Resting postures in terrestrial mammalian herbivores

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For ruminants and arboreal herbivores (sloths and colobine monkeys), an influence of digestive physiology on resting postures has been postulated that is linked to the interplay of digestive anatomy and the gravity vector. To further explore this putative relationship, we observed 253 individual terrestrial mammalian herbivores at zoological gardens, noting 29,478 resting events in 36 species during the day and 7,383 resting events of 18 species at night, providing a catalogue of mammalian resting postures. We confirm the constraint of ruminants to sternal recumbency and expand this observation to camelids, which rely on a similar sorting mechanism in their forestomach for rumination, but which use lateral recumbency to a slight but distinctively larger proportion. Generally, larger herbivores rest more in a standing position, and use lateral recumbency more when lying. The use of lateral recumbency in large hindgut fermenters (perissodactyls, elephants) and nonruminant foregut fermenters (macropods, hippos) corresponds to the concept that there is no interplay between gravity and digestive physiology in these species. By contrast, peccaries, hyraxes, and hystricomorph rodents never used lateral recumbency. While this may be related to body size, body shape, or other species-specific characteristics, it also suggests that the interplay of gravity and digestive processes, in particular with the colonic separation mechanism in hystricomorph rodents, should be further investigated.

Key words: camelid, colonic separation mechanism, elephant, gravity, herbivore, recumbency, rest, ruminant, sleep

Resting behavior is considered important for physical recuperation, whether only by relaxation of the musculoskeletal system (wakeful rest) or also for the central nervous system (sleeping rest—Phillips 2002; Siegel 2005; Gonfalone and Jha 2015). Implications and associations of the duration of rest, in particular of sleep, have been investigated in ecological and evolutionary contexts (Capellini et al. 2008; Samson and Nunn 2015). Compared to the overall relevance of rest, the specific postures adopted by animals during rest have received less comprehensive attention. The positions that animals adopt for resting depend on a variety of factors. In terms of anatomical properties, a broad, barrel-shaped torso combined with short legs (as in hippopotamuses) may make a lateral lying position less likely than a sternal one; in contrast, a more keeled torso combined with long legs (as in macropods) may make a sternal position less likely than a lateral one. In equids, the peculiar patellar locking mechanism facilitates a relaxation of the antigravity musculature of one leg in a standing position (Hermanson and Macfadden 1996).

Environmental conditions that play a role comprise the shape of the substrate (branches for arboreal animals versus flat surfaces for terrestrial animals), the incline of the substrate (flat versus sloped—McGlone and Morrow-Tesch 1990), or the nature of the substrate (soft and malleable versus hard—Haley et al. 2000; Greening et al. 2013). Both the available space as well as environmental temperatures will determine whether and how often standing, more spacious and more surface-exposing lying postures like lateral lying, or more compact postures like sternal recumbency will be adopted (Russell 1971; Duncan 1985; Hänninen et al. 2003; Raabymagle and Ladewig 2006; Terrien et al. 2011). In terms of social behavior, animals that seek physical contact during resting may adopt more compact resting postures than animals that rest without physical contact to conspecifics (Sale 1970; Sowls 1974). Moreover, animals may choose their resting position depending on their physical status. For example, individuals that are less mobile may avoid lying rest, presumably due to the difficulty of getting up again, or due to discomfort in the case of late-term pregnancy (Coomer and Fouché 2010; Schiffmann et al. 2018a). The same may apply for perceived safety status, when animals avoid lying rest as compared to standing rest, or lateral lying as compared to sternal recumbency, to retain a better view over their

surroundings and a better chance to escape or defend themselves immediately (Schiffmann et al. 2018a). Correspondingly, species at a higher risk of predation may have less recumbent rest (Lesku et al. 2006), and domestic animals may show a resting behavior less tuned to predator avoidance than their nondomesticated counterparts (Stodart and Myers 1964).

In herbivores, the anatomy and physiology of the digestive system may represent an additional factor that influences the range of postural options during resting. Mammalian herbivores typically rely on microbial fermentation of plant cell walls, which requires a voluminous compartment in the digestive tract to harbor the microbiota (Stevens and Hume 1998). Mammalian herbivores can be categorized as foregut and hindgut fermenters, depending on whether the fermentation chamber is located prior to the glandular stomach (in foregut fermenters such as ruminants, camelids, hippos, peccaries, colobine monkeys, sloths, macropods) or after the small intestine (in hindgut fermenters such as perissodactyls, lagomorphs, rodents, many primates, elephants—Müller et al. 2013; Langer and Clauss 2018). Foregut systems with an additional sorting mechanism facilitate the strategy of rumination, common to ruminants and camelids, where mainly large particles are submitted to repeated mastication (Lechner-Doll et al. 1991). Hindgut systems with an additional sorting mechanism (the "colonic separation mechanism") facilitate the strategy of cecotrophy, where microbial protein is sequestered in a certain kind of feces (cecotrophs) that are reingested at defecation (Björnhag 1987).

In theory, the position of the fermentation chamber, and the presence of a sorting mechanism, may determine whether digestive physiology affects resting behavior. Such an effect would be expected to be linked to the gravity vector. For example, arboreal foregut fermenters (sloths and colobine monkeys) apparently prefer a sitting resting posture, which may be related to the eructation of fermentation gases (Clauss 2004; Matsuda et al. 2017). In ruminants and camelids, the sorting mechanism in the forestomach uses the functional density of digesta particles as the main discrimination criterion in a flotation-sedimentation system (Baumont and Deswysen 1991; Lechner-Doll et al. 1991) that is dependent on gravity. Therefore, ruminants are theoretically limited to a sternal resting position in order to maintain a constant positioning of their forestomach anatomy with respect to the gravity vector (Balch 1955). Whereas newborn ruminants, in which the forestomach is not fully developed yet and which mainly ingest milk, may also rest in lateral recumbency, sternal recumbency soon becomes the only quantitatively important lying resting position with the onset of rumination (Jarman 1977; Pucora and Clauss 2018). A similar difference in the use of lateral and sternal recumbency has been reported in lying rest in camelids (Khan et al. 1998). By contrast, regardless of an increase in the rest spent standing with age, no similar change in lying rest from a lateral to a sternal position is evident in horses over ontogeny (Boy and Duncan 1979).

Due to the similarity of the forestomach sorting mechanism between camelids and ruminants (Lechner-Doll et al. 1991; Dittmann et al. 2015), similar constraints as in ruminants

should apply to camelids. In nonruminant foregut fermenters, even though regurgitation and remastication of digesta has been reported in some species (reviewed in Matsuda et al. 2011; Vendl et al. 2017), there is no evidence for a sorting mechanism (Clauss et al. 2004; Schwarm et al. 2008, 2009, 2013; Munn et al. 2012; Matsuda et al. 2015), and therefore, no constraint on resting positions due to this reason is expected.

Whether the colonic separation mechanism of coprophagic hindgut fermenters also depends on a specific gravity vector has not been investigated. In rodents and lagomorphs, three morphologically different types of colonic separation mechanisms have been described: a "wash-back mechanism" in lagomorphs, and two different "mucus-trap" mechanisms in hystricomorph and myomorph rodents (Hume and Sakaguchi 1991; Björnhag and Snipes 1999; Hagen et al. 2018). Whereas the morphological structures of the lagomorph and myomorph colonic separation mechanism occur on all sides of the colon (and hence cannot require a particular positioning in relation to gravity), the characteristic groove that facilitates the colonic separation mechanism in hystricomorph rodents (Snipes et al. 1988) only occurs on the colon's mesenteric side. The hystricomorph colonic separation mechanism could therefore theoretically be affected by the gravity vector. Recent findings of differential particle marker retention in a large hystricomorph rodent, the capybara (*Hydrochoerus hydrochaeris*), where the putatively denser marker was retained less intensively than putatively less dense markers (Kiani et al. 2019), further support that hypothesis.

The aim of the present study was to characterize the postural resting behavior of mammalian herbivores to test whether the predicted differences between ruminant foregut fermenters and nonruminant herbivores can be demonstrated, and to explore whether hystricomorph rodents show a preference for a resting posture that maintains a constant position of the digestive tract to the gravity vector.

MATERIALS AND METHODS

Animals.—No animals were directly handled during the course of this study; only observations of animals in their usual surroundings were performed without modifying these environments. A total of 253 individuals of 38 mammalian species were observed in four zoos across Switzerland and Germany between July 2015 and April 2016; for 18 species, observations were available for daytime and nighttime behaviors. Observations were limited to healthy adult individuals of either sex. Animals were housed in their usual zoo enclosures. During the night, only three of the five common hippos (*Hippopotamus amphibius*) included in the study had access to a water pool. Feeding occurred several times per day in accordance with the specific dietary regimen determined by the respective zoos for each species. Animals were categorized into four digestion types: nonruminant foregut fermenters (NRFF), ruminant foregut fermenters (RFF), non-coprophageous hindgut fermenters (NCHF), and coprophageous hindgut fermenters (CHF).

Observations.—Daytime observations were made during the operating hours of the zoos at three distinct time points: morning

(0900 to 1000–1100 h), early afternoon (1200 to 1300–1400 h), and late afternoon (1500 to 1600–1700 h). Observations involved walking between animal enclosures and performing instantaneous scan sampling, noting the resting positions of individuals; for each time point, a minimum of 10 observations per species were taken at a minimum time interval of 5 min. Nighttime observations were made using infrared cameras (ABUS TVCC60030, Wetter, Germany; Visortech PX-1159-919, Germany) mounted in an unobtrusive location and portable monitors and recorders (ABUS TVVR20000, Wetter, Germany; Visortech PX-1207-919, Pearl GmbH, Buggingen, Germany; Olympus OEV143, Tokyo, Japan). Cameras were set to begin recording at 2200 h and finish recording at 0500 h. Video footage was later analyzed for resting behavior using the same sampling interval rate as required for the respective species during the daytime, ranging between every 5 and 13 min, for the entire duration of the video.

The calculated number of observations per individual was variable because not all individuals could be observed at all times. This generally occurred more often during camera nighttime observations if animals moved out of the cameras' range.

The following resting positions were recorded: standing rest, lying rest in sternal recumbency, lying rest in lateral recumbency, lying rest in dorsal recumbency, sitting rest (see Supplementary Data SD1, Table S1 for more detailed definitions). Rumination was the only activity that did not preclude the classification of a posture as resting, following Belovsky and Slade (1986). Unfortunately, it was not recorded whether rumination occurred or not. Dorsal recumbency was only observed very sporadically in two macropod species and was not included in analyses. Individual data were averaged per species (Supplementary Data SD1, Table S2). Results are presented as a proportion of total time spent in rest, in nonstanding rest, in lying rest (excluding sitting), and in lateral recumbency (excluding sternal recumbency).

Statistical analyses.—Comparisons between daytime and nighttime activity were only completed for NCHF ($n = 10$). Paired samples were less than $n = 6$ and thus insufficient for nonparametric tests of NRFF ($n = 1$), RFF ($n = 3$), and CHF ($n = 4$).

Differences in resting positions between digestive types were analyzed with nonparametric means using a general linear model (GLM) on ranked data as in many cases, the data violated the assumption of equal variance. Digestion type (following Müller et al. 2013) entered the model as a fixed factor, and (ranked) body mass (taken from Jones et al. 2009) was included as a covariable. Sidak's test on estimated marginal means was used to compare digestion types post hoc. All analyses were performed using SPSS 25.0 (IBM, New York, New York). The significance level was set to 0.05.

RESULTS

Species-specific data on resting positions are presented in Supplementary Data SD1, Table S2. In total, 29,478 individual resting observations were made during the day, and 7,387 at night.

Among the NRFF, macropods were never observed in sternal but always in lateral recumbency. In contrast, peccaries never lay on their side, whereas hippos used lateral recumbency sporadically, but not more than sternal recumbency. Haphazardly, hippos used a sitting posture. *Macropus giganteus* was the only species in which dorsal recumbency was observed at a relevant proportion (0.01 of all rest). Among RFF, lateral recumbency was never observed in any ruminant, but haphazardly in three of the four camelid species.

Among NCHF, elephants and some equid species were never observed to lie down during the day. The only species that used, when lying, lateral recumbency more often than sternal recumbency were the elephants. Equids were never observed to use lateral recumbency during the day; in contrast, tapirs and rhinos did. At night, all perissodactyls used lateral recumbency to some extent. Among the NCHF, only hyraxes and warthogs (*Phacochoerus africanus*) ever rested in a sitting posture. Sitting was observed in all but one CHF species (hystricomorph rodents). CHF species were observed only very sporadically in lateral recumbency.

Day versus night.—Analysis of standing and lying as a proportion of total resting between day and night found a significant difference between the amount of standing rest (and hence also lying rest) when comparing all 18 species ($P = 0.001$). Within digestion types, this difference was significant in NCHF ($P = 0.005$), which spent more rest in a lying position at night. In the single NRFF species (hippopotamus) as well as in the three RFF species (all camelids), a similar difference appeared to exist, but not in CHF (Fig. 1A). Comparing the time spent in sternal or lateral recumbency (in proportion of total lying time), there was again a significant difference when comparing all 18 species ($P = 0.003$), with a significant difference in NCHF ($P = 0.008$), which spent a higher proportion of lying rest in lateral recumbency at night. Again, a similar difference appeared to exist in the single NRFF species. In contrast, the preference for sternal recumbency in RFF and CHF did not appear to change between day and night (Fig. 1B).

Body mass and digestion types.—Body mass had an effect on the proportion of resting time spent standing (with larger species spending more time in standing rest; Fig. 2A), and on the time spent sitting (with smaller species spending more time sitting), during the day but not at night (Table 1). Yet, even with including body mass in the model, differences between digestion types were also significant, with NRFF and NCHF spending significantly more rest standing than CHF during the day (Fig. 2B). Additionally, RFF (and during the day, also CHF) spent significantly more rest in sternal recumbency than NCHF (Table 1). Among the NCHF, elephants and equids used lying rest to a much lower proportion than tapirs and rhinos, both during the day and at night (Fig. 2A).

Considering only nonstanding rest, body mass only had a significant effect on the proportion of the rest spent sitting during the day, and on the rest spent in sternal and lateral recumbency at night (Table 2). During the day, RFF rested more in sternal recumbency than NCHF; at night, they rested more in sternal recumbency than CHF (Table 2). Considering only lying rest
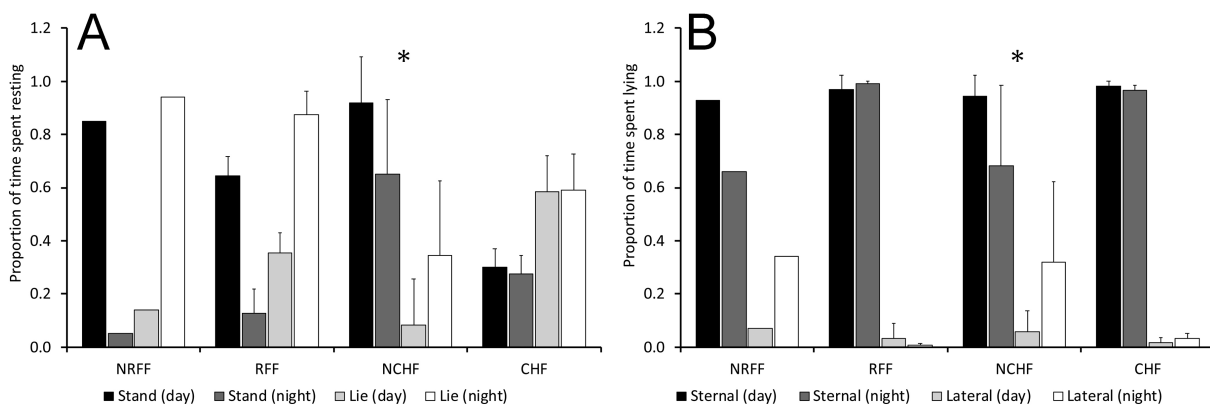
Fig. 1.—Comparison of resting positions during the day and the night in 18 species of mammalian herbivores of four digestion types (nonruminant foregut fermenters—NRFF, $n = 1$; ruminant foregut fermenters—RFF, $n = 3$; non-coprophageous hindgut fermenters—NCHF, $n = 10$; coprophageous hindgut fermenters—CHF, $n = 4$; species means ± SD). (A) Difference between standing and lying rest, (B) difference between lying rest in sternal or lateral recumbency. Note that for NRFF, only one species (*Hippopotamus amphibius*) was observed during both day and night. The asterisk indicates significant differences between day and night in NCHF.
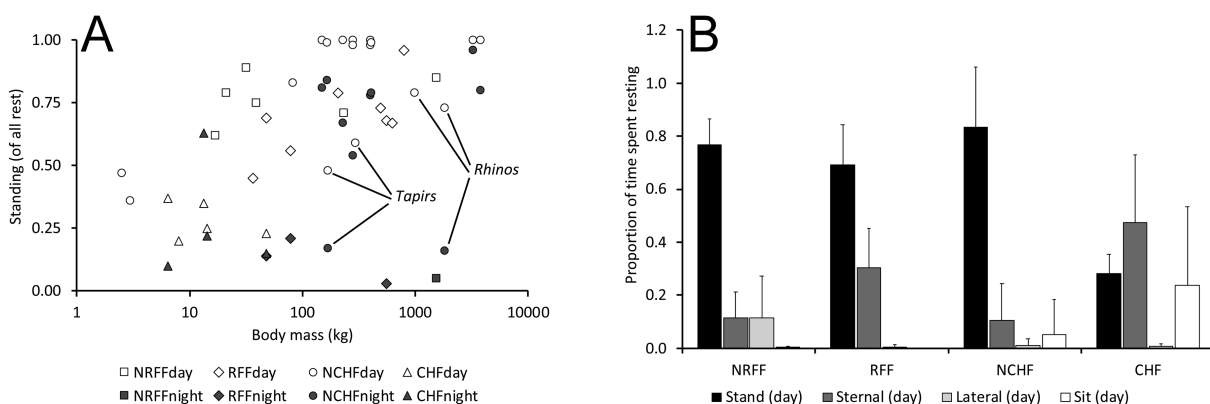
Fig. 2.—(A) Relationship between body mass (on a log-scale) and the proportion of rest spent in a standing position at day and night, and (B) the proportion of time spent resting in a standing, sternal recumbent, lateral recumbent, and sitting posture during the day in mammalian herbivores of four digestion types (nonruminant foregut fermenters—NRFF, $n = 6$ during the day and 1 at night; ruminant foregut fermenters—RFF, $n = 8$ day, 3 night; non-coprophageous hindgut fermenters—NCHF, $n = 17$ day, 10 night; coprophageous hindgut fermenters—CHF, $n = 5$ day, 4 night; species means ± SD). Note in NCHF, tapirs and rhinoceroses spent more time nonstanding than equids and elephants.

(i.e., excluding sitting), body mass again had a significant effect at night, with larger species using more lateral recumbency (Fig. 3); macropods were outliers, because they were never classified as resting in sternal recumbency. Apparent differences between digestion types for the lying posture (Fig. 1B) were neither significant during the day nor at night (Table 2), even though RFF nearly exclusively used sternal recumbency. Note that those equids species that did lie down during the day, and could therefore be compared in their lying posture with RFF, did so in sternal recumbency, and observations at night, when equids did lie in lateral recumbency, included only three RFF species.

Generally, there was no evident lateral lying preference in the data set, except for both hippo species that only lay on their right side during the day (but not during the night), and for all CHF that, if they did rest in lying during the day, did so on their left side (but not during the night). This led to a significant effect of digestion type on the daytime (but not the nighttime) data (Table 2). These patterns are most likely the effect of the

very sparse occurrence of lateral lying rest (Figs. 1B and 2B); side bias was mostly present in species that were observed very rarely in lying rest, and side use became more balanced as the observations of lying rest increased (Fig. 4).

DISCUSSION

This study presents data on the use of different resting positions by a variety of captive mammalian herbivores. The results corroborate the preference of ruminants for sternal recumbency that has been linked to the interplay of their digestive anatomy and physiology with the gravity vector, and expands this concept to camelids, which are also functional ruminants. By contrast, both nonruminant foregut fermenters and large hindgut fermenters appear less constrained in the choice of their resting posture, choosing lateral recumbency more often, albeit with species-specific differences. Small hindgut fermenters, represented exclusively by hystricomorph rodents in the present study, showed a clear preference for sternal over lateral

Table 1.—Effects of digestion type (nonruminant foregut fermenters—NRFF; ruminant foregut fermenters—RFF; non-coprophageous hindgut fermenters—NCHF; coprophageous hindgut fermenters—CHF) and body mass on the proportion of resting time spent standing, in sternal recumbency, lateral recumbency, and sitting, in the standing-inclusion model (tests performed on ranked data).

Position		F-statistic	$d.f.$	P-value	Post hoc comparisons[a]
Daytime observations					
Standing	Digestion	5.197	4,30	0.003	NRFF, NCHF > CHF
	Body mass	12.184	1,30	0.002	
Sternal	Digestion	5.793	4,30	0.001	CHF > NRFF
	Body mass	0.579	1,30	0.453	RFF, CHF > NCHF
Lateral	Digestion	2.214	4,30	0.091	
	Body mass	1.098	1,30	0.303	
Sitting	Digestion	1.456	4,30	0.240	
	Body mass	7.116	1,30	0.012	
Nighttime observations					
Standing	Digestion	5.072	3,13	0.015	
	Body mass	0.176	1,13	0.681	
Sternal	Digestion	7.594	3,13	0.003	RFF > NCHF
	Body mass	0.496	1,13	0.494	
Lateral	Digestion	2.312	3,13	0.124	
	Body mass	1.101	1,13	0.313	
Sitting	Digestion	2.597	3,13	0.097	
	Body mass	0.104	1,13	0.753	

[a]Only significant results are displayed.

Table 2.—Effects of digestion type (nonruminant foregut fermenters—NRFF; ruminant foregut fermenters—RFF; non-coprophageous hindgut fermenters—NCHF; coprophageous hindgut fermenters—CHF) and body mass on the proportion of resting time spent in sternal recumbency, lateral recumbency, and sitting, in the standing-exclusion model, on the proportion of lying time spent in sternal or lateral recumbency, and on the proportion of lateral recumbency spent on the left or right side (tests performed on ranked data).

Position		F-statistic	$d.f.$	P-value	Post hoc comparisons[a]
Nonstanding rest					
Daytime observations					
Sternal	Digestion	2.857	4,30	0.041	RFF > NCHF
	Body mass	0.240	1,30	0.628	
Lateral	Digestion	2.815	4,30	0.043	
	Body mass	0.013	1,30	0.909	
Sitting	Digestion	1.243	4,30	0.314	
	Body mass	5.184	1,30	0.030	
Nighttime observations					
Sternal	Digestion	3.817	4,30	0.037	RFF > CHF
	Body mass	8.214	1,30	0.013	
Lateral	Digestion	3.629	3,13	0.042	
	Body mass	7.665	1,13	0.016	
Sitting	Digestion	2.597	3,13	0.097	
	Body mass	0.104	1,13	0.753	
Lying rest[b]					
Daytime observations					
Sternal	Digestion	2.230	4,24	0.096	
	Body mass	0.031	1,24	0.862	
Nighttime observations					
Sternal	Digestion	3.205	3,13	0.059	
	Body mass	6.825	1,13	0.021	
Lateral lying rest[b]					
Daytime observations					
Left	Digestion	4.654	4,7	0.038	
	Body mass	5.224	1,7	0.056	
Nighttime observations					
Left	Digestion	0.712	3,10	0.567	
	Body mass	2.775	1,10	0.127	

[a]Only significant results are displayed.
[b]Only results for sternal recumbency and left side lying are displayed, as lateral recumbency and right side lying represent their reciprocal values.

recumbency; a lack of similar-sized herbivores with a different resting posture pattern does not allow conclusions whether this is due to body size or other biological characteristics.

Study constraints and representativeness.—An important constraint of the present study, in spite of the large number of individual resting observations, is the sole focus on resting postures, with data acquisition not allowing the determination of daily activity budgets. Therefore, the data have a qualitative character, indicating a preferred resting posture, but not how much time is actually spent resting. With respect to the digestive strategy of rumination, it therefore cannot be evaluated whether ruminants rest more (using a part of their resting time
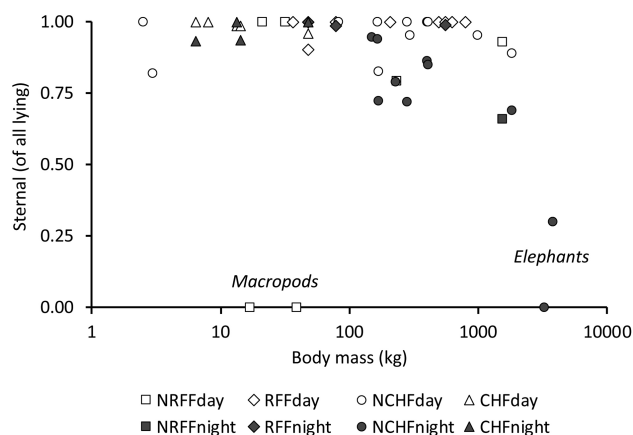
Fig. 3.—Relationship between body mass (on a log-scale) and the proportion of sternal recumbency of all lying rest during the day and at night in mammalian herbivores of four digestion types (nonruminant foregut fermenters—NRFF; ruminant foregut fermenters—RFF; non-coprophageous hindgut fermenters—NCHF; coprophageous hindgut fermenters—CHF). Note that macropods appear as outliers with no sternal recumbency.
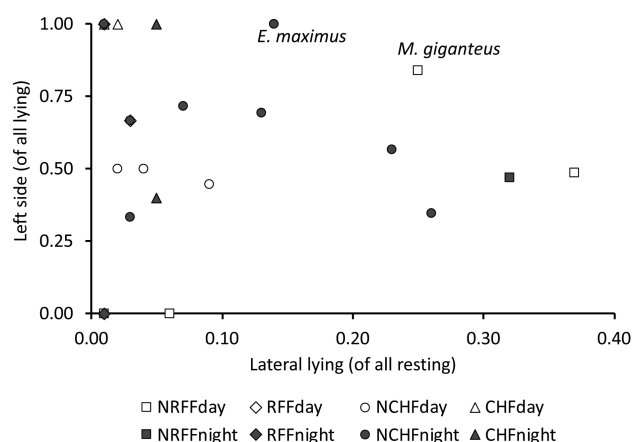

Fig. 4.—Relationship between the proportion of lateral rest (of all rest) and the proportion of this rest spent on the left body side during the day and the night in 36 species of mammalian herbivores of four digestion types (nonruminant foregut fermenters—NRFF; ruminant foregut fermenters—RFF; non-coprophageous hindgut fermenters—NCHF; coprophageous hindgut fermenters—CHF; species means). Note that extreme values for lying on the left or right side are related to a low frequency of lateral recumbency and hence most likely a spurious finding.

actively, i.e., ruminating) than other herbivores. The laterality of sternal recumbency (i.e., whether the torso is perfectly vertical, or slightly tilted toward the left or right, with legs protruding to the one or other side), a state important in ruminants that tend to prefer sternal recumbency on their left side when ruminating (Balch 1955; Grant et al. 1990), was not recorded. Additionally, data were not recorded for specific individuals, so that laterality could not be assessed on an individual basis. For further studies, particular attention should be directed at choosing species not only for their digestive strategy, but for their body shape characteristics, such as limb and neck proportions and torso shape, and at recording a variety of additional information on the specific environment, such as temperature and substrate.

An evident second constraint of the present study is the reliance on captive animals, which were exposed to various, unrecorded degrees of visitor exposure during the daytime. The provision of food, the food's high digestibility, and the protection from predators have been suggested repeatedly as reasons why animals are less active in captivity, possibly resulting in different activity, resting, and sleeping patterns (e.g., in giraffes, *Giraffa camelopardalis*—Veasey et al. 1996; in sloths, *Bradypus variegatus*—Rattenborg et al. 2008). Differing conditions across zoos will also affect the resting behavior (Veasey et al. 1996). To what extent the postures adopted during rest are affected by this cannot be assessed in the present study.

Nevertheless, there are indications that the data collected in the present study are representative for the species in question. Data from a pilot study performed in 2011, which only recorded whether animals used sternal or lateral recumbency when lying down, yielded similar results to the present study (Fig. 5), with the macropod species using only lateral recumbency, the
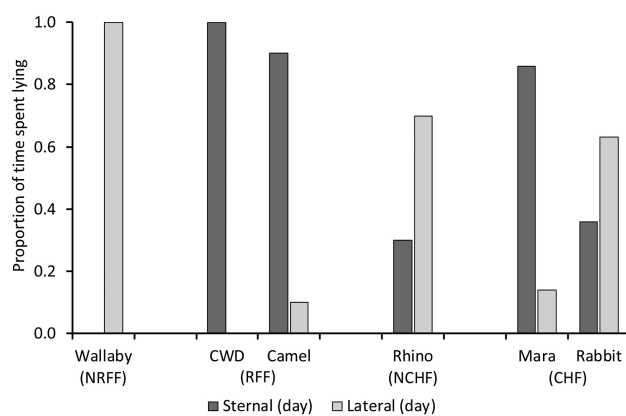
Fig. 5.—Proportion of sternal and lateral recumbency (of total time observed lying) in six herbivore species (groups of free-ranging Bennet's wallaby [*Macropus rufogriseus*], Chinese water deer [*Hydropotes inermis*], and mara [*Dolichotis patagonum*]; n = 5 Bactrian camels [*Camelus bactrianus*], n = 5 white rhinoceros [*Ceratotherium simum*], observed for 10 consecutive days once every early morning and every early afternoon at a zoological collection; n = 7 domestic rabbits [*Oryctolagus cuniculus*], observed for 10 consecutive days once every morning by private owners) representing four digestion types (nonruminant foregut fermenters—NRFF; ruminant foregut fermenters—RFF; non-coprophageous hindgut fermenters—NCHF; coprophageous hindgut fermenters—CHF). Data from unpublished pilot study by S. Baker and M. Clauss in 2011.

ruminant and camelid species preferring sternal recumbency (but a small proportion of lateral recumbency in the camelid), ample use of lateral recumbency in the rhinoceros species, and again a clear preference for sternal recumbency in a hystrico-morph rodent. Additionally, the data generated in the present study match several reports from the literature on the respective species or digestion types (see below).

There was a greater incidence of lying at night compared to during the day. Although the data cannot reliably indicate whether this also translated into a larger amount of time spent resting, this result is not surprising given that the majority of the study species were diurnal. The removal of visitor stimulus at night allows animals the opportunity to relax, which sub-sequently results in a distinct resting position and eventually sleep (Gonfalone and Jha 2015). The only exception was the group of coprophageous hindgut fermenters, which included only species that are either nocturnal or biphasic.

Ruminants and camelids (RFF).—For ruminants, the clear preference for sternal recumbency described for domestic (Balch 1955) as well as nondomestic species (Jarman 1977; Caboń-Raczyńska et al. 1987; Tobler and Schwierin 1996) was confirmed both in the present and the pilot study. In spite of a large body of literature on ruminant activity budgets in which "lying rest" is recorded as part of the activity budget, the pos-ture is hardly ever specified, most likely because most biolo-gists take sternal recumbency for granted. As expected, and in accord with the literature (de Lamo et al. 1998; Khan et al. 1998), sternal recumbency was also the preferred resting pos-ture of camelids in both the present (Supplementary Data SD1, Table S2) and the pilot study (Fig. 5), but unexpectedly, cam-elids showed a slight yet distinctive use of lateral recumbency, also noted in adult dromedaries (*Camelus dromedarius*) by Khan et al. (1998). This slight difference between ruminant and camelid resting may be due to the generally lower level of food intake in camelids as compared to ruminants (Dittmann et al. 2014); with a putatively slower forestomach digestion process, camelids are more tolerant of interruptions of the forestomach sorting mechanism compared to ruminants.

With respect to a body-mass effect, Belovsky and Slade (1986) found, in a sample of free-ranging North American prai-rie rodent and ruminant species, that the time spent inactive (and its components, time spent lying and time spent inactive standing) decreased with body mass. Recalculating their data to express rest in a lying and standing posture, however, does not show an effect of body mass on the postures chosen, in contrast to our study where smaller ruminants rested more in a lying posture during the day than larger ones (Fig. 2A). In a sample of four African ruminant species, du Toit and Yetman (2005) found that the proportion of day rest spent standing increased with body mass from steenboks (*Raphicerus camp-estris*) to giraffes, as for ruminants in our study. These authors follow Jarman (1974) in linking lying rest to a hiding behav-ior, a strategy more likely to be used by smaller species. This contrasts with domestic ruminants, where Ruckebusch (1972) found cattle to spend more of their reduced wakefulness lying compared to sheep.

Equids, rhinos, and tapirs (NCHF).—Equids are known to spend a large proportion of their resting time in a standing position (Duncan 1980; Lamoot and Hoffmann 2004), using the patellar locking mechanism to relieve one of the hindlimbs (Hermanson and Macfadden 1996). The absence of such a mechanism in tapirs and rhinos possibly explains the observa-tion that these species use lying rest more often than horses (Fig. 2A). Comparing domestic horses not only to domestic ruminants, but also to the domestic pig (a hindgut fermenter), Ruckebusch (1972) found horses to spend much more time in standing rest. This author also reported that horses spend the majority of their lying rest in sternal recumbency, similar to our study. The resting postures adopted by the zoo equids of the present study at night resembled closely those observed in free-ranging horses (Duncan 1980; Supplementary Data SD1, Fig. S1), with a certain proportion of lying rest. Whether this implies an unnatural resting pattern during the daytime at the zoo remains to be investigated, as for other free-ranging equids that were observed during daylight hours, conflicting results were reported, with hardly any other rest than in a standing posture in different zebra groups (Joubert 1972; Neuhaus and Ruckstuhl 2002) and lying rest at daytime making up a propor-tion of about 0.2 of total rest in a zebra bachelor group and nonlactating females (Neuhaus and Ruckstuhl 2002).

Equids might avoid lying rest during daytime as an antipreda-tor behavior. Neuhaus and Ruckstuhl (2002:1440) cite Estes (1991) as claiming that lying zebras are "much more likely to be taken by lions" than standing ones. As another reason for a reluctance by large animals to use lateral rest, an impairment of lung ventilation was demonstrated in anesthetized horses (McDonell et al. 1979; Sorenson and Robinson 1980) and rhi-noceroses (Morkel et al. 2010). However, the fact that lying rest does occur, but more often at night (Fig. 3), indicates that factors inducing vigilance are more likely limiting the use of lying, and particularly lateral lying rest, during daylight hours. In free-ranging black rhinos (*Diceros bicornis*), sternal recum-bency was reported as the nearly exclusive lying rest posture during the day (Goddard 1967), similar to the findings in the present study (Supplementary Data SD1, Table S2).

To date, there are no indications for sorting mechanisms (Hummel et al. 2018) or other gravity-dependent processes in the digestive physiology of perissodactyls. The fact that they include lateral recumbency in their resting repertoire to a much larger proportion than ruminants and camelids suggests that their digestive processes are independent of gravity.

Elephants (NCHF).—Of all nondomestic mammals, el-ephants are probably the species whose resting behavior has been investigated most thoroughly (reviewed in Schiffmann et al. 2018a). Adult elephants rest mainly in a standing posi-tion, although the anatomy of their knee joint does not allow a patellar locking mechanism as in equids (Weissengruber et al. 2006). Nevertheless, lying rest in lateral recumbency has been documented in elephants independent of age. Its duration seems to decrease with increasing age, although extraordinarily long lying bouts of up to 8.5 h have been reported in a geriatric Asian elephant (*Elephas maximus*—Schiffmann et al. 2018b).

A strong side preference in individual elephants has been reported, as also evident in our elephant data (Fig. 4), but no general species-wide laterality is detectable in elephant lying rest (Schiffmann et al. 2018a). Several observational studies reported leaning behavior (when an elephant gives part of its body weight to an environmental structure while standing) in free-ranging as well as captive elephants (McKay 1973; Tobler 1992; Weisz et al. 2000; Wuestenhagen et al. 2000). Taking into account that this behavior occurred mainly in elephants expressing reduced lying rest, Schiffmann et al. (2018a) hypothesized leaning to function as substitute for lateral recumbency. In contrast to other larger-sized herbivores resting mainly in sternal recumbency, elephants prefer a lateral position for lying rest, as also documented in the present study (Fig. 3). Sternal rest is considered uncommon in elephants, and it is assumed that elephants would suffer hypoxia when resting in a sternal position for an extended duration (Benedict and Lee 1938; Pienaar et al. 1966; Harthoorn 1973; Tobler 1992). The present findings, with one individual African elephant (*Loxodonta africana*) resting extensively in this position (Fig. 3), together with anecdotal observations (C. Schiffmann, pers. obs.), suggest that sternal recumbency may not be as uniformly detrimental as commonly thought. As for perissodactyls, two facts suggest that the digestion of elephants functions independently of gravity: no sorting mechanism in their digestive tract has been reported so far, and they can adopt lateral lying postures for prolonged periods of time.

Warthogs and hyraxes (NCHF).—Domestic pigs use, in increasing preference, sitting, sternal recumbency, and lateral recumbency as resting postures (Ekkel et al. 2003), if the space provided to them allows the fully stretched-out lateral position, and the same postural preference (with a low proportion of sitting and a high proportion of lateral recumbency) was reported for wild boars (*Sus scrofa*—Gundlach 1968). While sitting was also observed in the warthog of the present study, lateral recumbency was not (Supplementary Data SD1, Table S2). Whether free-ranging warthogs use some form of lateral recumbency in their burrows is, to our knowledge, unknown, and it was not possible in the present study to record their nighttime behavior. The difference from domestic pigs may be due to a generally higher vigilance in nondomestic species, as reported for rabbits, where domestic rabbits rested more above ground in an outside enclosure than free-ranging wild rabbits (Stodart and Myers 1964). In a comparison of domestic pig and wild boar sows' behavior after birth, the domestic animals spent significantly more time lying than the nondomestic animals (Gustafsson et al. 1999), and wild boars generally spend less daytime resting than domestic pigs (Robert et al. 1987). No evidence for a digesta sorting mechanism in pigs has been presented so far.

Hyraxes often rest in close contact with conspecifics in formations called huddling (several animals in close contact) or heaping (with animals positioned on the backs of huddling conspecifics), and these require sternal recumbency (Sale 1970). With increasing environmental (and hence also substrate) temperature, resting hyraxes change from a sitting to a crouched (hunched) to a prone (flat) sternal posture, with

hindlegs stretched out backwards in the latter (Sale 1970; Brown and Downs 2005, 2007). As also reflected in our data (Supplementary Data SD1, Table S2), lateral recumbency is not mentioned as a resting posture in hyraxes. In the present study, resting events scored as standing possibly represent a crouched sternal, and events scored as sternal represent a prone resting posture. Additionally, hyraxes were often observed in a sitting position. In total, the resting position of hyraxes did not so much resemble that of other NCHF, but rather that of similar-sized rodents, and is a strong indication that general body shape and limb length may be the main determinants of resting positions rather than digestive physiology. Hyraxes have a digestive tract anatomy that is very peculiar among mammals (reviewed in Langer 2017). Regurgitation and remastication of digesta has been claimed for the hyrax (Hendrichs 1963, 1965; Van Doorn 1972), as well as coprophagy (Gaylard and Kerley 1997), but these observations have also been challenged (Fischer 1992) and cannot be considered conclusive. So far, a digesta sorting mechanism in the digestive tract of hyraxes has not been investigated.

Hystricomorph rodents (CHF).—The hystricomorph rodents of the present study resembled ruminating foregut fermenters in their preference for sternal recumbency (Figs. 1 and 2B), with the addition that they also rested sitting, which represents a similar posture as sternal recumbency with respect to the gravity vector. Sternal recumbency was reported to be the typical resting posture in capybaras by Lord (1991), who also reported that the animals adopted lateral recumbency to allow birds to take ectoparasites from their fur, and in free-ranging nutria (*Myocastor coypus*—Gosling 1979). For porcupines (*Hystrix* spp.), limited evidence for sternal recumbency being the typical resting posture exists in a drawing from Felicioli et al. (1997), and in the fact that juveniles are nursed from axillary nipples the mother presents in a sitting position (Tohmé and Tohmé 1980), and it appears intuitive to assume that the presence of spines make this resting posture the most likely one. The mara (*Dolichotis patagonum*), in spite of its comparatively long limbs, did not use lateral recumbency in the present study (Supplementary Data SD1, Table S2) and used it only to a small proportion in the pilot study (Fig. 5); resting animals in a photograph in Kessler et al. (2009) lie in sternal recumbency or sit, and in a study on the species' behavioral ecology, Taber (1987) described the lying of maras as "sphynx posture."

Thus, the hystricomorph rodents investigated appear limited in their resting behavior to a posture that keeps the relation to the gravity vector constant. This is in line with the prediction that due to the nature of the anatomical structure facilitating cecotroph formation in this group (cf. considerations on the hystricomorph colonic separation mechanism above), one might expect a similar constraint in resting position as observed in ruminants. However, this result is far from conclusive. On the one hand, a functional theory on, and evidence for, gravity playing a role in the hystricomorph colonic separation mechanism remain to be produced. On the other hand, aspects of body size and body shape as well as vigilance need to be further clarified. The finding of the pilot study that domestic rabbits, which have a "wash-back"

colonic separation mechanism whose anatomical structures are on all sides of the colon, but which also have particularly long hindlimbs, use lateral recumbency to a much higher degree than the hystricomorph rodents of the present and the pilot study (Fig. 5), justifies further investigation of this question.

Macropods, peccaries, and hippos (NFRR).—In macropods, the proportions of the hindlimbs prevent these animals from attaining a resting posture that would be comparable to sternal recumbency in other species. However, Schürer (1978) differentiated the lateral lying posture of macropods further, depending on whether both front legs are in contact with the ground and the head held up, or whether a part of the neck was in contact with the ground; unfortunately, this distinction was not made in the present study. However, Schürer (1978) did not differentiate quantitatively between these positions, and only stated that smaller macropods use standing rest more often than lying rest. For lying, this author also observed no side preference. Lentle (1998) reported more standing rest during the day, and a higher proportion of lying rest during the night in tammar wallabies (*Macropus eugenii*). The only postural association with digestion processes is the observation that merycism, the process of regurgitation and remastication of digesta, is only reported for macropods in standing positions (Lentle 1998; Vendl et al. 2017). However, the fact that this behavior apparently does not occur in a predictable, consistent manner in macropods (Vendl et al. 2017), the absence of evidence for a sorting mechanism in their forestomach (Schwarm et al. 2009, 2013; Munn et al. 2012), and the present observations that they use lateral recumbency on either side (Supplementary Data SD1, Table S2), indicates that this animal group does not require a constant positioning with respect to the gravity vector for their digestive physiology.

Peccaries exclusively used sternal recumbency for lying rest in the present study (Supplementary Data SD1, Table S2). Few information on postures in these species exists. A photograph in Sowls (1978) shows two peccaries in sternal recumbency, and a drawing in Sowls (1974) depicts a group of peccaries resting with body contact in a sternal position. Peccaries nurse their young usually in a standing position (Sowls 1974) and not in lateral recumbency as domestic pigs. No indication for a sorting mechanism in the peccary forestomach exists (Schwarm et al. 2009, 2013), but the forestomach anatomy comprises a ventral blind sac that will trap dense material such as sand (Schwarm et al. 2010). Therefore, the apparent avoidance of a lateral resting posture in peccaries is curious, and remains to be explained.

To our knowledge, no information about the resting behavior of pygmy hippos (*Hexaprotodon liberiensis*) exists. Common hippos (*Hippopotamus amphibious*) typically rest in water, but they require shallow water to do so, and they have been seen resting on land (Eltringham 1999; Dell et al. 2016). Common hippos did not rest on land in a study on a zoo exhibit with a large pool with varying depths that allowed resting in the water (Blowers et al. 2012). In the present study, common hippos in one zoological facility did not have access to a water pool at night, but the other group that did have access also rested on land. During the day, with access to their pools, hippos rested in the water in a standing position, and also rested in sternal recumbency on land.

During the night, lateral recumbency was used more frequently (Supplementary Data SD1, Table S2). Whereas Pluhácek and Basrtosová (2011) observed two female hippos that preferred to nurse while lying on their left side, the sparse daytime occurrences of lying rest suggested a preference for the right side, whereas the nighttime observations, with a larger number of animals using lateral recumbency, did not suggest any side preference (Supplementary Data SD1, Table S2). As described for the peccary forestomach, the hippopotamus forestomach comprises blind sacs (Langer 1988) that will trap dense material (Wings et al. 2008). However, no evidence for a functional sorting mechanism in hippos exists (Schwarm et al. 2008, 2013), and their use of lateral recumbency correspondingly indicates no digestion-related constraint on resting posture.

Conclusions.—The present study investigated the prediction that digestive physiology may influence resting postures adopted by herbivores (Clauss 2004; Matsuda et al. 2017). It presents a catalogue of resting postures for a wide range of terrestrial mammalian herbivores. Considering an interrelation between digestive physiology and resting postures, it corroborates the well-known use of sternal recumbency in ruminants (Balch 1955) and expands it to camelids, while showing that camelids also use lateral recumbency to a small but larger extent than taxonomic ruminants (Supplementary Data SD1, Table S2; Fig. 5). Other large herbivores are observed in lateral recumbency more often (Table 2; Figs. 1 and 3), suggesting that digestive physiology does not constrain their resting positions, but species-specific peculiarities unrelated to digestive physiology, such as the patellar locking mechanism in equids (Hermanson and Macfadden 1996), affect the proportion of rest spent in the different postures. In general, larger herbivores not only spend more rest in a standing position (Table 1; Fig. 2A), but also use lateral recumbency more often when lying (Table 2; Fig. 3). Therefore, it cannot be decided whether the exclusive use of sternal lying rest in peccaries, hyraxes, and hystricomorph rodents reflects a body size and body shape-related pattern, or is linked to digestive physiology. While studying the different conditions that affect species-specific resting postures is of further interest, the present study particularly raises the question about the function of the hystricomorph colonic separation mechanism and its putative relation to the gravity vector.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Table S1 (ethogram), Table S2 (species-specific data), Fig. S1 (comparison of equid data of

the present study to data from free-ranging horses from Duncan 1980).

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