



Research article

Feeding management of giraffe towards positive welfare

Sarah Depauw¹, Leen Verbist¹, Jeroen M.G. Stevens¹ and Marina Salas²

10 disee University of Applied Sciences, Agro- and Biotechnology, Sint-Niklaas, Belgium ²Antwerp Zoo Centre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp, Belgium

Correspondence: Sarah Depauw, email; sarah.depauw@odisee.be

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Abstract

This study prioritised positive affective states while modifying the feeding management of five giraffes at Zoo Planckendael and monitored the impact on indicators of both negative and positive welfare. Observations were conducted day and night over a 10-day winter period before and one year after implementing the following feeding management changes: 1) increased fibre and decreased sugar and starch content in the diet; 2) inclusion of five browse species year-round, accounting for a minimum 10% of total dry matter intake, including browse with thorns; 3) increased daily feeding frequency (from two to three times) of pellets, produce and browse, with the highest browse provision in the evening; and 4) all food offered required tongue manipulation. Results indicate improved positive welfare, with significant increases in daytime feeding (from 24.5% to 43.4% of observed time), night-time feeding (from 17.6% to 28.7%) and nocturnal rumination (from 26.7% to 38.7%), and the complete replacement of mouth feeding with tongue feeding. Oral abnormal repetitive behaviours decreased during the day (from 2.9% to 2.0%) and significantly decreased at night (from 1.0% to 0.6%). The absence of recumbency during the day might indicate negative welfare and warrants further investigation. Overall, the Five Domains animal welfare model proved valuable in optimising feeding strategies that promote positive affective states like pleasure, gastrointestinal comfort and engagement, which led to increased positive welfare in giraffes after implementing the new feeding management regime. Round-the-clock observations and positive welfare indicators provide broader insights into giraffe welfare, highlighting potential for future zoo nutrition research.

Introduction

The study of giraffe welfare in zoos is an active and ongoing area of research (Bashaw et al. 2016; Lewton and Rose 2020; Normando et al. 2018; Patel et al. 2019; Razal et al. 2017). Inadequate nutrition management has been associated with health issues such as ruminitis, hoof problems and the occurrence of abnormal behaviours in captive giraffes (Bashaw et al. 2001; Baxter and Plowman 2001; Clauss and Dierenfeld 2008; Gage 2019; Gattiker et al. 2014; Hummel et al. 2006). The main focus of giraffe welfare and feeding management research revolves around the investigation of oral abnormal repetitive behaviours and development of reduction strategies (Baxter and Plowman 2001; Enevoldsen et al. 2022; Fernandez et al. 2008; Gussek et al. 2018; Hummel et al. 2006; Orban et al. 2016). However, this approach deviates from contemporary

animal welfare definitions which state that overall quality of life is enhanced by promoting positive welfare (Boissy et al. 2007; Mellor 2016; Wolfensohn et al. 2018).

The World Association of Zoos and Aquaria (WAZA) animal welfare strategy (Mellor et al. 2015) recommends that zoos and aquariums utilise the Five Domains model, which includes nutrition, environment, health, behaviour and mental state, to assess animal welfare. The model refers to an animal's overall affective experiences, which are influenced by a variety of internal and external factors related to its physical and social environment. According to the model, ensuring good welfare is not solely about avoiding negative experiences. Instead, animals must be given opportunities to experience positive affective states such as pleasure, engagement, gastrointestinal comfort, satiety and contentment (Mellor and Beausoleil 2015; Mellor 2016). However, within the domain of zoo

animal nutrition, there is a lack of studies addressing how feeding management can contribute directly to positive animal welfare. Zoological institutions place insufficient emphasis on eliciting positive emotional states through effective feeding management.

Significant progress has been made in defining potential indicators of positive welfare in various animals, including farm animals (Rowe et al. 2022), pets (Polgár et al. 2019) and zoo animals (Manteca et al. 2016; Miller et al. 2021). However, a comprehensive assessment of welfare indicators specific to giraffes is still pending. Ward and Hosey (2020) advocate for the adoption of welfare concepts and procedures developed in an agricultural context, as they can prove beneficial and applicable to zoos (Salas et al. 2018). Ruminants, including giraffes, share common physiological and behavioural characteristics that make welfare assessment frameworks suitable for diverse species. Given the considerable advancements in welfare assessment for ruminant farm animals, research conducted on farm ruminants (Mattiello et al. 2019; Papageorgiou and Simitzis 2022) was utilised as the basis for establishing welfare indicators specifically tailored to giraffes for this study.

The act of consuming food elicits purposeful behaviours within an animal's environment, and the concept of this behaviour being rewarding suggests that animals presumably experience a form of pleasure when obtaining food, which contributes to a positive mental state (Mellor 2015). In the case of ruminants, including wild giraffes, a significant amount of time is allocated to feeding. It constitutes the primary diurnal activity for giraffes, accounting for up to 75% of their time. During night-time hours, giraffes typically dedicate approximately 22% of their time to feeding, which can increase to 34% on nights with greater illumination (Pellew 1984; Veasey et al. 1996). Hence, duration of feeding was used in this study as an indicator of positive welfare. According to the Five Domains animal welfare model, 'masticatory pleasures' is an affective state that can be influenced by feeding strategies (Mellor and Beausoleil 2015). Giraffes use their prehensile tongue, which can extend up to 45 centimetres in length, to delicately pluck leaves while avoiding thorns (Dagg 2014). The term 'masticatory pleasures' is replaced here with 'tongue work' to render it more relevant to the feeding behaviour of giraffes, and is included as a potential indicator of positive welfare.

Rumination plays a crucial role in maintaining the well-being of ruminants. In cows, the majority of rumination occurs when in a resting position or during the night (Kilgour et al. 2012). Ruminating while lying down is considered an indication of positive welfare, as it typically reflects the state of healthy, calm and unstressed cows (Phillips 2002). In wild giraffes, nocturnal activities are also primarily characterised by rumination. However, in contrast to cows, giraffes exhibit a lower proportion of rumination while lying down during daytime hours, with a peak occurring around midday, which accounts for approximately 10% of their overall activity (Pellew 1984). In this study, duration of rumination is used as an indicator of positive welfare, and rumination was recorded in both standing and lying down positions.

Duration and quality of sleep has also been proposed as a measure for stress and animal welfare (Manteca et al. 2016). Mammalian sleep can be categorised into two primary states: deep sleep or rapid eye movement (REM) sleep (also called paradoxical sleep) and non-REM sleep (Siegel 2005). Alterations in social behaviour, environmental factors and health conditions can lead to immediate modifications in REM sleep patterns (Siegel 2011). REM sleep significantly decreases in adult giraffes following a stressful event (Sicks 2013). Ruckebusch (1972) demonstrated that non-REM recumbency sleep and cud chewing can occur simultaneously in cows. Cows can transition as quickly into REM sleep when they cease rumination as cows that are not ruminating. This phenomenon was recently confirmed in

lesser mouse-deer *Tragulus kanchil* (Lyamin et al. 2022). Given an expected increase in rumination following implementation of the new feeding management (Hummel et al. 2006), the tendency of ruminants to dedicate more time to rumination at night compared to the day (Beauchemin 2018), the understanding that rumination and non-REM sleep are not mutually exclusive in ruminants (Ruckebusch 1972) and well-studied sleeping behaviour in giraffes (Tobler and Schwierin 1996), it was intriguing to investigate potential modifications to both REM and non-REM sleep during this study. By examining sleep patterns, a deeper understanding of the effects of feeding management on sleeping behaviour and the overall well-being of the giraffes was sought.

The primary objective of this study was to provide an example in giraffes of how to enhance feeding management towards positive affective states. To optimise feeding management, the Five Domains animal welfare model was used. The study aimed to evaluate the impact of modified feeding management on the overall welfare of giraffes. The traditional focus was shifted from observing indicators of negative welfare, such as oral abnormal repetitive behaviour, to assessing indicators of positive well-being. This approach aligns with contemporary understanding of animal welfare, which emphasises the promotion of positive welfare.

Materials and methods

Subjects

A herd of five Kordofan giraffes Giraffa camelopardalis antiquorum at Zoo Planckendael (Belgium) was observed before and after a change in feeding management. This herd consisted of two adult females, two subadult males and one juvenile female (Table 1). Their indoor living space, which spanned 178 m², featured four large stables and a central area. In addition, they shared an outdoor enclosure of 7325 m² with four addax Addax nasomaculatus, five Mhorr gazelles Nanger dama mhorr, and 49 helmeted guinea fowls Numida meleagris in 2020. In 2021, the helmeted guinea fowl were isolated as a preventative measure for the avian influenza outbreak in Belgium. In 2021, in contrast to the prior year, the giraffes were also permitted access to indoor areas during visitor hours. During the winter months, all giraffes were housed indoors at night-time due to the cold temperatures. The giraffes were provided with food around 0900 (indoors and outdoors), 1400 (indoors and outdoors) and 1600 (indoors), after which they were kept indoors for the night.

Changes in feeding management to improve animal welfare

To optimise feeding management for improved welfare, positive affective states that can be influenced by the nutrition domain described in the Five Domains Model of animal welfare were focused on (Mellor and Beausoleil 2015). These affective states include pleasure, engagement, gastrointestinal comfort,

Table 1. Information about the giraffes observed in this study.

Name	Sex	Date of birth	Remarks
Barbie	Female	31 Jan 2000	Lactating in 2020
Diamant	Female	26 Jun 2002	
Matombu	Male	01 Nov 2017	
Twiga	Male	10 Jun 2018	Son of Barbie
Valeye	Female	12 Jan 2020	Daughter of Barbie, was still nursing during observations in 2020

satiety, and contentment. The selected positive affective states were transformed into specific objectives for the newly proposed feeding management (Figure 1).

To promote gastrointestinal comfort and satiety, dietary fibre content was increased and starch and sugar components reduced (Baxter and Plowman 2001; Gussek et al. 2018; Hummel et al. 2006). This was achieved by substituting high-starch pellets with an alternative product which contained less starch (<5%, fresh matter basis) and higher fibre (neutral detergent fibre>40%, acid

detergent fibre>30%, fresh matter basis), and by a 20% decrease in the amount of pellet given daily. Carrots and all fruit items were removed from the diet. To encourage consumption of lucerne hay, the amount of green vegetables was reduced; a maximum of 1 kg of green vegetables was permitted for training and enrichment purposes. To offer variety in smell, taste and texture, a minimum of five browse species were provided daily throughout the year, including fresh rose leaves, which accounted for at least 10% of total dry matter intake. To mimic natural browsing behaviour,

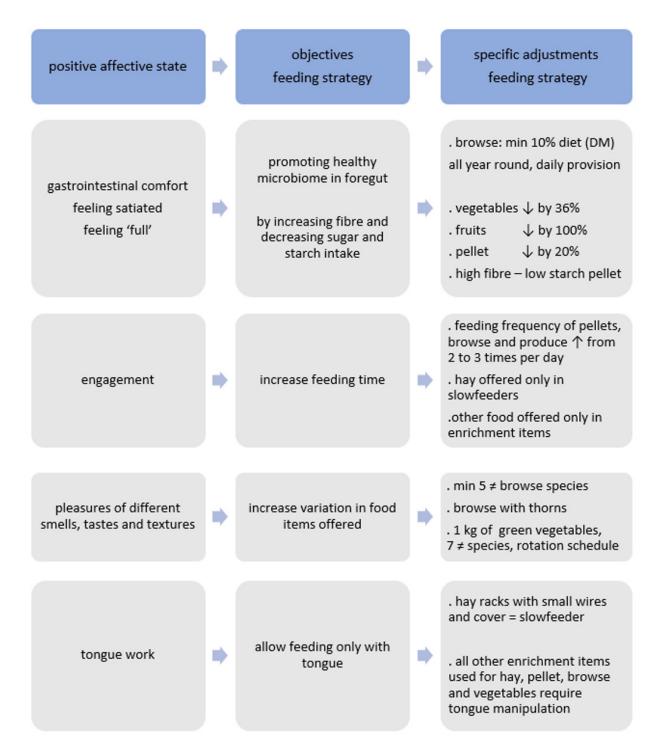


Figure 1. Moving from the assessment of affective states related to nutrition (Mellor et al. 2015) to the development of objectives and specific adjustments in the feeding management for captive giraffes.

access to thorny vegetation such as blackberry was provided, as wild giraffes frequently forage on leaves from trees possessing spiked branches (Parker and Bernard 2005; Pellew 1984). Seven different species of green vegetables were offered on a weekly basis using a rotation schedule.

The feeding frequency of pellets, browse and produce was increased from two to three times a day, with the highest supply of browse occurring during the final feeding session to promote increased nocturnal browsing (Duggan et al. 2016). The new diet was provided exclusively via slow feeders and enrichment devices that required tongue manipulation, further emulating natural feeding behaviour. The giraffes had unrestricted access to lucerne hay through ten wired hay racks with covers, with five strategically placed indoors and an additional five located outdoors in different areas. Dried leaves, fresh rose leaves, green vegetables and pellets were consistently presented in feeders constructed from materials like PVC tubes or barrels, designed to necessitate tongue manipulation. Each feeding instance included at least nine of these feeders which were suspended both indoors and outdoors at different locations.

Data collection

Body condition was scored for all giraffes before the start of observations in 2020 and 2021. Behavioural observations were conducted for ten randomly selected days, in November 2020 (before the change in feeding management) and in December 2021 (one year after implementation of the new feeding management). Each day, data were collected for a total of 12 hours: 4 hours during the daytime period (0800–1600) and 8 hours during the night-time period (1600–0800). To ensure a comprehensive observation schedule, a twelve-hour block system was implemented, with each block lasting two hours. Within each two-hour block, three 20-minute randomised observation sessions were conducted, resulting in a total of 120 hours of observations per study period (40 hr during daytime and 80 hr during night-time). Night-time observations were conducted using footage from four infrared

cameras (Hikvision Full HD 2.8MP, viewing angle 107°, infrared night vision up to 40 m) placed in each corner of the stable and one in the central area. The behaviour of each giraffe was recorded with continuous focal sampling. Due to the short duration of head flick/rolls, this behaviour was evaluated using all-occurrence sampling. All observations were recorded using ZooMonitor (Ross et al. 2018; Wark et at. 2019).

To assess the impact of the altered feeding management on welfare, both positive and negative welfare indicators were scored (Table 3). Negative welfare indicators include the time spent displaying abnormal repetitive behaviours, such as pacing, licking non-food objects and tongue rolling (Baxter and Plowman 2001; Fernandez et al. 2008; Orban et al. 2016; Veasey et al. 1996), and head flick/rolls (Duggan et al. 2016), which were observed in certain giraffes prior to the study. Positive welfare indicators include the division of feeding time into feeding using the tongue versus the mouth, and the division of rumination time into rumination while standing versus lying down. Sleeping behaviour as an indicator of welfare was also investigated, classified into three categories: standing sleep, recumbent sleep and paradoxical (REM) sleep, as previously described in captive giraffes (Tobler and Schwierin 1996).

Data analysis

Total duration of behaviours (in seconds) were computed for each day and night from the dataset for both years, per giraffe, each consisting of ten observation days and nights. To address the considerable variation in the duration of different behavioural bouts, statistical analyses were performed on the calculated totals (in seconds) using JMP Pro statistical software. This was made feasible by the uniform time span of observations both prior to and following the alteration in feeding management. Results were expressed as a percentage of observed time. Group-level analyses were generated using a linear mixed model, with the year (2020 and 2021) treated as a fixed effect and the individual giraffes considered the random effect. The effect of adapted feeding

Table 2. Zoo diet and calculated nutritional composition (using Zootrition®) for the giraffes housed in Zoo Planckendael during winter season both prior to and following the alteration in feeding management (i.e., 2020 and 2021).

Zoo diet for an adult giraffe of 800 kg – winter season			Macronutrient composition				
	Weight as fed	Before 2020	After 2021			Before 2020	After 2021
Lucerne hay*	g	ad lib, min 5400	ad lib, min 6000	Moisture	%	31.5	18.2
Browse: dried leaves**	g	500	1000	Crude protein	% DM	16.6	18.4
High fibre pellet	g	4500	3500	Crude fat	% DM	2.7	3.2
Carrots	g	1400	-	Crude fibre	% DM	22.3	28.6
Green vegetables	g	1400	1000	Crude ash	% DM	9.8	10.4
Fruits	g	800	-	NFE	% DM	48.6	39.5
Branches to peel***		ad lib	ad lib	Starch	% DM	8.6	3.2
Mineral lick		ad lib	ad lib	Sugar	% DM	5.6	4.3
KNZ Wild®				NDF	% DM	39.3	45.7
				ADF	% DM	27.2	33.1
				ADL	% DM	3.4	8.1

Lucerne hay was always offered ad libitum. The specified minimum amount helps zoo staff in assessing whether there is sufficient lucerne intake. **When fresh rose leaves were available, the quantity specified for dried leaves in 2021 was tripled. ***Branches to peel were not included when calculating the macronutrient composition.

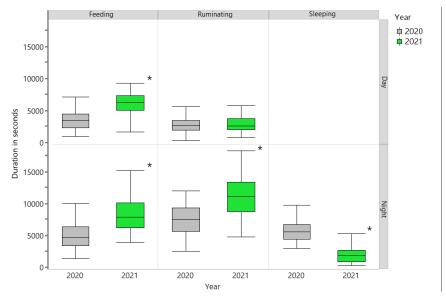


Figure 2. Mean total time giraffes were engaged in feeding, ruminating, and sleeping behaviour during the day and night before and after the change in feeding management (i.e., 2020 and 2021); averaged for all ten 24 hour-cycles and all five giraffes * Significant P values (P<0.001).

management at the individual level was tested by a two-sample t-test for equal means. When the assumption of normality was not met, a log transformation of the response was used. Head flick/rolls, which were quantified in terms of the number of occurrences (n) rather than the total duration in seconds, were analysed at group level using a generalised linear mixed model with negative binomial distribution and log link using statistical SAS software. On the individual level, a Wilcoxon rank sum test was used. All P values ≤ 0.05 were deemed significant.

Results

Throughout the study, the body condition score of all giraffes remained stable, with all individuals falling within the range of 4 to 5 on a 1–9 scale. The average time spent eating, ruminating and sleeping before (2020) and after (2021) implementation of the new feeding management is presented in Figure 2. There was a significant increase in diurnal (24.5% to 43.4%, P<0.001) and nocturnal (17.5% to 28.7%, P<0.001) feeding time. The giraffes spent an average of 19.8% (in 2020) and 20.1% (in 2021) of

Table 3. Ethogram of selected giraffe behaviours used as positive and negative welfare indicators (based on Tobler & Schwierin 1996; Orban et al. 2016)

Behaviour	Behaviour Description
Feeding with mouth	Mouth is in contact with non-cud food items for purpose of consumption, includes mastication of non-cud. The mouth reaches for the food without really sticking out the tongue
Feeding with tongue	Tongue is in contact with non-cud food items for purpose of consumption, includes mastication of non-cud. The tongue comes out of the mouth and curls around the food, then the food is pulled in
Ruminating lying down	Giraffe in recumbency, lower jaw moves horizontally to upper jaw and back to starting position in succession of five or more occurrences resulting in the mastication of cud. Also includes regurgitation and swallowing of cud
Ruminating standing	Giraffe standing, lower jaw moves horizontally to upper jaw and back to starting position in succession of five or more occurrences resulting in the mastication of cud. Also includes regurgitation and swallowing of cud
Paradoxical (REM) sleep	In a lying position, a giraffe bends its neck and head towards the side of its body. The individual lets the neck and top of the head rest on the hip or on the ground next to the hind legs. The eyes are completely closed
Recumbent sleep	In a lying position, the eyes are relaxed and do not blink, no rumination, the neck remains in a vertical position but closer to the ground than when they are awake, and the neck and head do not move
Standing sleep	Standing motionless, the ears are directed backward and are also immobile, and the neck is closer to the ground than when they are awake
Pacing	Locomotion occurring in a repeated pattern between two locations
Licking	Tongue is repetitively moved across non-food, stationary item, typically a structural component of exhibit such as wall, fence, or tree
Tongue-rolling	Tongue is continuously moved or rolled in and out of mouth, most often involving a food item that is not actively being masticated or ruminated
Head flick/rolls	The head/neck is twisted around in the air without any purpose or reason

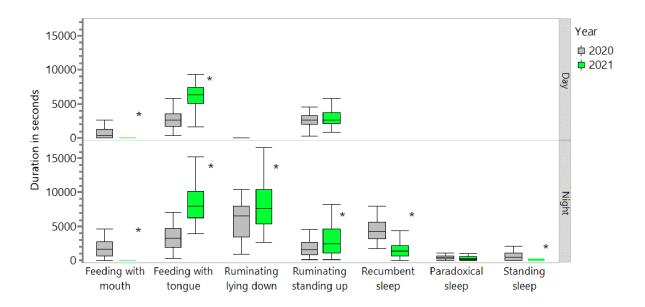


Figure 3. Mean (+SD) total time giraffes were engaged in feeding, ruminating, and sleeping behaviour during the day and night before and after the change in feeding management (i.e., 2020 and 2021); averaged for all ten 24 hour-cycles and all five giraffes. * Significant P values (P<0.001)

observed daytime ruminating. In both study periods, the giraffes ruminated more at night than during the day. In 2020, the giraffes spent 26.6% of observed night-time ruminating, which significantly increased to 38.7% in 2021 (P<0.001). Sleeping behaviour was not observed during the daytime in either study period. The mean duration of sleep during the night significantly decreased, dropping from 19.8% in 2020 to 6.9% in 2021 (P<0.001).

During the day, the giraffes spent on average 5.1% of the observed time feeding with their mouth, which significantly decreased to 0.1% in 2021 (P<0.001; Figure 3). In contrast, feeding with the tongue significantly increased during the day, more than

doubling its duration from 19.4% to 43.3% (P<0.001). Feeding with the mouth significantly declined at night, decreasing from 6.3% in 2020 to 0.0% in 2021 (P<0.001). Conversely, feeding with the tongue significantly increased, more than doubling from 11.3% to 28.7% (P<0.001). The giraffes spent on average 19.2% (2020) and 20.1% (2021) of observed daytime ruminating while standing. Ruminating while recumbent was not observed during the daytime. However, at night, ruminating both standing up and lying down significantly increased. Ruminating while standing increased from 6.0% in 2020 to 10.6% in 2021 (P<0.05). Mean time spent ruminating while lying down increased from 20.7% to 28.1%

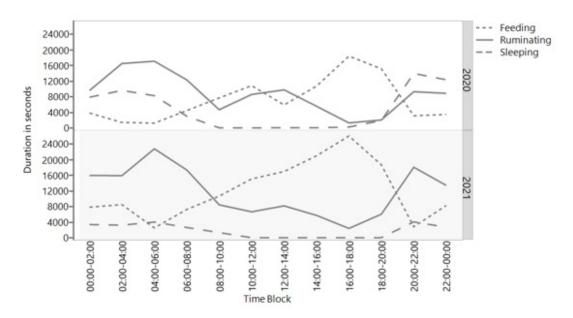


Figure 4. Patterns of feeding, ruminating, and sleeping behaviour before and after the change in feeding management (i.e., 2020 and 2021); divided into 2-hour time blocks; averaged for all five giraffes and all ten 24-hour cycles.

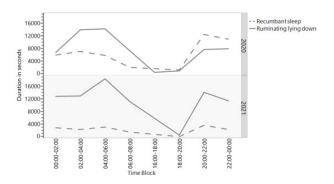


Figure 5. Nocturnal patterns of ruminating in lying and standing position and recumbent and standing sleep before and after the change in feeding management (i.e., 2020 and 2021); divided into 2-hour time blocks; averaged for all five giraffes and all ten-night cycles.

(P<0.001). Sleeping behaviour was subdivided into paradoxical, standing and recumbent. Paradoxical sleep remained comparable between the two study periods, accounting for 1.4% in 2020 and 1.2% in 2021. However, there was a significant decrease in recumbent sleep from 15.9% in 2020 to 5.4% in 2021 (P<0.001). Similarly, standing sleep also significantly decreased from 2.5% to 0.4% (P<0.001).

The patterns of feeding, ruminating and sleeping across the 24 hr period are shown in Figure 4. In both years, the giraffes increased their feeding behaviour between 0400 and 0600. Feeding behaviour peaked at 1000–1200 and 1600–1800 in 2020, while a peak was observed only at 1600–1800 in 2021. Rumination slightly peaked in 2021 at 1200–1400 and 2000–2200. A distinct peak in rumination was observed at 2000–2200 and 0400–0600 in 2021, while no such peak was observed during daytime hours. Sleeping behaviour was not observed during daytime hours and was highest at 2000–2200 in both study periods.

Figure 5 provides an overview of the nocturnal patterns of ruminating lying down and recumbent sleep. While the giraffes were predominantly in recumbent sleep between 1800 and 0000 in 2020, this behaviour decreased drastically in 2021 and was replaced by an increase in rumination while laying down.

At the group level, there was a non-significant decrease in total oral abnormal repetitive behaviour (object-licking + tonguerolling) from 2.9% to 2.0% during daytime hours. However, overall the group exhibited a significant decrease in this behaviour from 1.0% to 0.6% (P<0.05). The mean time each individual giraffe performed total oral abnormal repetitive behaviours is presented in Figure 6. These behaviours decreased in all three adult giraffes during the day in 2021 (Barbie: 3.5% to 2.9%, Diamant: 5.4% to 1.8%, Matombu: 2.8% to 1.5%). The decrease was only statistically significant for Diamant (P<0.05). In contrast, the subadult giraffes Twiga and Valeye exhibited a non-significant increase in total oral abnormal repetitive behaviour (1.2% to 1.4% and 1.8% to 2.3% respectively). During night-time hours, results varied among individuals. While Diamant exhibited a significant decrease in this behaviour from 2.4% to 0.6% (P<0.05) and Valeye showed a nonsignificant decrease from 1.7% to 0.1%, the other giraffes showed a slight non-significant increase in this behaviour. Barbie increased oral abnormal repetitive behaviour from 0.5% to 0.7%, Matombu from 0.4% to 1.1% and Twiga from 0.2% to 0.4%.

Table 4 presents the average percentage of object licking, tongue-rolling and pacing, both at group level and individually, during day and night. It also includes the number of head flicks/ rolls exhibited per day and night. Diamant showed the highest percentage of object-licking and was the only giraffe showing a significant decrease (P<0.05) during the day. There was a significant decrease in night-time object licking at the group level, from 1.0% to 0.5% (P<0.05). The decrease was observed in all individuals. Tongue rolling was rarely observed and non-significantly decreased for all animals during the day, with the exception of Twiga who slightly increased this behaviour from 0.0% to 0.3%. At night, a slight increase in tongue-rolling at the group level was observed. Pacing during the day decreased non-significantly in all adult giraffes. Twiga increased pacing from 2.1% to 5.1%, whereas Valeye did not perform this behaviour. Pacing during the night was seldom observed, with no significant differences between the study periods. The number of head flick/rolls during the day varied among individuals. This behaviour was mainly performed by Barbie and Twiga. Barbie exhibited a significant night-time increase in this behaviour, with occurrences rising from 7.2 to 18.9, while Valeye showed a significant daytime increase from 0.1 to 1.3 occurrences (P<0.05). In contrast, Diamant significantly reduced this behaviour from 1.6 to 0.1 occurrences during the day and from 1.2 to 0.1 occurrences during the night (P<0.05).

Patterns of abnormal repetitive behaviours across the 24-hr period are shown in Figure 7. Object licking peaked during both study periods at 1000–1200 and 1800–2000. However, the intensity of the peaks varied between the study years. In 2020, the highest peak occurred in the evening, while in 2021 it occurred in the morning. Tongue-rolling in 2020 showed a peak only at 1000–1200. It was more dispersed in 2021, with the highest peak occurring at 1600–1800. Pacing and head flick/rolls were highest at 0800–1000 and 1200 and around 1400 in 2020. In 2021, these behaviours peaked at the same time in the morning but occurred one time block later in the afternoon compared to 2020.

Discussion

The primary aim of this study was to improve the feeding management of a herd of Kordofan giraffes with the ultimate goal of promoting positive affective states. The Five Domains animal welfare model (Mellor and Beausoleil 2015) was valuable in optimising feeding management. By considering the model's domains, ways in which the composition and presentation of the giraffes' diet could elicit putatively positive experiences for the animals such as pleasure, gastrointestinal comfort, satiety, engagement and contentment were examined. This approach emphasises the significance of enhancing the animals' overall well-being through thoughtful and purposeful adjustments to the

feeding regime. The impact of the modified feeding management on the giraffes' welfare was assessed by observing indicators of both negative and positive welfare, in line with contemporary animal welfare definitions that prioritise the promotion of positive affective states. Research conducted on farm ruminants was used as the basis for establishing welfare indicators specific to giraffes.

In ruminants, feeding behaviour is considered an indicator of positive welfare (Mattiello et al. 2019; Papageorgiou and Simitzis 2022). Although wild giraffes allocate up to 75% of their daytime to feeding, captive giraffes often do not even reach half of this (Baxter and Plowman 2001; del Castillo et al. 2005; Hosie and Turner 2000; Pellew 1984; Veasey et al. 1996). In this study, diurnal feeding significantly increased from 25% of observed time

Table 4. Mean (Standard Deviation (SD)) percentage of observed time (both day and night) the giraffes engaged in object licking, tongue-rolling and pacing, and mean number of observations (N) (both day and night) giraffes were engaged in head flick/rolls before and after the change in feeding management (i.e., 2020 and 2021); averaged for all five giraffes and all ten 24 hour-cycles. * Significant p-values (p < 0.05)

	Daytime						
	2020	2021	Probability	2020	2021	Probability	
Object licking (9	% (SD))						
Group	2.7 (3.5)	2.9 (2.1)	0.176	1.0 (1.4)	0.5 (0.7)	0.006*	
Barbie	2.8 (3.3)	1.8 (1.8)	0.391	0.5 (0.9)	0.5 (1.1)	0.366	
Diamant	5.4 (4.4)	1.8 (1.8)	0.019*	2.4 (2.2)	0.5 (0.5)	0.020*	
Matombu	2.5 (4.8)	1.5 (1.1)	0.819	0.4 (0.5)	0.1 (0.2)	0.513	
Twiga	1.2 (1.5)	1.4 (1.4)	0.497	0.2 (0.3)	0.0 (0.1)	0.335	
Valeye	1.8 (1.1)	2.3 (1.7)	0.464	1.7 (0.9)	1.1 (0.8)	0.160	
Tongue-rolling ((% (SD))						
Group	0.2 (1.1)	0.1 (0.3)	0.195	0.0 (0.0)	0.0 (0.3)	0.335	
Barbie	0.9 (2.4)	0.0 (0.1)	0.346	0.1 (0.1)	0.3 (0.4)	0.144	
Diamant	0.1 (0.2)	0.0 (0.0)	0.331	0.0 (0.0)	0.0 (0.1)	-	
Matombu	0.3 (0.8)	0.0 (0.0)	0.256	0.0 (0.0)	0.0 (0.0)	-	
Twiga	0.0 (0.1)	0.3 (0.7)	0.262	0.0 (0.0)	0.3 (0.6)	0.155	
Valeye	0.0 (0.0)	0.0 (0.0)	-	0.0 (0.0)	0.0 (0.1)	-	
Pacing (% (DS))							
Group	1.7 (3.6)	1.5 (3.6)	0.493	0.2 (0.7)	0.1 (0.2)	0.167	
Barbie	5.1 (6.6.)	2.1 (2.3)	0.464	0.9 (1.2)	0.3 (0.5)	0.077	
Diamant	0.7 (0.9)	0.0 (0.0)	0.311	0.0 (0.1)	0.0 (0.0)	-	
Matombu	0.7 (1.2)	0.3 (0.4)	0.494	0.0 (0.0)	0.0 (0.0)	-	
Twiga	2.1 (2.4)	5.1 (6.5)	0.445	0.2 (0.6)	0.0 (0.0)	0.299	
Valeye	0.0 (0.0)	0.0 (0.0)	-	0.0 (0.0)	0.0 (0.0)	-	
Head flick/rolls	(n (SD))						
Group	19.0 (23.6)	30.1 (46.1)	0.300	5.9 (15.1)	5.0 (9.6)	0.220	
Barbie	36.4 (20.1)	67.8 (48.6)	0.064	7.2 (5.1)	18.9 (13.9)	0.018*	
Diamant	1.6 (2.7)	0.1 (0.3)	0.017*	1.2 (1.9)	1.1 (0.3)	0.038*	
Matombu	5.2 (3.8)	4.1 (3.4)	0.270	1.5 (2.2)	0.7 (1.1)	0.342	
Twiga	51.6 (12.3)	77.4 (49.4)	0.162	19.4 (30.4)	5.2 (4.7)	0.068	
Valeye	0.1 (0.3)	1.3 (2.1)	0.049*	0.0 (0.0)	0.3 (0.9)	0.500	

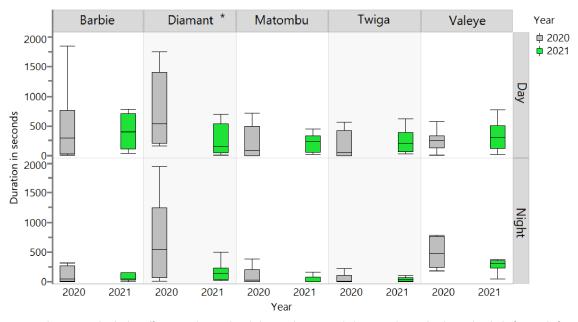


Figure 6. Mean total time an individual giraffe engaged in total oral abnormal repetitive behaviours during the day and night before and after the change in feeding management (i.e., 2020 and 2021); averaged for all ten 24 hour-cycles. * Significant P values (pP<0.05)

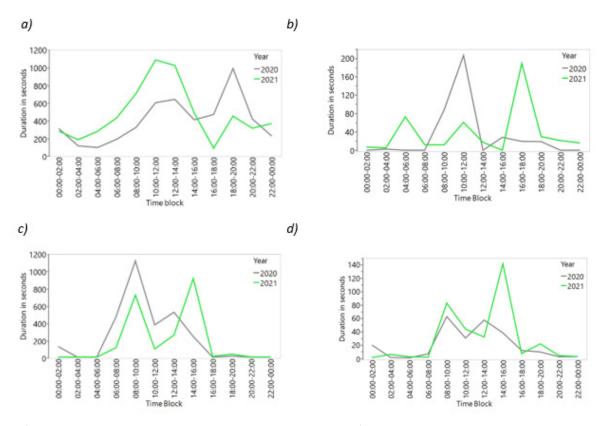


Figure 7. 24/7 patterns of a) object licking, b) tongue-rolling, c) pacing, and d) head flick/rolls before and after the change in feeding management (i.e., 2020 and 2021); divided into 2-hour time blocks; averaged for all five giraffes and all ten 24-hour cycles.

to 43% following the adaptation of feeding management. Schüßler et al. (2015) report a higher feeding time of 48%, attributed to the availability of browse for ad libitum consumption. Due to logistical limitations, providing browse for ad libitum consumption was not feasible in the present study. The modified feeding management also induced a significant increase in nocturnal feeding time, from 18% to 29%. This aligns more closely with nocturnal feeding patterns observed in wild giraffes, which range between 22% and 34% of observed time (Pellew 1984). A comprehensive study involving 63 giraffes from 13 different EAZA zoos revealed that nocturnal feeding periods varied significantly, ranging from 19% to 39% of observed time (Burger et al. 2021). Thus, the results of the current study fall within the upper range of nocturnal feeding patterns observed in both captive and wild giraffes. Before the shift in feeding management, Barbie was actively lactating and likely experiencing a heightened demand for food, which would naturally lead to an increase in feeding time. The significant increase in Barbie's feeding time following the adjustment in feeding management, even though she had ceased lactating by that point, provides further confirmation of the effectiveness of the new feeding approach.

Given the browsing nature of giraffes, characterised by leafplucking using their tongues while avoiding thorns (Dagg 2014), tongue feeding was included as a potential indicator of positive welfare. On average, the giraffes in this study allocated 21% of their daytime and 36% of their night-time to feeding using their mouths. However, through the exclusive implementation of enrichment items that require tongue manipulation and the provision of slow-feeders in the form of wired hay racks with covers, mouth-based feeding was successfully eliminated, resulting in 100% utilisation of tongues for feeding in 2021. Thus the modified feeding management led to an overall increase in feeding time, during both the day and night, and exclusive tongue usage, which can be considered indicators of improved giraffe welfare. These results emphasise the importance of considering an animal's feeding behaviour and demonstrate that for giraffes, any form of direct mouth access to food should be prevented.

In their natural habitat, giraffes display a distinct biphasic feeding pattern, characterised by peaks in feeding activity occurring three hours after dawn and before dusk, with reduced feeding during the midday heat (Pellew 1984). However, in the present study, feeding patterns were likely influenced by the zookeepers' feeding routine; feeding behaviour showed an increase a few hours after sunrise (0800-0845) without a distinct feeding peak. This can be attributed to the fact that the giraffes were only fed between 0900 and 1000, when the giraffes were allowed access to their cleaned outdoor enclosure where feeding stations were refilled. The provision of fresh browse, hay and pellets during this time likely contributed to the continuous increase in feeding duration throughout the morning. Before altering feeding management, giraffes showed a noticeable rise in feeding between 1200 and 1400 when they were fed again by the zookeepers. However, following implementation of modified feeding management aimed at promoting extended feeding periods, giraffes exhibited heightened feeding behaviour throughout the day, with a peak occurring only at 1600-1800 when housed indoors. The typical reduced feeding activity at midday, observed in the wild and before the change in feeding management, was not present. The dietary change and division of pellets, produce and browse into three feeding times instead of two likely induced a higher intake of roughage between zookeepers' designated feeding sessions. This is supported by the unaltered body condition score of the giraffes in 2021 despite a 20% decrease in pellets and 75% reduction in produce. Notably, during the post-change observations, giraffes were given unrestricted access to both the indoor and outdoor areas, unlike before the dietary adjustment. This may have influenced feeding behaviour, as the animals had access to both indoor and outdoor feeding stations. Currently, the impact on captive giraffe welfare of the absence of the typical two-phase feeding pattern observed in wild giraffes remains uncertain. In the wild, the midday rest is linked to very high temperatures around noon, which do not occur at comparable intensity in temperate zone zoos. This difference highlights the need for further investigation of ways to encourage increased feeding times in captive giraffes.

Ruminating behaviour is a well discussed indicator of positive welfare in ruminants (Mattiello et al. 2019; Papageorgiou and Simitzis 2022). In the present study, modifying feeding management did not impact the overall duration of rumination during the day. On average, the giraffes dedicated approximately 20% of their time to rumination, which closely aligns with mean percentages for wild giraffes reported by Pellew et al. (1984) and slightly exceeds values documented by Veasey et al. (1996). However, typical peaks in rumination observed at midday in the wild and related to high ambient temperatures were not observed; this could be due to the zookeepers' feeding routine, as explained previously. Following alteration of feeding management, overall rumination time significantly increased during the night from 27% to 39%, bringing values closer to reported levels of approximately 50% in wild giraffes (Pellew et al. 1984). Recumbency was the primary posture observed for rumination, with peaks occurring shortly after sunset and in the early morning, which is consistent with natural activity budgets (Pellew et al. 1984). The nocturnal increase in rumination time further suggests that the modifications in feeding management led to an overall improvement in welfare.

The observations raise a significant possible welfare concern, as the giraffes displayed a complete absence of rumination in recumbency during daytime hours. Furthermore, it is striking that these giraffes did not lie down at all throughout the day, even outside of observation periods (data not shown). In cows, increased lying time, the ability to adopt appropriate lying postures and the ease of transitioning between standing and lying positions may serve as indicators of positive welfare (Matiello et al. 2019). Veasey et al. (1996) attribute variations in the percentage of recumbent behaviour among zoos with differences in enclosure substrate. Specifically, they found that giraffes housed in hardstand paddocks laid down less than those in grass paddocks. The giraffes in this study had access to a variety of substrates, including grass, straw pellets, pieces of concrete, dolomite (albeit limited), sandpits and soil with grass. The giraffes were housed in a mixed-species exhibit which might have influenced their resting behaviour. Wild giraffes engaging in recumbency during the day and its association with positive welfare in ruminants highlights the significance of assessing this parameter for giraffe welfare. Evaluating the importance of recumbency and rumination in captive giraffes, as recommended by Razal et al. (2018), could provide valuable insights into their welfare. Additionally, investigating the environmental factors influencing giraffe's recumbent behaviour is warranted.

Ruminants have complex digestive systems and spend a significant portion of their waking hours feeding and ruminating. As a result, their sleep is often fragmented into shorter intervals, with REM sleep being scarce and of short duration, likely due to increased vulnerability to predation during this sleep stage (Tobler and Schwierin 1996). In the present study, the change in feeding management did not impact paradoxical (REM) sleep, which accounted for only 1.2 to 1.4% of the giraffes' nocturnal activity. These findings align with previous research conducted on both wild and captive giraffes, as well as other free-ranging ruminants such as blue wildebeest *Connochaetes taurinus* and Arabian oryx *Oryx leucoryx* (Burger et al. 2020, 2021; Davimes et al. 2018; Malungo et al. 2021). In contrast, a significant decrease

in non-REM recumbent sleep was observed, from an average of 16% of observed time to 5.4%. However, this decrease was accompanied by an almost equal increase in rumination while recumbent, so that the total time spent recumbent was not affected. During the study, recumbent sleep and ruminating while lying down were treated as separate behaviours, although they can occur simultaneously (Lyamin et al. 2022; Ruckebusch 1972). Tobler and Schwierin (1996) reported non-REM sleep in giraffes while standing, a phenomenon also observed in other ruminants (Ruckebusch 1972). In the current study, this interpretation of standing sleep was incorporated into observations. However, due to limited research on standing sleep in giraffes and ruminants as a whole, the classification of this behaviour as actual sleep remains controversial. Nonetheless, a notable reduction in standing sleep was observed following the alteration in feeding management, which was accompanied by an increase in rumination while standing. Based on the available data, it is not possible to definitively determine whether the giraffes were in a non-REM sleep state while engaging in standing or recumbent rumination. However, the most significant and crucial finding in terms of positive welfare is the observed increase in rumination during both recumbency and standing. This indicates that the modification in feeding management had a positive impact on rumination, which is considered an important aspect of overall giraffe welfare.

The observed percentages of total oral abnormal repetitive behaviours in this study were low compared to previous studies (Baxter and Plowman 2001; Fernandez et al. 2008; Koene and Visser 1997; Orban et al. 2016). Prior to the alteration in feeding management, the herd engaged on average 2.9% of its daytime in this behaviour, which is much lower than the 17% recently reported in captivity (Orban et al. 2016). Furthermore, the occurrence of nocturnal abnormal repetitive behaviour, with an individual maximum observation of 2.4%, was significantly lower when compared to previous studies reporting rates of up to 15% (Duggan et al. 2016). Additionally, all giraffes reduced this behaviour during the night compared to the daytime, which is in contrast to previous findings (Duggan et al. 2016; Veasey et al. 1996). When considering the herd as a whole, average daytime oral abnormal repetitive behaviours decreased non-significantly from 2.9% to 2.0%. Object-licking and tongue-rolling are frequently observed in captive giraffes. Similar to other ungulates, these behaviours are believed to arise from frustrated feeding motivation caused by restricted food or nutrient intake, as well as shorter durations for food processing when compared to natural conditions (Bashaw et al. 2001; Bergeron et al. 2006). An increase in fibre and browse, the use of complex feeders requiring tongue manipulation and guest feeding programmes have previously proven to reduce these abnormal behaviours in giraffes (Baxter and Plowman 2001; Fernandez et al. 2008; Koene and Visser 1997; Orban et al. 2016). However, these studies did not provide a clear picture of giraffe behaviour throughout the day and night, but rather focused on specific periods with high incidences of oral abnormal repetitive behaviours or were limited to daytime observations.

The current study provides a broader perspective on the behaviour of giraffes throughout the day and night, aligning more closely with the 24/7 animal welfare concept. This concept highlights the importance of continuous care for animal well-being, taking into account various life stages, biological rhythms and seasonal variations (Brando and Buchanan-Smith 2018). Animal care and behavioural research often conform to human schedules rather than the animals' natural rhythms. For a more thorough assessment of welfare indicators, behavioural observations should be conducted during times when staff are absent, such as evenings and nights. Day and night observations of giraffes by Duggan et al. (2016) failed to establish conclusive evidence for a significant impact of changes in feeding management on oral

abnormal repetitive behaviours during the day, although there was a negative correlation between feeding and oral stereotypies. In the current study, the new feeding management did lead to a significant reduction in total oral stereotypic behaviour during the night, from 1% to 0.6%. Diamant, the oldest female, exhibited the highest occurrence of object-licking, while tongue-rolling was rarely observed. This higher incidence is consistent with the notion that stereotypies become more prevalent with age in giraffes and other animals (Baxter and Plowman 2001; Mason 1991; Veasey et al. 1996). Although abnormal repetitive behaviour generally becomes more difficult to reduce in older animals (Mason 1991), Diamant demonstrated the highest significant decrease in both diurnal and nocturnal object licking, from 5.4% to 1.8% during the day and 2.4% to 0.5% during the night. Subadults Twiga and Valeye, who were likely still in the process of developing stereotypic behaviour, showed a slight non-significant increase in diurnal object licking. Twiga also demonstrated a 24/7 increase in tongue rolling after the change in feeding management, although these values are still very low. The limited sample size, individual variations, age differences and notably, the substantial withinindividual variation observed on different days may account for the lack of statistical significance in these changes at a group level. Overall, when considering the herd as a whole, the decrease in object-licking during the day and the significant decline during the night confirms that the altered feeding management had a positive impact on giraffe welfare.

Notably, aligning with the current results, Duggan et al. (2016) found that oral stereotypies peaked either concurrently with feeding sessions or shortly thereafter. This behaviour has also been observed in cattle (Redbo 1990). A survey of stereotypic behaviour in giraffes found that giraffes performed more object-licking behaviour when fed more often during the day (Bashaw et al. 2001). Hence, it is recommended to compare various methods of extending feeding time in giraffes, some of which do not require the involvement of zookeepers. These methods may include the utilisation of timed feeders, augmenting the quantity of complex feeders or enhancing the complexity of the feeders (Fernandez et al. 2008; Sasson-Yenor and Powell 2019).

In the present study, giraffes commonly engaged in locomotor stereotypical behaviour such as pacing and head flicks/rolls when they were unable to access the paddock or stable while zookeepers were cleaning these areas and refilling the feeding stations. These behaviours were rarely observed at night and likely indicate anticipatory behaviour (Krebs et al. 2022). During the daytime, the herd engaged in pacing behaviour for approximately 1.7% of the observed time in 2020 and 1.5% in 2021. Due to the short duration of head flick/rolls, this behaviour was evaluated using all-occurrence sampling. Throughout the daytime, the herd exhibited this behaviour an average of 19 times per day, increasing to 30 times per day partly due to the subadult giraffes who both increased this behaviour while aging. This observation confirms that stereotypes tend to develop as animals mature. However, Diamant displayed a significant decrease in this behaviour during both day and night, highlighting distinct individual differences. The anticipatory pacing and head flick/rolls observed could be attributed to motivation for feeding, which aligns with the findings of Duggan et al. (2016). While the experience of anticipation itself is intrinsically rewarding, when there is a scarcity of positive events or occurrences in an animal's life, those events, such as feeding sessions, may hold exceptional significance to the animals. Therefore, it is important not to disregard anticipatory behaviour as it serves as an indicator of the current equilibrium between positive and negative experiences in an animal's life (Podturkin et al. 2022; Watters 2014). Hence, future investigations aiming to increase feeding time in giraffes through approaches other than simply increasing feeding frequency should also evaluate effects on



Figure 8. Night-time images captured in Zoo Planckendael depict a giraffe guarding system. Two giraffes can be observed in paradoxical sleep at the bottom, while two other giraffes are in a recumbent position and one giraffe is standing.



Figure 9. Daytime images captured at Dublin Zoo exhibit a herd with a notable occurrence of simultaneous recumbent behaviour. Photo: Clodagh Walsh

anticipatory behaviours. While pacing is commonly considered an anticipatory behaviour, it may also be influenced by the diet itself. This has been previously demonstrated in giraffes; an increased intake of browse during night-time resulted in decreased pacing behaviour (Duggan et al. 2016).

The findings emphasise the importance of a holistic approach in zoo nutrition research. It is crucial to consider both positive and negative welfare indicators to gain a comprehensive understanding of impacts on animal welfare. These data highlight the significance of assessing animal welfare throughout a 24-hour period, rather than solely during human working hours. This aligns with the 24/7 approach advocated for by Brando and Buchanan-Smith (2018) to enhance overall welfare. The current study focused on a few indicators of positive welfare suggested for ruminants. More research is needed to scrutinise other potential indicators of positive welfare such as social affiliative behaviours (Papageorgiou and Simitzis 2022). The characteristics of rumination such as chewing cycles, which have been previously studied in giraffes (Schüßler and Greven 2017), hold potential interest for assessment. However, evaluating these characteristics using night cameras might be challenging. Synchronisation of lying and feeding behaviours has been proposed as an important indicator of positive welfare in ruminants. It suggests reduced competition among individuals, allowing subordinate animals to access feeding resources in the company of conspecifics (Mattiello et al. 2019; Papageorgiou and Simitzis 2022). Exploring the synchronisation of these behaviours in exotic ruminants like giraffes would provide valuable insights.

A limitation of behavioural synchronisation as a potential welfare indicator relates to the relatively small herd sizes commonly observed in captivity. This could introduce bias when interpreting synchronisation levels. Some species in the wild, including giraffes, exhibit natural guarding systems, which may persist in captivity, leading to some animals guarding while others rest (Shukla et al. 2021). Consistent with observations in both wild and captive giraffes (Burger et al. 2020, 2021), in the current study there were no instances where all animals were observed sleeping

or resting simultaneously. Instead, some individuals within the group were observed standing or feeding, while others rested in close proximity (Figure 8). Therefore, further investigation into the potential of behavioural synchrony (Figure 9) as a positive welfare indicator is encouraged, but caution should be exercised when interpreting results.

Conclusions

Feeding management should prioritise enhancing positive affective states for giraffes and other animals rather than solely focusing on reducing negative welfare. The Five Domains welfare model is a valuable tool to carefully examine how composition and presentation of giraffes' diets could elicit positive experiences such as pleasure, gastrointestinal comfort, satiety, engagement and contentment. The management changes outlined in this study resulted in a feeding regimen necessitating tongue manipulation for the entire diet, not just specific enrichment items. Providing the complete diet in this manner could have advantages for other species.

The feeding management investigated in this study led to a significant rise in positive welfare indicators and a notable decline in negative welfare indicators. However, while feeding time and tongue feeding showed significant increases during both the day and night, rumination time and rumination in recumbency only increased significantly during the night. Additionally, at the group level, oral stereotypic behaviour decreased significantly only during the night. Exclusively focusing on reducing negative indicators, like stereotypic behaviour, may neglect broader aspects of animal welfare that contribute to overall well-being. Comprehensive evaluations of giraffe welfare, including nutritional research, should encompass both positive and negative welfare indicators and be based on observations throughout the day and night. More research is needed to define welfare indicators for giraffes specifically. Recumbency and rumination in recumbency are potential indicators of positive welfare in giraffes that warrant further investigation.

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References

- Bashaw M.J., Tarou L.R., Maki T.S., Maple T.L. (2001) A survey assessment of variables related to stereotypy in captive giraffe and okapi. *Applied Animal Behaviour Science* 73(3): 235–247.
- Bashaw M.J., Sicks F., Palme R., Schwarzenberger F., Tordiffe A.S.W., Ganswindt A. (2016) Non-invasive assessment of adrenocortical activity as a measure of stress in giraffe (*Giraffa camelopardalis*). *BMC Veterinary Research* 12(1): 235. doi:10.1186/s12917-016-0864-8
- Baxter E., Plowman A.B. (2001) The effect of increasing dietary fibre on feeding, rumination and oral stereotypies in captive giraffes (*Giraffa camelopardalis*). *Animal Welfare* 10(3): 281–290. doi:10.1017/S0962728600024052
- Beauchemin K.A. (2018) Invited review: Current perspectives on eating and rumination activity in dairy cows. *Journal of Dairy Science* 101(6): 4762–4784. doi:10.3168/jds.2017-13706
- Bergeron R., Badnell-Waters A.J., Lambton S., Mason G. (2006) Stereotypic oral behaviour in captive ungulates: Foraging, diet and gastrointestinal function. In: Mason G., Rushen J. (eds.). Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare. Wallingford, UK: CABI Books, 19–57. doi:10.1079/9780851990040.0019
- Boissy A., Arnould C., Chaillou E., Désiré L., Duvaux-Ponter C., Greiveldinger L., Leterrier C., Richard S., Roussel S., Saint-Dizier H., Meunier-Salaün M., Valance D., Veissier I. (2007) Emotions and cognition: A new approach to animal welfare. *Animal Welfare* 16(S1): 37–43. doi:10.1017/S0962728600031717
- Brando S., Buchanan-Smith H.M. (2018) The 24/7 approach to promoting optimal welfare for captive wild animals. *Behavioural Processes* 156: 83–95. doi:10.1016/j.beproc.2017.09.010
- Burger A.L., Fennessy J., Fennessy S., Dierkes P.W. (2020) Nightly selection of resting sites and group behavior reveal antipredator strategies in giraffe. *Ecology and Evolution* 10(6): 2917–2927. doi:10.1002/ecc3.6106
- Burger A.L., Hartig J., Dierkes P.W. (2021) Biological and environmental factors as sources of variation in nocturnal behavior of giraffe. Zoo Biology 40(3): 171–181. doi:10.1002/zoo.21596
- Clauss M., Dierenfeld E.S. (2008) The nutrition of "browsers". In: Fowler M.E., Miller R.E. (eds.). Zoo and Wild Animal Medicine: Current Therapy. St Louis, Missouri: Saunders Elsevier, 444–454.
- Dagg A.I. (2014) Giraffe: Biology, Behaviour and Conservation. Cambridge, UK: Cambridge University Press. doi:10.1017/CBO9781139542302
- Davimes J.G., Alagaili A.N., Bhagwandin A., Bertelsen M.F., Mohammed O.B., Bennett N.C., Manger P.R., Gravett N. (2018) Seasonal variations in sleep of free-ranging Arabian oryx (*Oryx leucoryx*) under natural hyperarid conditions. *Sleep* 41(5): zsy038. doi:10.1093/sleep/zsy038
- del Castillo S.M., Bashaw M.J., Patton M.L., Rieches R.R., Bercovitch F.B. (2005) Fecal steroid analysis of female giraffe (*Giraffa camelopardalis*) reproductive condition and the impact of endocrine status on daily time budgets. *General and Comparative Endocrinology* 141(3): 271– 281. doi:10.1016/j.ygcen.2005.01.011
- Duggan G., Burn C.C., Clauss M. (2016) Nocturnal behavior in captive giraffe (*Giraffa camelopardalis*)—A pilot study. *Zoo Biology* 35(1): 14– 18. doi:10.1002/zoo.21248
- Enevoldsen E.M.E., Møller-Lassesen K., Larsen N., Gert O.E.S., Holmegard R., Jensen S.E., Pagh S., Pertoldi C., Jensen T.H., Alstrup A.K.O., Johansen K. (2022) The influence of feeding opportunities of six zoohoused Giraffa camelopardalis rothschild: The influence of feeding opportunities. *Genetics and Biodiversity Journal* 6(2): 103–126.
- Fernandez L.T., Bashaw M.J., Sartor R.L., Bouwens N.R., Maki T.S. (2008) Tongue twisters: Feeding enrichment to reduce oral stereotypy in giraffe. *Zoo Biology* 27(3): 200–212. doi:10.1002/zoo.20180
- Gage L.J. (2019) Giraffe husbandry and welfare. In: Miller R.E., Lamberski N., Calle P.P. (eds.). Fowler's Zoo and Wild Animal Medicine Current Therapy, Volume 9 . St Louis, Missouri: WB Saunders, 619–622. doi:10.1016/B978-0-323-55228-8.00087-4

- Gattiker C., Espie I., Kotze A., Lane E.P., Codron D., Clauss M. (2014) Diet and diet-related disorders in captive ruminants at the national zoological gardens of South Africa. *Zoo Biology* 33(5): 426–432.
- Gussek I., Große-Brinkhaus C., Südekum K.H., Hummel J. (2018) Influence of ration composition on nutritive and digestive variables in captive giraffes (*Giraffa camelopardalis*) indicating the appropriateness of feeding practice. *Journal of Animal Physiology and Animal Nutrition* 102(2): e513–e524. doi:10.1111/jpn.12790
- Hosie L., Turner H. (2000) Oral behaviours performed by giraffes at Chester Zoo. *Proceedings of the 2nd Annual Symposium on Zoo Research*, Paignton Zoo Environmental Park, Paignton, Devon, UK, 6–7 July 2000. London, UK: Federation of Zoological Gardens of Great Britain and Ireland, 137–142.
- Hummel J., Clauss M., Baxter E., Flach E.J., Johanson K. (2006) The influence of roughage intake on the occurrence of oral disturbances in captive giraffids. In: Fidgett A., Clauss M., Eulenberger K., Hatt J.M., Hume I., Janssens G.P.J., Nijboer J. (eds.). *Zoo Animal Nutrition* Vol. III. Fürth, Germany: Filander, 235–252. doi:10.5167/uzh-3523
- Koene P., Visser E.K. (1997) Tongue playing behaviour in captive giraffes. Mammalian Biology - Zeitschrift für Säugetierkunde 62: 106–111.
- Kilgour R.J., Uetake K., Ishiwata T., Melville G.J. (2012) The behaviour of beef cattle at pasture. *Applied Animal Behaviour Science* 138(1-2): 12-17. doi: 10.1016/j.applanim.2011.12.001
- Krebs B.L., Chudeau K.R., Eschmann C.L., Tu C.W., Pacheco E., Watters J.V. (2022) Space, time, and context drive anticipatory behavior: Considerations for understanding the behavior of animals in human care. Frontiers in Veterinary Science 9: 972217. doi:10.3389/fvets.2022.972217
- Lewton J., Rose P.E. (2020) Evaluating the social structure of captive Rothschild's giraffes (*Giraffa camelopardalis rothschildi*): Relevance to animal management and animal welfare. *Journal of Applied Animal Welfare Science* 23(2): 178–192. doi:10.1080/10888705.2019.15736 82
- Lyamin O.I., Siegel J.M., Nazarenko E.A., Rozhnov V.V. (2022) Sleep in the lesser mouse-deer (*Tragulus kanchil*). Sleep 45(7): zsab199. doi:10.1093/sleep/zsab199
- Malungo I.B., Gravett N., Bhagwandin A., Davimes J.G., Manger P.R. (2021) Sleep in two free-roaming blue wildebeest (Connochaetes taurinus), with observations on the agreement of polysomnographic and actigraphic techniques. *IBRO Neuroscience Reports* 10: 142–152. doi:10.1016/j.ibneur.2021.02.005
- Manteca X., Amat M., Salas M., Temple D. (2016) *Animal-based indicators* to assess welfare in zoo animals. CABI Reviews. Wallingford, UK: CABI Books. doi:10.1079/PAVSNNR201611010
- Mason G.J. (1991) Stereotypies: A critical review. *Animal Behaviour* 41(6): 1015–1037. doi: 10.1016/S0003-3472(05)80640-2
- Mattiello S., Battini M., De Rosa G., Napolitano F., Dwyer C. (2019) How can we assess positive welfare in ruminants? *Animals* 9(10): 758. doi:10.3390/ani9100758
- Mellor D.J. (2015) Positive animal welfare states and reference standards for welfare assessment. *New Zealand Veterinary Journal* 63(1): 17–23. doi:10.1080/00480169.2014.926802
- Mellor D.J. (2016) Updating animal welfare thinking: Moving beyond the "Five Freedoms" towards "A Life Worth Living". *Animals* 6(3): 21. doi:10.3390/ani6030021
- Mellor D.J., Beausoleil N.J. (2015) Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare* 24(3): 241–253. doi:10.7120/09627286.24.3.241
- Mellor D.J., Hunt S., Gusset M. (2015) Caring for Wildlife: The World Zoo and Aquarium Animal Welfare Strategy. WAZA Executive Office. https://www.waza.org/wp-content/uploads/2019/03/WAZA-Animal-Welfare-Strategy-2015_Landscape.pdf
- Miller L.J., Lauderdale L.K., Bryant J.L., Mellen J.D., Walsh M.T., Granger D.A. (2021) Behavioral diversity as a potential positive indicator of animal welfare in bottlenose dolphins. *PloS ONE* 16(8): e0253113. doi:10.1371/journal.pone.0253113
- Normando S., Pollastri I., Florio D., Ferrante L., Macchi E., Isaja V., De Mori B. (2018) Assessing animal welfare in animal-visitor interactions in zoos and other facilities. A pilot study involving giraffes. *Animals* 8(9): 153. doi:10.3390/ani8090153
- Orban D.A., Siegford J.M., Snider R.J. (2016) Effects of guest feeding programs on captive giraffe behavior. *Zoo Biology* 35(2): 157–166. doi:10.1002/zoo.21275
- Papageorgiou M., Simitzis P.E. (2022) Positive welfare indicators in dairy animals. *Dairy* 3(4): 814–841. doi:10.3390/dairy3040056
- Parker D.M., Bernard R.T.F. (2005) The diet and ecological role of giraffe (*Giraffa camelopardalis*) introduced to the Eastern Cape, South Africa.

- 1267(2): 203-210. doi:10.1017/S0952836905007399
- Patel F., Wemelsfelder F., Ward S.J. (2019) Using qualitative behaviour assessment to investigate human-animal relationships in zoo-housed giraffes (*Giraffa camelopardalis*). *Animals* 9(6): 381.
- Pellew R.A. (1984) The feeding ecology of a selective browser, the giraffe (*Giraffa camelopardalis tippelskirchi*). *Journal of Zoology* 202(1): 57–81. doi:10.1111/j.1469-7998.1984.tb04288.x
- Phillips C.J.C. (2002) *Cattle Behaviour and Welfare*, 2nd edition. Wiley-Blackwell Science.
- Podturkin A.A., Krebs B.L., Watters J.V. (2022) A quantitative approach for using anticipatory behavior as a graded welfare assessment. *Journal of Applied Animal Welfare Science* 26(3): 463–477. doi:10.1080/1088 8705.2021.2012783
- Polgár Z., Blackwell E.J., Rooney N.J. (2019) Assessing the welfare of kennelled dogs—A review of animal-based measures. *Applied Animal Behaviour Science* 213: 1–13. doi:10.1016/j.applanim.2019.02.013
- Razal C.B., Bryant J., Miller L.J. (2017) Monitoring the behavioral and adrenal activity of giraffe (*Giraffa camelopardalis*) to assess welfare during seasonal housing changes. *Animal Behavior and Cognition* 4(2): 154–164. doi:10.12966/abc.03.05.2017
- Redbo I. (1990) Changes in duration and frequency of stereotypies and their adjoining behaviours in heifers, before, during and after the grazing period. *Applied Animal Behaviour Science* 26(1–2): 57–67. doi:10.1016/0168-1591(90)90087-T
- Ross M.R., Niemann T., Wark J.D., Heintz M.R., Horrigan A., Cronin K.A., Shender M.A., Gillespie K. (2018) Zoo *Monitor* (Mobile Application Software). Available online: https://zoomonitor.org
- Rowe E., Mullan S. (2022) Advancing a "Good Life" for farm animals: Development of resource tier frameworks for on-farm assessment of positive welfare for beef cattle, broiler chicken and pigs. *Animals* 12(5): 565. doi:10.3390/ani12050565
- Ruckebusch Y. (1972) The relevance of drowsiness in the circadian cycle of farm animals. *Animal Behaviour* 20(4): 637–643. doi:10.1016/s0003-3472(72)80136-2
- Salas M., Manteca X., Abáigar T., Delclaux M., Enseñat C., Martínez-Nevado E., Quevedo M.Á., Fernández-Bellon H. (2018) Using farm animal welfare protocols as a base to assess the welfare of wild animals in captivity—Case study: Dorcas gazelles (*Gazella dorcas*). *Animals* 8(7): 111. doi:10.3390/ani8070111

- Sasson-Yenor J., Powell D.M. (2019) Assessment of contrafreeloading preferences in giraffe (*Giraffa camelopardalis*). Zoo Biology 38(5): 414–423. doi:10.1002/zoo.21513
- Schüßler D., Gürtler W.D., Greven H. (2015) Aktivitätsbudgets von Rothschildgiraffen (*Giraffa camelopardalis rothschildi* Lydekker, 1903) in der "Zoom Erlebniswelt Gelsenkirchen". *Der Zoologische Garten* 84(1–2): 61–74. doi:10.1016/j.zoolgart.2015.01.002
- Schüßler D., Greven H. (2017) Quantitative aspects of the ruminating process in giraffes (*Giraffa camelopardalis*) fed with different diets. *Zoo Biology* 36(6): 407–412. doi:10.1002/zoo.21386
- Shukla I., Kilpatrick A.M., Beltran R.S. (2021) Variation in resting strategies across trophic levels and habitats in mammals. *Ecology and Evolution* 11(21): 14405–14415. doi:10.1002/ece3.8073
- Sicks F. (2013) Paradoxer Schlaf als Parameter zur Messung der Stressbelastung bei Giraffen (*Giraffa camelopardalis*). Johann Wolfgang Goethe-University, Frankfurt am Main: Doctoral dissertation.
- Siegel J.M. (2005) Clues to the functions of mammalian sleep. *Nature* 437(7063): 1264–1271. doi:10.1038/nature04285
- Siegel J.M. (2011) REM sleep: A biological and psychological paradox. Sleep Medicine Reviews 15(3): 139–142. doi:10.1016/j.smrv.2011.01.001
- Tobler I., Schwierin B. (1996) Behavioural sleep in the giraffe (*Giraffa camelopardalis*) in a zoological garden. *Journal of Sleep Research* 5(1): 21–32. doi:10.1046/j.1365-2869.1996.00010.x
- Veasey J.S., Waran N.K., Young R.J. (1996) On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator. Animal Welfare 5(1): 13–24. doi:10.1017/S0962728600018297
- Ward S.J., Hosey G. (2020) The need for a convergence of agricultural/laboratory and zoo-based approaches to animal welfare. *Journal of Applied Animal Welfare Science* 23(4): 484–492. doi:10.1080/108887 05.2019.1678038
- Wark J.D., Cronin K.A., Niemann T., Shender M.A., Horrigan A., Kao A., Ross M.R. (2019) Monitoring the behavior and habitat use of animals to enhance welfare using the ZooMonitor app. *Animal Behavior and Cognition* 6(3): 158–167. doi:10.26451/abc.06.03.01.2019
- Watters J.V. (2014) Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. *Zoo Biology* 33(4): 251–256. doi:10.1002/zoo.21144
- Wolfensohn S., Shotton J., Bowley H., Davies S., Thompson S., Justice W.S.M. (2018) Assessment of welfare in zoo animals: Towards optimum quality of life. *Animals* 8(7): 110. doi:10.3390/ani8070110