69743	**0.28273**	**55.45998**	**−2.467**	**0.01675***
Contraception	−0.30120	0.28258	64.09569	−1.066	0.29048
Subspecies	−0.21704	0.21291	57.60093	−1.019	0.31228
EC model					
Intercept	3.13387	0.36859	15.38650	8.502	3.34e−07***
Age	−0.07197	**0.01685**	**48.41278**	**−4.272**	**9.02e−05***
Motherhood	−0.61128	0.27269	52.57134	−2.242	**0.0292***
Bull present	−0.37606	0.31550	9.11354	−1.192	0.2634
Stable (individually)	−0.29852	0.30676	27.87865	−0.973	0.3388
Stable (all together)	0.15968	0.42862	12.33669	0.373	0.7158
Group size	−0.01549	0.03697	6.31454	−0.419	0.6890
Enclosure size	0.10342	0.08444	5.87745	1.225	0.2675

Note: Codes to interpret the estimate: Age 1 month per interval; sex 0 = female, 1 = male; *motherhood/ contraception/bull present/stable* 0 = no, 1 = yes, subspecies 0 = Rothschild's giraffe, 1 = Reticulated giraffe; *group size one individual per interval; enclosure size* 1 m^2 per interval. Significant effects are marked with asterisks.

Abbreviations: EC, environmental conditions; IC, individual characteristics; REM, rapid eye movement.

*$p < .05$.
**$p < .01$.
***$p < .001$.

3.2 | Variation in standing activities and REM sleep between individuals and zoos during the dark phase

To characterize behavioral variation during the dark phase, we fitted two null models for standing activities and REM sleep with random effects. Each model analyzed 606 nights, 63 animals, and 13 zoos. For standing activities, the highest variability and the highest standard deviation was found for individuals (161.19 ± 12.696), while variability was considerably lower among zoos (60.33 ± 7.767). The null model for REM sleep showed higher variability among individuals (0.8242 ± 0.9078). Interestingly, almost no variability was found among zoos (0.0000 ± 0.000). We used ANOVA to determine whether the two random effects *ID* and *zoo* were significant or not. The model for standing activities was statistically significant both for ID

$\chi^2(1) = 283.65$, $p < .001$ and zoo $\chi^2(1) = 5.2903$, $p < .05$. The model for REM sleep was statistically significant for ID $\chi^2(1) = 108.37$, $p < .001$, but not for zoo $\chi^2(1) = 0$, $p > .05$.

3.3 | Sources of variation in standing activities and REM sleep

Factors showing a significant influence on the nocturnal standing activities were determined on an individual basis for each giraffe (Table 1). Age, subspecies, and motherhood significantly affected standing activities. Nocturnal standing activities increased with increasing age and motherhood (1 year older 0.7% more active and 11.6% more active as nursing cow). Giraffe of the two subspecies Rothschild's and reticulated giraffe differed significantly in their activity levels, Rothschild's giraffe spent 14.6% more time on standing activities than reticulated giraffe. In contrast, neither sex nor contraception had a significant influence, although male giraffe showed 2.6% less sanding activities than females. Due to the significant influence of age, subspecies and motherhood on standing activities, these three variables were included in the EC model. Similar to standing activities, REM sleep was significantly affected by the age of an individual, as REM sleep time decreased with increasing age (0.1% per year). Furthermore, a nursing mother slept significantly less (0.7%) than other giraffe of the same age. Neither sex, contraception nor subspecies showed a significant effect on REM sleep. As age and motherhood had significant influence on REM sleep, these two variables were included in the EC model. In contrast to our expectations, environmental conditions had no influence on the nocturnal behavior. This indicates that neither enclosure size nor group size had an influence on how active animals were. Social factors, such as the presence of a bull, or how animals were stabled during the night also did not show any impact on standing activities. Exclusively enclosure size slightly tended to be significant. Per 100 m² increasing enclosure size, standing activities decreased by 3.5%. For REM sleep behavior, none of the assessed environmental or social factors showed a significant influence.

3.4 | Backward reduced fixed-effect step model

The overall model, given by the backward reduced fixed-effect step model method, defined nocturnal standing activities of giraffe as a function of age, subspecies and motherhood (fixed effects) with ID and zoo as random effects: *standing activities ~age + motherhood + subspecies + (1 | ID) + (1 | zoo)*. REM sleep was defined as a function of age and motherhood: *REM sleep ~age + motherhood + (1 | ID)*.

4 | DISCUSSION

4.1 | Nightly activity from 17:00 to 7:00

This study comprehensively describes the nightly activity with special focus on REM sleep of captive giraffe. Our results present a nightly activity budget under "normal" conditions without any extraordinary events (e.g., transport, birth, and death) during the observation period. The results obtained are consistent with previous studies on activity budgets and REM sleep patterns (Sicks, 2012; Takagi et al., 2019; Tobler & Schwierin, 1996). Individuals may vary in behavior because of their different fundamental behaviors or their behavioral flexibility in different situations (Searle et al., 2010). Therefore, large-scale studies with a large number of animals and different husbandry conditions are necessary to gain general conclusions. For management reasons it would be helpful to understand why animals behave differently within the same environment, for example, in a zoo. This study found significant differences in activity budgets between all individuals and among all zoos. Even giraffe living in the same zoo showed significantly different activity budgets. Surprisingly, we found great variance in the activity budgets of Rothschild's and reticulated giraffe, although there was no age difference between the animals studied from the two subspecies. On average, Rothschild's giraffe spent more time on standing activities than reticulated giraffe while showing similar REM sleep behavior.

4.2 | Variation in standing activities and REM sleep behavior during the dark phase

The results of this study confirm our hypothesis that individual attributes determine behavior patterns most, with social and environmental factors having less impact. We determined a remarkable effect of age, motherhood and subspecies on nocturnal standing activities. Social cues and housing conditions did not show a crucial impact during the dark phase. We confirm that behavioral inter-zoo-variation derives from variation in ages of individuals and subspecies of individuals and is less influenced by social factors or enclosure conditions (Figure 3). Even though the analyzed environmental predictor variables did not show significant effects on giraffe's behavior under normal housing conditions, other studies have already shown that special situations clearly influence their behavior. For instance, transportation of a giraffe, changes in enclosure design, social group characteristics, or feeding regime resulted in different daily and nocturnal activity budgets (Duggan et al., 2016; Razal et al., 2017; Sasson-Yenor & Powell, 2019; Sicks, 2012; Tarou et al., 2000). An in-depth look at the actual nocturnal behavior during dark phase revealed that REM sleep differed between individuals but not among zoos. Regarding the influence of individual characteristics on REM sleep, we found that only age and motherhood were effective. REM sleep in general is a very sensitive behavioral state. Changes in social patterns, environmental conditions or health status are reported to provoke immediate changes in REM sleep patterns (Sicks, 2012; Siegel, 2011). Due to this high sensitivity to internal and external stimuli, observing this behavioral state can be a reliable method to draw conclusions regarding animal welfare. Behavior, defined as "movement, social interaction, cognition and learning" (Breed & Moore, 2016), is the constantly adjustment of an organism. This constant process of adaptation automatically leads to behavioral
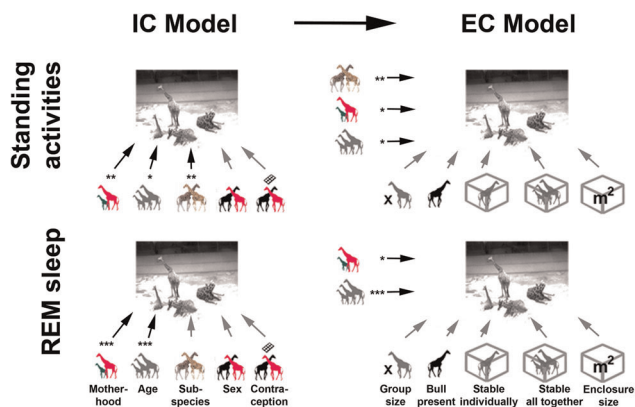
FIGURE 3 Stepwise evaluation of influencing factors on standing activities (upper series of illustrations) and REM sleep (lower series of illustrations) regarding the individual characteristics (IC model) and environmental conditions (EC model). Significant effects are marked with asterisks ($p < .001 = ***$, $p < .01 = **$, $p < .05 = *$) [Color figure can be viewed at wileyonlinelibrary.com]

variation over time. Findings of our study confirm that variation in behavior occurs within the same animal. These results underpin the need of covering an appropriate observation period. The "normal" range of behavior patterns therefore has to be defined individually for each animal with respect to its individual characteristics.

4.3 | Influence of individual characteristics

In this study, individual characteristics were found to be the variables affecting nightly activity budgets as well as nocturnal behavior most. These results are confirmed by several other studies on ruminants in which age, reproductive state and parenthood also show a strong influence on standing activities or REM sleep (Green, 1992; Mramba et al., 2017; Ruckstuhl & Neuhaus, 2009; Scheijen et al., 2020; Sicks, 2012). However, we could not confirm an influence of sex on both variables in giraffe. This contradicts other studies pointing out that sex dimorphism in ungulates is often accompanied by differences in activity budgets. These studies propose that sexual differences in activity budgets should be most pronounced in ruminants with sexual size dimorphism, less pronounced in hindgut fermenters and absent in monomorphic ungulates (Ruckstuhl, 1998; Ruckstuhl & Neuhaus, 2000; Yearsley & Pérez-Barbería, 2005). For instance, sexes of monomorphic African oryx (*Oryx gazella*) do not differ in their total time of active behavior (Ruckstuhl & Neuhaus, 2009), whereas dimorphic blue sheep (*Pseudois nayaur*) show different activity budgets between males and females (Liu et al., 2017). To keep zoo populations vital and genetically diverse, the administration of contraceptives may be necessary under certain circumstances. The effect of these contraceptives on the behavior of zoo animals, however, has been little researched to date. Our results could not find any influence on the nocturnal activity budget of giraffe. Since recent studies have shown that behavior of wild giraffe correlates with individual hormone levels and reproductive cycle (Scheijen

et al., 2020), this would also be of special interest for captive giraffe. To better understand this complex relationship between contraceptives and activity profile, a large-scale study that determines an animal's hormone level and links it to behavioral observations is needed. Our study showed that the nightly activity budget differed significantly depending on the subspecies. Recent multilocus analyses of giraffe subspecies have proposed that there are four genetically distinct clades, suggesting the existence of four separate species (Fennessy et al., 2016). According to these studies, Rothschild giraffe and reticulated giraffe belong to two different species that separated as genetic lines more than 0.5 million years ago (Bock et al., 2014). Although it has been shown that in captivity some giraffe subspecies hybridize (Gray, 1972), explicit gene flow analyses revealed less than one migrant per generation between the closely related Rothschild giraffe and the reticulated giraffe (Winter et al., 2018). This finding of limited gene flow may support our hypothesis that the basic activity levels at night may have developed differently in both genetic lines. In this context, different environmental conditions (e.g., vegetation type or predation pressure) could have been possible drivers in the past for this divergent development. Sleeping under a higher risk of predation affects the balance between activity and inactivity or REM sleep (Lima et al., 2005). Furthermore, our data showed that the percentages of feeding behavior and REM sleep did not differ between the two subspecies. Rather, the differences were based on the percentages in lying or standing and walking. This behavioral constancy of feeding and REM sleep may further indicate that these are essential behaviors and that neither subspecies nor environmental conditions lead to percentage changes in activity budgets of giraffe.

4.4 | Environmental conditions

According to the EAZA standards for the accommodation and care of animals in zoos and aquaria, member zoos are expected to provide a high standard of accommodation (including space, illumination, and social needs) for all the animals in their care (EAZA, 2014). Since these standards are constantly being reviewed and improved, the findings of this study provide important information on the influence of environmental and social conditions on nocturnal behavior. For interpreting the results of the present study, it is important to note that the collected data set only included zoos fulfilling EAZA standards.

The impact of social cues on behavior is a controversially discussed topic (Favreau et al., 2009; Greco et al., 2017). Our results did not show any significant influence of social conditions on standing activities or REM sleep behavior during the night. However, predetermined social group characteristics in stables can be important factors that should be considered in the analyses of behavior patterns of captive giraffe. Although wild giraffe live in social groups characterized by fission–fusion dynamics, they are organized in multiple social levels which are consistent to matrilineal-based societies (Carter, Brand, et al., 2013; Van der Waal et al., 2014). Zoo studies on giraffe confirmed such social structures. Females thereby showed social preferences regarding

which other females they prefer to associate with (Bashaw et al., 2007; Horova et al., 2015; Muller, Cantor, et al., 2018). Regarding Horova et al. (2015), formation of hierarchy could be a mechanism to prevent interindividual conflicts over limited resources. Variation in giraffe behavior was also observed after changes in group characteristics due to management reasons, transport, birth or death (Bashaw, 2011; Bercovitch, 2012; Sicks, 2012; Tarou et al., 2000). Therefore, future studies should concentrate on the relationships and the social backgrounds of giraffe kept together in one zoo.

All examined zoos fulfilled or exceeded the required EAZA management and husbandry standards for giraffe (EAZA, 2006). This is an important consideration when discussing the delicate topic of how enclosure size affects animal welfare. Our results show that giraffe behavior was not affected by zoo specific housing conditions. Interestingly, giraffe tended to show less standing activities with increasing enclosure size (3.5% per additional 100 m²). Own observations in the zoo as well as in the field lead to the assumption that giraffe provide a guarding system during resting phases (Burger, Fennessy, et al., 2020; Burger, Hartig, et al., 2020). At no time were all animals of an observed group seen sleeping at the same time. On the contrary, some group members were seen standing or feeding, while others rested nearby. The lying animals were in relatively close proximity to the waking animals. When the animals were close together, they usually positioned themselves in such a way that many sight lines were covered. If the animals were a little further apart, their gaze was always directed toward the more open area, while they often lay with their backs to single bushes or trees or fixed objects in the zoo. We could not find any correlation between enclosure size and the position of the individual animals during resting periods, but this would be an interesting approach for further research. In this context, Bashaw (2011) observed captive giraffe under two different management regimes to identify what aspects of their behavior are similar across zoos. The author stated that giraffe activity budgets are similar across zoos, confirming other results, where enclosure size correlated positively with ruminating behavior and locomotor activity (Veasey et al., 1996). Our results could not confirm these findings, as there was no impact of the independent variables enclosure size and group size on the dependent variables standing activities and REM sleep. Nevertheless, enclosure design and construction materials were reported to affect behavior in mammals, especially in primates (gorillas & chimpanzees), Malayan sun bears (*Helarctos malayanus*), tigers (*Panthera tigris*), African elephants (*Loxodonta africana*), and sitatunga (*Tragelaphus spekii*; Breton & Barrot, 2014; De Rouck et al., 2005; Greco et al., 2017; Rose & Robert, 2013; Ross et al., 2009; Tan et al., 2013; Valuska & Mench, 2013). In addition to the variables presented, the time of feeding and the quantity and quality of food are also likely to have an influence on giraffe's nocturnal activity budgets. Duggan et al. (2016) showed that different types and amounts of food provided lead to significant changes in time spent feeding per night. In addition, their study found a negative correlation between total feeding time and stereotypical behavior. Our results confirm a general variation in nocturnal feeding behavior, which can presumably be attributed to,

among other factors, different feeding regimes across zoos and individual food preferences. For future studies, it would be interesting to expand the present study to more zoos across countries and to include further predictor variables of enclosure conditions, such as, for example, temperature, humidity, or enclosure materials. In addition, future studies could record the distance between individual animals, and patterns of vigilance sharing (where animals preferentially sleep if another animal is standing), and focus on further social and environmental influences to validate our results and to optimize the future development of management programs and husbandry guidelines for zoos.

5 | CONCLUSION

Zoos provide great opportunities for studying and analyzing animal behavior patterns in relation to the animal's environment. While zoos are characterized by a profound knowledge of animal behavior and raising interesting research questions, they often do not have the man-power to process large-scaled studies on their own (Hutchins et al., 2019; Watters et al., 2009). For this study we cooperated with many zoos and were able to present detailed nightly activity budgets of captive giraffe. We showed that behavior patterns were not influenced by sex, contraception, enclosure size or social cues. Among the environmental factors examined in this study, light was the only one having a strong impact on standing activities. Individual variables likely affecting nocturnal behavior of captive giraffe were age, motherhood, and subspecies. Older and nursing individuals spent more time on standing activities. Similarly, Rothschild's giraffe spent more time on standing activities than reticulated giraffe. The results of our study thus indicate that when analyzing species-specific behavioral patterns and activity budgets, it is important to adequately consider individual differences.

CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author with permission from participating zoos. Data available on request due to privacy/ethical restrictions.

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