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Impacts of dietary modifications on the behaviour of captive western lowland gorillas (*Gorilla gorilla gorilla*)

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Abstract
Behavioural profiles of captive and wild *Gorilla gorilla gorilla* have been shown to differ greatly, with captive gorillas moving and foraging much less than their wild counterparts and often experiencing high levels of obesity and cardiovascular disease. Captive gorillas are typically fed an energy-dense diet and housed in relatively small enclosures compared to wild gorillas that forage for large quantities of fibrous fruits and foliage over expansive home ranges. These differences could be one of the leading factors driving behavioural and health problems observed among captive gorillas. This study examined behavioural profiles of captive gorillas fed experimental diets more nutritionally similar in both nutrient content and volume to those seen in the wild, particularly with the addition of woody browse and tamarind seed. It was predicted that when gorillas ate the experimental diets, they would display behavioural patterns more similar to their wild counterparts. The study found that feeding woody browses led to a reduction in coprophagy and regurgitation/reingestion (R/R) behaviours, but the addition of tamarind seed led to increased rates of coprophagy. These findings could be an important addition to management strategies in improving health and well-being among captive gorillas.

Introduction

Behavioural profiles of gorillas (*Gorilla gorilla*) differ greatly between free-ranging and captive-housed individuals, particularly with captive individuals foraging less and showing lower activity levels than their wild counterparts (Less et al. 2014; Cabana et al. 2018; Fuller et al. 2018). For example, gorillas at the San Francisco Zoo engaged in less feeding and foraging (29% vs 57%–67%) and higher rates of resting (43% vs 21%–29%) (Smith unpublished data) during daylight hours than observed in wild lowland gorillas (Remis 1994; Masi et al. 2009). These behavioural differences can be readily attributed to the time wild gorillas spend seeking out significant quantities of relatively low quality, high fibre foods (Remis et al. 2001) over a large home range. Conversely, captive gorillas live in relatively small spaces and eat smaller amounts of energy-dense, low fibre, low-tannin diets that likely differ from those consumed during their evolutionary history (Popovich et al. 1997; Jenkins et al. 1998). Tannins are defensive polyphenols found in plants and generally reduce the quality of herbivore foods (Hagerman and Klucher 1986). Nevertheless, certain tannins and other polyphenols have been reported to also improve health parameters including reducing blood pressure and lipid levels in humans (Chung et al. 1998; Scalbert et al. 2005a, b) and are anti-parasitic in various animal species (Hoste et al. 2006; Rothman et al. 2009).

The combination of relative inactivity and energy dense diets may contribute to chronic health issues among captive gorillas, including elevated levels of cholesterol and low-density lipoproteins, obesity and high rates of heart disease related deaths, particularly among relatively young silverbacks (Kenny et al. 1994; Schulman et al. 1995; Scott et al. 1995; Schmidt et al. 2006; Strong et al. 2016; Cabana et al. 2018). Additionally, some gorillas in captivity have been reported to exhibit heightened rates of undesired behaviours relative to their wild counterparts (Gray 1965; Burks 2001; Cordoni et al. 2006; Less et al. 2014; Fuller et al. 2018), including body rocking, pacing, regurgitation/reingestion (R/R) (Gould and Bres 1985; Ruempler 1992; Lukas 1999), and coprophagy (Akers and Schildkraut 1985). However, coprophagy, particularly seed reingestion, has been observed in wild primates, including gorillas and other African apes (Harcourt and Stewart 1978; Krief et al. 2004; Graczyk and Canfield 2003; Payne et al. 2008; Sakamaki 2010; Bertolani and Pruetz 2011; Beaune et al. 2017; Masi and Breuer 2018). If seeds are not chewed upon initial consumption, coprophagy has been suggested to facilitate access to nutrients otherwise unavailable by softening the seed coating (Krief et al. 2004; Masi and Breuer 2018). Additionally, passage through the gut potentially reduces the presence of antifeedants (compounds produced by plants to discourage ingestion) in wild diets, (Beaune et al. 2017), allowing for safe consumption once initially processed, referred to as the "toxicity reduction hypothesis" (Masi and Breuer 2018).

The presence of undesired behaviours in captive animals may be related, at least in part, to differences in feeding and foraging between captivity and native environments. For example, some carnivores, who in their wild habitat have large home ranges, exhibit undesired behaviours (i.e. pacing) when living in relatively small captive enclosures (Clubb and Mason 2003, 2007). Likewise, wild gorillas require a large home range to find sufficient quantities of low-quality foods. As gorillas in captivity have small enclosures relative to their wild home ranges, easily accessible energy-dense foods, and a potential for boredom, they might display undesired behaviours (particularly those that are diet related such as R/R) that are not often observed in the wild (Lawrence and Rushen 1993).

While it is difficult to mimic the size of a natural home range in captivity, altering captive diets to add volume and make them nutritionally more similar to those seen in the wild (including seasonality) is predicted here to improve captive gorilla health and wellbeing and bring behavioural profiles more in line with those seen in the wild. The effects of experimental diets on levels of obesity, digestion and biomarkers of health among the gorillas in this study will be addressed separately (Smith et al. in prep).

The present study predicted that altering captive gorilla diet to more closely resemble foods eaten in the wild (Calvert 1985; Masi 2008; Mondika 2006; Remis et al. 2001; Rogers et al. 1990) would act as behavioural enrichment as it should require foraging for, consumption of, and processing of a higher volume of more fibrous foods. When consuming the higher fibre experimental diets, it was expected that captive gorillas would be more active, experience enhanced satiation, and exhibit reduced frequency of undesired behaviours such as R/R, and coprophagy that might result from boredom or lack of satiety. As such, integrating behavioural and physiological research with dietary studies on gorillas should assist captive management efforts.

Methods

Permission for this study was granted by the Purdue University Animal Care and Use Committee (#09-080) and the Oklahoma City Zoo's IACUC board. All dietary trials were overseen by the veterinary and nutrition teams at the Oklahoma City Zoo.

Subjects and housing

This study was conducted between June 1 and December 20, 2010 at the Oklahoma City Zoo (Oklahoma City, OK). At that time, the Oklahoma City Zoo (OKC Zoo) was home to 10 western lowland gorillas (*Gorilla gorilla gorilla*). The gorillas were separated into the two groups as follows: Group One (one silverback, three adult females, one juvenile female) and Group Two (one silverback, one adult female with nursing juvenile, one adult female, one juvenile male, and one unweaned juvenile male). While the social groups had identical indoor enclosures, the outdoor yards differed. Group One had outdoor access to 5,852 m² of usable space, including a large waterfall, while Group Two had access to 1,951 m² of usable space and a large climbing structure.

Behavioural data collection

Behavioural observations were collected daily during the study period between 0900 and 1700 hours. A total of 415 hours of behavioural data were collected, with 213 hours collected on Group One and 202 hours collected on Group Two (approximately 50 hours per group per diet treatment; eight hours per day during daylight hours). Both group scan and continuous focal-animal sampling methods were employed (Altmann 1974), using a previously created behavioural ethogram (Smith unpublished data) (Table 1). Scan and focal samples were conducted on alternate days. Scan samples were taken every minute within 30 minute blocks (amount of blocks varied day to day depending on weather and access to animals), while focal follows were conducted for 30 minutes at a time. For analysis, scan samples were subsampled every five minutes to increase the likelihood that samples were independent of one another.

Specific attention was paid to feeding and foraging behaviours, social behaviours, food intake, undesired behaviours (particularly coprophagy and R/R) and overall activity budgets, with the unit of analysis being individual behaviours. The experimental diet portion of the study included four dietary manipulations which were conducted on both gorilla groups. Temperature and rainfall data were collected through the use of national weather databases (weather.com and wunderground.com).

Dietary trials

The gorillas were sequentially fed a series of isocaloric experimental diets differing in fibre and tannin levels over four distinct dietary trials (Table 2). Equal numbers of observation hours per group were collected during each dietary trial. Dietary trials one and two were higher in insoluble fibre (measured as neutral detergent fibre, NDF) than dietary trials three and four, supplied primarily through the addition of woody browse. Additionally, dietary trials two and three contained a source of dietary tannins from tamarind fruits and seeds versus dietary trials one and four. Woody browse is available at OKC only during the summer months and thus was offered during the first two dietary trials of this study. Woody browse was only offered indoors, as it was collected through the day and distributed at the end of the day while it was still fresh. Condensed tannin concentrations were analysed for all woody browse samples at the Primate Nutritional Ecology Lab, Hunter College, USA.

Dietary trial one (Group One: June 1–July 13; Group Two: June 1–July 19) (Average Temperature: 33°C) consisted of the typically fed zoo diet composed of Mazuri® maintenance biscuits (5MA2; Land O'Lakes, Minneapolis, MN) and fresh produce, with the experimental addition of at least 200 g of woody browse per gorilla per day (Table 2). In the second dietary treatment (Group One: July 14–September 17; Group Two: July 20–September 22) (average temperature: 34°C), each gorilla was offered an experimental diet composed of Mazuri® leafeater commercial primate biscuit (5MO2), fresh produce, at least 200 g of woody browse (high in fibre and tannins), approximately 91 g (per gorilla) of tamarind fruit and seeds (high in tannins), and a soluble fibre supplement (psyllium) consisting of 96 g (per gorilla) of Metamucil® (The Proctor and Gamble Company, Cincinnati, OH) and banana. The Metamucil® supplement for each group was created by mashing 480 g of product into 325 g of banana, dividing the mixture into five equal portions and freezing. During the midday feeding,

Table 1. Captive gorilla behavioural ethogram.

Undesired		
RR	Regurgitation & Reingestion	regurgitating and reingesting food/regurgitant
HB	Head Bang	repeated lifting and dropping of the head
RK	Rock	rocking, standing or sitting
PC	Pace	walking a path repeatedly
EC	Ear Cover	covering one or both ears with hands, arms, or shoulders
SM	Self-Mutilation	injuring self
CP	Coprophagy	eating feces
DU	Drink Urine	drinking urine
GT	Grind Teeth	grinding teeth
Feeding/Foraging		
EA	Eat	eating food
FG	Forage	foraging for food
Locomote		
CL	Climb	climbing up or down an object or structure
LO	Locomote	walking or running bipedally or quadrupedally
Other		
MO	Manipulate Object	manipulating object manually
SY	Solitary Play	playing with an object or playing by self
GS	Groom Self	cleaning self with hands or mouth
HI	Human Interaction	interacting physically or verbally with a zoo visitor or staff
OV	Out of View	out of view
RP	Raspberry	pursing lips and blowing air through them
DF	Defecate	defecating
UR	Urinate	urinating
Tension		
YA	Yawn	opening the mouth and showing teeth
SS	Scratch Self	scratching self with hand
TM	Tense Mouth	pursing lips
RG	Rigid Stance	walking or standing with stiff arms
UD	Undirected Display	charging or throwing an item without an intended target
JA	Jaw-Clenching	clenching jaw repeatedly (closed or open mouth, but without showing teeth)
CS	Clasp Self	grabbing and holding arms or legs, with one or both hands
PR	Palm Raspberry	placing hand against pursed lips and blowing
Resting		
SI	Sit	standard definition
STA	Stand	standard definition
SLE	Sleep	standard definition
LA	Lay	lay without sleeping
LE	Lean	standing or sitting, but leaning against a wall or structure
NE	Nest	fold leaves, or pack hay/wood wool to create a nest and lay or sit in it

Social		
Affiliative		
MZ	Muzzle to Muzzle	placing mouth on another gorilla's mouth
EM	Embrace	hugging
SL	Social Locomotion	walking side by side
GR	Allogroom	grooming another gorilla
SP	Social Play	playing with another gorilla
Aggressive		
DD	Directed Display	charging or throwing an item without an intended target
CB	Chest Beat	pounding on chest
SQ	Slap Object or Ground	hitting the ground or an object with an open hand
HQ	Hoot	vocalising through an "o" shaped mouth
ST	Stare	focusing eyes on one individual
AT	Arm Toss	rapid raising and dropping of arms
OM	Open Mouth	opening mouth with no teeth showing
PG	Pig Grunt	making low, short grunting sounds, in rapid succession
LU	Lunge	lurching forward toward an individual
AT	Attack	aggressive physical contact (i.e. hit, pull, etc.)
DP	Displace	taking over the physical location of another individually
BI	Bite	aggressively biting another individual
CH	Chase	running after another individual
GR	Growl	performing low grumbling vocalization
Submissive		
AV	Avoid	walking or running away (when not receiving an attack) from another individual
CR	Crouch	head turned down, with bent arms and legs
FL	Flee	running away (when receiving an attack) from another individual
PR	Present	turning backside or part of body (with stooped head) toward another individual, slowly approaching
RG	Rapid Glance	quickly looking at another individual and then looking away
Dominance		
REC AV	Receive Avoid	receiving a walk or run away (when not attacking) from another individual
REC RG	Receive Rapid Glance	receiving a quick look from another individual
Sexual		
SOL	Solicit	similar to "present", but with the intention of breeding
REC SOL	Receive Solicit	receive a "present" with the intention of breeding
COP	Copulate	standard definition

Table 2. Diet and nutritional differences of daily offered food among dietary trials in Experimental diets at Okc Zoo.

		Dry matter %	Dietary trial 1	Dietary trial 2	Dietary trial 3	Dietary trial 4
Food offered per gorilla (total g(DM g)	Fruit (grapefruit, grape, kiwi, pear, pineapple)	15	952.56 (142.88)	952.56 (142.88)	952.56 (142.88)	952.56 (142.88)
	Leafy green vegetables (Bok choy, collards, kale)	10	1088.61 (108.86)	1088.61 (108.86)	1088.61 (108.86)	1088.61 (108.86)
	Other vegetables (broccoli, celery, cucumber, eggplant, scallion)	8	1360.8 (108.6)	1360.8 (108.6)	1360.8 (108.6)	1360.8 (108.6)
	Root vegetables (carrot, sweet potato, turnip)	20	816.48 (163.3)	816.48 (163.3)	816.48 (163.3)	816.48 (163.3)
	Maintenance biscuit	95	453 (430.35)	0	0	453 (430.35)
	Leafeater biscuit	95	0	453 (430.35)	453 (430.35)	0
	Peanut	95	90.72 (86.18)	90.72 (86.18)	90.72 (86.18)	90.72 (86.18)
	Metamucil (Soluble fibre source)	95	0	96 (91.2)	96 (91.2)	0
	Tamarind (Tannin source)	7	0	91 (63.7)	91 (63.7)	0
	Woody browse (Insoluble fibre source)	5	200 (100)	200 (100)	0	0
Nutritional composition	Total DMI		1140.439	1295.339	1195.339	1040.439
	% Neutral Detergent Fibre NDF		23.87	22.59	19.47	19.64
	NDF Amount (g)		269.82	297.6	236.52	201.58
	Crude Protein CP		17.59	16.87	18.52	18.01
	% Tannin in dry matter (%) (Browse and Tamarind)		8.77193	12.64093	5.330544	0
	% Tannin diet DM		0.219298	0.290741	0.106611	0
	Kcal/gram		3.15	2.93	2.94	3.17
	Total Kcal		3560.7	3776.71	3483.34	3253.62

each individual received one supplement patty, fed by hand to ensure complete consumption. The third dietary trial (Group One: September 18–October 29; Group Two: September 23–November 2) (average temperature: 26°C) comprised diet two, without the addition of browse, and the fourth dietary trial (Group One: October 30–December 7; Group Two: November 3–December 15) (average temperature: 14°C) duplicated the original pre-trial diet, composed of Mazuri® maintenance commercial primate biscuit (5MA2) and fresh produce, without the addition of browse (Table 2).

Statistical analysis

Statistical analyses included G-test Tests for Independence and Kruskal-Wallis H Tests, with Bonferroni correction for multiple tests. G-tests were used as non-parametric alternatives to t-tests. All statistics were run in SPSS 25.0, Minitab 16.0 and a G-Test Calculator (McDonald, 2009).

Results

Overall gorilla behaviour

Overall, during the study, the gorillas at OKC spent the majority of their time resting (50.8%), followed by feeding and foraging (28.6%). Behaviour varied significantly by sex and age class (G=39.078, df=12, P<0.01), with males resting more (65.6% vs females at 48.6% and juveniles at 42.8%), and females feeding and foraging more than other individuals (30.1% vs males at 27.8% and juveniles at 25.33%). Juveniles locomoted more than others (8.1% vs males at 2.3% and females at 3.8%) and engaged more frequently in both social (17.5% vs males at 0.8% and females at 4.6%) and undesired behaviours (coprophagy and R/R) (0.8% vs male at 0.2% and female at 0.4%).

There were no significant differences in behaviours seen between groups, though behavioural trends were noted between groups (Table 3). The silverback of Group One fed and foraged,

Table 3. Individual average activity budgets (%)

	Group 1				
Behaviour	Silverback 1	Adult female 1	Adult female 2	Adult female 3	Juvenile female 1
Rest	61.5 ±0.4	54.3 ±0.04	41.7 ±0.3	48.9 ±0.4	40 ±0.3
Feeding/Foraging	30.3 ±0.2	32 ±0.2	32.3 ±0.2	26.9 ±0.2	27.5 ±0.2
Locomote	1.7 ±0.01	2.7 ±0.02	4.1 ±0.03	2.6 ±0.02	4.9 ±0.04
Social	0.8 ±0.01	1.6 ±0.01	5.5 ±0.04	5.8 ±0.04	9.6 ±0.1
Other	0.1 ±0	1.1 ±0.01	0.7 ±0.01	0.6 ±0	2.5 ±0.02
R/R	0 ±0	0 ±0	0 ±0	0.4 ±0	±0
Coprophagy	0.1 ±0	0.4 ±0	0.5 ±0.	±0	0.4 ±0.
Other undesired	0 ±0	0 ±0	0 ±0	0 ±0	0 ±0
Out of view	5.5 ±0.04	7.9 ±0.1	15.2 ±0.1	14.9 ±0.1	15.2 ±0.1
	Group 2				
Behaviour	Silverback 2	Adult female 4	Adult female 5	Juvenile male 1	Juvenile male 2
Rest	69.4 ±0.5	48.4 ±0.3	58 ±0.4	47 ±0.3	38.5 ±0.3
Feeding/Foraging	25.3 ±0.2	34.3 ±0.2	27.4 ±0.2	26.9 ±0.2	23.8 ±0.2
Locomote	2.8 ±0.02	4.7 ±0.03	3.9 ±0.03	6.8 ±0.1	9.4 ±0.04
Social	0.9 ±0.01	2.6 ±0.02	3 ±0.02	13.5 ±0.1	21.5 ±0.1
Other	0.2 ±0.	1.3 ±0	1 ±0.01	0.3 ±0.	0.5 ±0
R/R	0 ±0	0 ±0	0 ±0	0.1 ±0	0 ±0
Coprophagy	0.2 ±0.	0 ±0.3	0.6 ±0	0.2 ±0.	0.1 ±0
Other undesired	0±0	0±0	0.1 ±0	1.2 ±0.01	0 ±0
Out of view	1.1 ±0.1	8.4 ±0.1	6.2 ±0.04	4.1 ±0.03	6.3 ±0.04

engaged in more "other" behaviours and was coded as out of view more often than the silverback of Group Two; but differences did not reach significance. As Group One used an outdoor grotto (Yard One) that did not allow for full visual access, the higher rates of "Out of View" can be explained. Group Two rested, locomoted, and displayed more undesired behaviours than Group One. The majority (52%) of social behaviours in Group Two were attributed to the youngest male juvenile.

Significant individual behavioural variation was seen among the gorillas (Kruskal-Wallis H Test=53.636, df=6, P≤0.001) (Table 3). All gorillas showed relatively similar rates of feeding and foraging and locomotion. The three youngest gorillas were the most social (9.6–21.5%), while the two silverbacks rested more (61.5% and 69.4%, respectively) than the others.

As captive silverbacks tend to have more health problems than other sex and age classes, their behavioural responses to the dietary trials were closely examined. Though the silverbacks in this

Table 4. Total frequency of behaviours across phases (%)

Behaviour	Trial 1	Trial 2	Trial 3	Trial 4
Rest	69.09 ±0.49	56.74 ±0.4	40.37 ±0.29	32.44 ±0.23
Feeding/ Foraging	9.67 ±0.07	23.3 ±0.16	37.78 ±0.27	48.25 ±0.34
Locomote	4.46 ±0.03	4.78 ±0.03	3.7 ±0.03	4.47 ±0.03
Social	5.36 ±0.04	6.8 ±0.5	8.75 ±0.06	5.49 ±0.04
Other	0.87 ±0.01	0.65 ±0	0.93 ±0.01	0.77 ±0.01
R/R	0.07 ±0.	0 ±0.	0 ±0.	0.12 ±0
Coprophagy	0 ±0	0.24 ±0.	0.42 ±0	0.49 ±0
Other undesired	0.07 ±0	0.1 ±0	0.09 ±0	0.33 ±0
Out of view	10.4 ±0.07	7.39 ±0.05	7.96 ±0.06	7.64 ±0.05
Total	100	100	100	100

Table 5. Frequency of behaviour across phases - frequency within each phase (%)

	Inside				Outside			
Behaviour	Phase 1	Phase 2	Phase 3	Phase 4	Phase 1	Phase 2	Phase 3	Phase 4
Rest	67.33 ±0.48	30.32 ±0.21	13.7 ±0.1	9.33 ±0.07	69.49 ±0.5	62.14 ±0.44	44.63 ±0.32	37.91 ±0.27
Feeding/ Foraging	15.17 ±0.11	54.14 ±0.38	74.42 ±0.53	81.27 ±0.57	9.32 ±0.12	16.51 ±0.12	32.7 ±0.23	39.14 ±0.28
Locomote	4.17 ±0.03	6.35 ±0.04	3.52 ±0.02	2.33 ±0.02	4.06 ±0.03	4.85 ±0.03	3.65 ±0.03	5.81 ±0.04
Social	7.83 ±0.06	6.88 ±0.05	7.39 ±0.05	4.27 ±0.03	5.13 ±0.04	6.38 ±0.05	7.76 ±0.05	5.73 ±0.04
Other	4.17 ±0.03	0.81 ±0.01	0.61 ±0	1.3 ±0.01	9.75 ±0.07	8 ±0.06	8.84 ±0.06	8.77 ±0.06
R/R	0 ±0	0 ±0	0 ±0	0.53 ±0	0.03 ±0	0 ±0	0 ±0	0.05 ±0
Coprophagy	0 ±0	0.42 ±0	0.3 ±0.	0.33 ±0	0.02 ±0	0.23 ±0.	0.44 ±0.	0.31 ±0
Other undesired	0 ±0	0.95 ±0.01	0.06 ±0	0.57 ±0	0.08 ±0.	0.09 ±0.	0.1 ±0	0.27 ±0
Out of view	1.33 ±0.01	0.14 ±0	0 ±0	0.07 ±0	2.11 ±0.01	1.8 ±0.01	1.88 ±0.1	2 ±0.1

study behaved differently from all other age and sex classes, they also behaved differently from each other throughout the study, with the silverback of Group One resting less (61.5% vs 69.4%) and feeding and foraging more (30.3% vs 25.3%) than the silverback of Group Two. Moreover, more undesired behaviours were recorded for the silverback of Group Two than of Group One during dietary trial four (1.3% vs 0%).

Differences in gorilla behaviour: dietary trials compared

Individual gorilla behaviours were examined to see if overall activity budgets and behaviours varied with experimental dietary manipulations (Table 4). Overall, mean behaviours significantly varied among dietary trials (G=49.632, df=18, P<0.01). On average, all gorillas rested the most (dietary trial one: 69.1%, dietary trial two: 56.7%) and foraged the least (dietary trial one: 9.6%, dietary trial two: 23.3%) during the high fibre dietary trials and rested the least (dietary trial three: 40.4%, dietary trial four: 32.4%) and foraged the most (dietary trial three: 37.8%, dietary trial four: 48.3%) during the low fibre dietary trials. Additionally, gorillas performed the least amount of undesired behaviours during dietary trial one (8% of all undesired behaviours), while undesired behaviours particularly increased during dietary trials two, three, and four (21%, 23%, 48% of all undesired behaviours, respectively). There were no significant differences in locomotive, social, and “other” behaviours across dietary trials.

In general, the silverbacks behaved significantly differently across dietary trials (G=53.427, df=18, P<0.001). While they did not behave significantly differently from one another during dietary trials one, two and four, they did in trial three (G=18.01, df=6, P<0.05). Overall, the silverback of Group One fed and foraged (30.34% vs 25.28%) more than the silverback of Group Two, who engaged more frequently in undesired (0.1% vs 0.28%) and social behaviours (0.8% vs 0.85%), and locomoted (1.7% vs 2.84%) and rested (61.48% vs 69.41%) more. Both silverbacks rested more (84.06% vs 44.72%) and fed less (8.51% vs 48.37%) in dietary trial one when fibre levels were high relative to dietary trial four when fibre levels were lower.

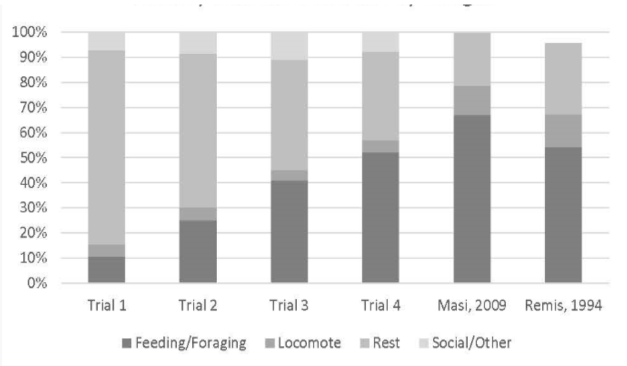

Figure 1. Activity budgets of OKC and wild gorillas. Wild data used is from Masi (2009) and Remis (1994).

The effects of temperature and fibre on gorilla behaviour

In order to determine if temperature was a confounding factor impacting overall gorilla behaviour, data were further analysed to compare behaviours while indoors compared to outdoors (Table 5). If temperature were a confounding factor, then it might be expected for gorilla behaviour to differ in a climate controlled (indoor) versus variable (outdoor) setting. Looking across all dietary phases, gorillas displayed significant differences in undesired (G=5.832, P<0.05), feeding and foraging (G=592.038, P≤0.001), “other” (G=5.294, P<0.05), and rest (G=446.749, P≤0.001) behaviours between indoor and outdoor enclosures (Table 5). When comparing behaviours within trials, it was found that gorillas did not display significant differences in indoor and outdoor behaviours in dietary trial one. In dietary trials two, three and four it can be seen that gorillas significantly fed more indoors (dietary trail two: G=215.476, P≤0.001; trial three:

G=80.843, P≤0.001; trial four: G=113.181, P≤0.001) and rested more outdoors (dietary trial two: G=125.798, P≤0.001; trial three: G=110.629, P≤0.001; trial four: G=165.98, P≤0.001). The only time that temperature was found to impact behaviour was a significant increase in coprophagy when gorillas were outdoors during dietary trial four, when it was colder (G=11.695; P≤0.001).

Discussion

This study examined behavioural changes among the captive gorillas at OKC during experimental dietary research intended to improve their health and well-being. One of the primary goals was to modify captive diets to be more nutritionally and functionally similar to those seen in the wild. Wild gorillas, who feed on high fibre foods, including woody browses, spend on average 50% of their day foraging (Masi 2008). It was hoped that activity budgets can more closely resemble those recorded for free-ranging gorillas, though it is acknowledged that additional methods should also be used in order to get a more comprehensive measure of well-being (Howell and Cheyne 2019).

As captive gorillas move and forage less than their wild counterparts, this study aimed to determine whether altering captive diets to bring them more in-line nutritionally and functionally with wild diets would have a positive impact on activity budgets, and potentially health (Cabana et al. 2018). While overall activity budgets of the OKC gorillas differed from those reported for wild gorillas (Figure 1), particularly in the case of silverbacks (Remis 1994; Masi 2008), coprophagy patterns followed those reported from field studies (Harcourt and Stewart 1978; Masi and Breuer 2018).

As a group, gorilla behaviour varied during each of the experimental dietary trials. Interestingly, though the gorillas had more outside access, more space, and access to woody browse during the summer months, the gorillas rested more, fed and foraged less, and engaged in undesired behaviour less frequently during those months. It is suggested that satiety had an impact on the reduction of foraging.

Frequencies of feeding and foraging behaviours were higher during dietary trials one and two, when the lower fibre diet was offered and woody browse was not available. These behavioural differences could be attributed to the gorillas feeling fuller while consuming the higher fibre diets, and thus not needing to feed and forage as much during the summer months. If temperature had played a role in behavioural expression, it would be expected to see gorillas resting more when outdoors in warmer months (dietary trials one and two). Moreover, it would be expected to see gorillas more active indoors compared to outdoors during those warmer months. However, these patterns were not observed, and in fact, gorillas exhibited the same behavioural patterns whether indoors or outdoors regardless of dietary trial. This is especially of interest during the first two dietary trials, when gorillas were offered woody browse only indoors, as it might be expected to see an increase in foraging and food processing as a result.

This study revealed the lowest rates of rare, but of interest, coprophagic behaviour when the gorillas were fed high tannin, high protein, high fibre woody browse during dietary trial one. The study found an increase in coprophagy in dietary treatments two and three, when tamarind was introduced, and the highest rates in dietary treatment four when the weather was coldest. Heightened rates of coprophagy in treatments two and three suggest that the gorillas may have been attempting to consume specific nutrients available in seeds whose protective coating had been softened during gut passage, as has been suggested for Dialium seed reingestion in wild gorillas (Masi and Breuer 2018) and chimpanzees (Krief et al. 2004). As both tamarind seed (Soong et al. 2004; Kumar and Bhattacharya 2008) and *Dialium* seeds (Rogers et al. 1990; Krief et al. 2004; Masi and Breuer 2018) are noted to have high protein, fibre and tannin content, this is of further interest.

Another explanation for heightened rates of coprophagy may have been the attempt to feed on fresh faeces as warm food in colder weather, as was seen in dietary treatment four, and also in wild mountain gorillas (Harcourt and Stewart 1978). This study suggests that there are multiple potential reasons for coprophagy in captive gorillas, none of which are maladaptive. Following the suggestion of Masi and Breuer (2018), further examination of coprophagy is necessary to better understand the driving mechanisms underlying this behaviour. Experimental dietary design in captivity is ideal for this line of inquiry.

Limitations

Though there was a period of two weeks between dietary trials for gorillas to biologically adjust to their new diets, behavioural data were still collected during the study, which could have led to potential behavioural carry-over from a previous trial. Additionally, due to the nature of the study, seasonal feeding schedule, timing and budgetary limitations, it was not possible to follow a research design of ABBBA (baseline diet, three experimental dietary trials, baseline diet), but instead a design of BBBA (three experimental dietary trials, baseline diet) was employed. In the future, it is advised to conduct experiments over multiple seasons, allow for longer adjustment periods, and design research based on the ABBBA model. This could also include sampling faeces and examining possible dietary effects on gut microbiome.

It should also be noted that wild gorillas forage throughout the entire day on high fibre foods, whereas the OKC gorillas were not fed ad-libitum, but on a three-meal schedule. Additionally, even with experimental high fiber diets, it is very difficult to create a nutritional composition similar to what is seen in the wild. For example, the highest NDF that was produced in the study was 23.87%, while NDF levels range between 41.03% and 67.41% (Calvert 1985; Masi 2008; Mondika 2006; Remis et al. 2001; Rogers et al. 1990).

Conducting similar dietary trials at multiple institutions, over a longer period of time, could help to tease apart potential impacts of dietary changes on captive gorilla activity budgets. Nevertheless, the addition of fibrous foods did seem to improve captive gorilla behavioural profiles, and may contribute to improving overall health, weight-management and well-being.

Conclusion

This study demonstrated that even moderate experimental dietary changes significantly altered activity budgets among the gorillas at OKC. The reduction in undesired behaviours with higher fibre diets is a useful finding for captive management. In this study, it is possible that higher fibre diets provided a satiety factor that reduced additional foraging; this observation in itself has implications for zoos concerned about weight management among gorillas.

The overall activity patterns of the gorillas at the Oklahoma City Zoo, like others in captivity, differed from those in the wild (Remis et al. 2001; Masi 2008); they rested more, fed and foraged less, locomoted less, and were more social than wild gorillas. An important, though unexpected, finding was the similarities of coprophagic behaviours between the gorillas housed at OKC and those in the wild. The least amount of undesired behaviours were observed when gorillas were fed a high fibre diet that did not include tamarind fruit. However, when tamarind fruit and seeds were introduced, an increase in undesired behaviours, particularly coprophagy, was observed. Moreover, the highest levels of coprophagy were observed when the gorillas were outdoors in the coldest months. Both of these behavioural patterns fit observations seen in the wild, and suggest that motivations for coprophagy in captive gorillas require further examination, and similar to other species, might be a normal behavior, depending on the circumstance (i.e. Hopper et al. 2016).

This study adds to the literature on captive gorilla activity budgets and demonstrates that dietary alterations do affect gorilla behavioural profiles. It provides options for zoos considering ways to reduce undesired behaviours with dietary strategies aimed at increasing satiety. Although in this study, tamarind seeds increased some behaviours considered undesirable in a zoo setting, the possible overall usefulness of high tannin foods for improving the health and wellbeing of captive gorillas may offset any possible negative side effects and should be further explored.

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