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Removing Milk from Captive Gorilla Diets: The Impact on Regurgitation and Reingestion (R/R) and Other Behaviors

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To test whether milk consumption facilitates performance of regurgitation and reingestion (R/R) in captive gorillas, an experiment was conducted in which milk was removed from the gorilla diet at Zoo Atlanta. The study was conducted using a withdrawal design (BTB), in which a baseline period (B) of 10 days was followed by a treatment period (T) of 10 days, followed by a return to the baseline feeding protocol (B) for 10 days. The experiment was conducted in two phases: first, identifying whether the incidence of R/R was decreased by replacing milk with an equal volume of diluted fruit juice, and second, identifying whether the incidence of R/R was decreased by replacing milk with a smaller volume of undiluted fruit juice. Removal of milk from the diet led to a significant decrease in R/R in both phases and an increase in feeding behavior during the first phase. Seasonal differences in baseline behavior were also observed. The current study provides evidence that removal of milk from the captive gorilla diet may reduce undesirable behaviors such as R/R and may be a step toward better approximating the natural diet for captive gorillas. Zoo Biol 18:515–528, 1999. © 1999 Wiley-Liss, Inc.

Key words: primate nutrition; abnormal behavior; rumination disorder in humans

INTRODUCTION

Mountain gorillas are primarily folivorous [Goodall, 1977; Fossey and Harcourt, 1977; Schaller, 1963; Watts, 1984, 1996], feeding on a wide range of herbaceous plant materials. In contrast, the natural diet of western lowland gorillas is composed largely of fruit when it is seasonably available [Kuroda et al., 1996; Nishihara, 1992,

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1995; Remis, 1997; Rogers et al., 1990, 1992; Tutin, 1996; Tutin and Fernandez, 1993; Williamson et al., 1990]. The fruit diet is diverse, with approximately 100 different types of fruit consumed [Kuroda et al., 1996; Nishihara, 1995; Remis, 1997; Rogers et al., 1992; Tutin and Fernandez, 1993; Williamson et al., 1990]. Western lowland gorillas also consume non-fruit food items such as leaves, bark, stems, seeds, and pith, which contribute to their relatively high-fiber, low-fat diet [Popovich et al., 1997]. Gorillas obtain most of the protein they need from leaves and shoots and most of the energy they require from high-fiber food items such as stems [Popovich et al., 1997; Rogers et al., 1990, 1992; Watts, 1996]. Wild gorillas do not consume animal products but do feed on insects, which make up a regular but relatively minor portion of the total diet [Kuroda et al., 1996; Nishihara, 1992; Tutin and Fernandez, 1992].

Unfortunately, it has proven difficult to replicate such a diverse diet for gorillas in captivity. Zoo nutritionists and managers often include a variety of fruits in the diet of captive gorillas, but cultivated fruits usually contain less protein and fiber, and more water and sugar, than those found in the native habitat [Popovich and Dierenfeld, 1997]. Captive gorillas are also fed leafy greens, other vegetables, natural browse items, cereals, and grains, in addition to nutritionally complete commercial primate biscuits which meet the majority of captive gorillas' nutritional needs [Popovich and Dierenfeld, 1997]. It is not uncommon for zoos to feed animal products such as meat, eggs, yogurt, or milk to gorillas even though these items are not nutritionally necessary and are not part of the western lowland gorilla's natural diet [Popovich and Dierenfeld, 1997].

Given their texture and tendency to spoil if left out, animal products are usually hand-fed to individual gorillas, unlike other food items that are easily scattered throughout exhibit space. From a behavioral standpoint, the consumption of handfed animal products may therefore consist of less extended processing or feeding time compared with scattered produce, browse, or forage items. Behavioral stereotypies have been associated with frustrated feeding motivation in confined animals fed nutritionally complete but diminutive meals and may contribute to the performance of regurgitation and reingestion (R/R) in captive gorillas [Lukas, 1999].

R/R refers to the voluntary, retrograde movement of food or fluid from the esophagus or stomach into the mouth [Lukas, 1999]. Common in captive gorillas, it has not been reported in wild populations. Although it has not been associated with health problems, it is unsightly to observe and may indicate deficiencies in the captive gorilla diet [Lukas, 1999]. A high rate of R/R in the indoor holding area at Zoo Atlanta [Lukas et al., 1997], especially at the end of the day, led to an examination of dietary factors that might influence such behavior at that time. As it was only offered at the evening meal, milk emerged as a factor that might uniquely contribute to the elevated levels of R/R in the post-prandial period. Milk was historically considered an essential item in the captive gorilla diet, but now appears to be a nutritionally redundant component of a complete diet composed of manufactured primate biscuits and produce items.

Gorilla regurgitation has been compared with rumination disorder in humans [Gold and Bres, 1986; Lukas, 1999]. Because post-meal rumination of food in humans is facilitated by large quantities of liquid [Shay and Johnson, 1984], late afternoon peaks of R/R may have been enhanced by the relatively large quantity of milk that each gorilla quickly consumed during the indoor evening meal at Zoo Atlanta.

Previous research suggests that post-prandial behavioral stereotypies in dairy calves are specifically elicited by ingestion of milk [de Passille and Rushen, 1997; de Passille et al., 1997]. Therefore, the impact of milk versus other liquids on eliciting R/R in gorillas was in question.

To test whether milk consumption influences the incidence of gorilla R/R, an experiment was conducted in which milk was removed from the gorilla diet. If late afternoon peaks in R/R were associated with consumption of milk at the evening meal, then removal of milk from the diet might result in a significant decrease in R/R at that time.

METHODS

Subjects

The subjects were seven male and 12 female western lowland gorillas at Zoo Atlanta. Ranging in age from 2 to 41 years, 11 subjects were captive born and eight were wild caught.

Diet Preparation and Analysis

Specific food items for each diet were chosen according to seasonal availability (see Appendix). A commercial primate biscuit (Lab Diet 5045, High Protein Monkey Diet, Purina Mills, Inc.®, Brentwood, MO) provided the basis for a nutritionally complete diet. The milk used in the baseline periods was non-fat powdered cow's milk mixed with water according to package directions. The type of juice (apple, orange, or pineapple) used in the treatment periods varied according to each individual's needs but remained consistent through each phase. A forage mix was scattered throughout the exhibit each day for the entire study. Favored food items were chosen that would not greatly add calories (sugar or fat) to the diet. By as-fed weight, the forage mix consisted of 40% miniature shredded wheat, 40% Cheerios®, 16% air-popped popcorn, and 4% raisins.

Preliminary formulation of the diets for each of the studies was done using the Animal Nutritionist® software program, which gave approximate nutritive values. After the study commenced, a sample of each diet was prepared for analysis. The sample diet was reduced in volume but composed of the same food products, in the same ratios, as the actual diet. The sample was diced and blended to a puree, which was frozen in thin layers in zip-locked freezer bags in a walk-in freezer set at 0°F. The frozen samples were then shipped on dry ice for analysis. Unopened cans of juice, a sample of forage mix, and a sample of powdered milk were also subjected to laboratory analysis. All food items underwent the same analysis at the same laboratory.

Procedure

In general, the normal daily husbandry remained unchanged for this study. The gorillas were fed four daily meals as illustrated in Table 1. The time and location of these meals remained constant throughout the study. An individual's diet was calculated according to food allowances (FA), where one FA was the amount of food provided for one adult female gorilla. The amounts offered to individuals in other age/sex classes were then based on this amount (Table 2).

Removal of milk from the diet was conducted using a withdrawal design

TABLE 1. Feeding protocol for gorillas at Zoo Atlanta

	AM indoor	AM outdoor	PM outdoor	PM indoor
Time fed	8:00–8:30	9:30–10:00	2:00–3:30	4:30–5:00
Location	Holding	Exhibit	Exhibit	Holding
Meal	1/2 biscuit ration	Vegetables	Fruit	1/2 biscuit ration milk
Method	Hand-fed to individuals	Scattered by keepers before gorillas occupied yard	Tossed by keepers into yard at feeding time	Hand-fed to individuals; milk offered in a large plastic cup

(BTB), in which a baseline period (B) of 10 days was followed by a treatment period (T) of 10 days, followed by a return to the baseline feeding protocol (B) for 10 days. One day of transition, in which no data were collected, was allotted between each period.

Because there are husbandry advantages to routinely administering liquid in a cup to individual gorillas, our goal was to replace the milk with a smaller volume of an alternative liquid. The experiment therefore consisted of two phases: first, identifying whether replacement of milk with an equal volume of fruit juice diluted with water reduced R/R and, second, identifying whether replacement of milk with a smaller volume of undiluted fruit juice reduced R/R. Phase 1 was conducted between November and December 1997, and Phase 2 was conducted between June and July 1998. In Phase 1, milk was replaced by fruit and vegetables in proportion to their caloric contribution in the baseline diet, with a portion of the fruit ration served as 8 oz of juice during the indoor evening meal instead of milk. To isolate the effect of removing milk from the diet (as opposed to reducing the amount of liquid in the diet), the juice was diluted with water to equal in volume the amount of milk that was offered during the baseline diet (32 oz). The replacement fruits and vegetables were added to the normal ration of fruits and vegetables and were fed during the outdoor morning (vegetables) and outdoor evening (fruit) meals as usual. Replacement values were based on exchanging equal proportions of energy (calories) rather than volume. The baseline and treatment diets for Phase 1 are presented in Table 3 in terms of nutritional composition for one FA.

In Phase 2, the baseline milk ration was replaced by fruit and vegetables in proportion to their caloric contribution in the baseline diet, with a portion of the fruit ration served as 8 oz of juice (undiluted) during the indoor evening meal instead of milk. As in Phase 1, replacement values were based on exchanging equal proportions of energy (calories) rather than volume. Similarly, the replacement fruits and vegetables were added to the normal ration of fruits and vegetables and were fed during the outdoor morning (vegetables) and outdoor evening (fruits) meals. The baseline and treatment diets for Phase 2 are presented in Table 4 in terms of nutritional composition for one FA.

TABLE 2. Food allowances for gorillas at Zoo Atlanta

Age class	Silverback	Blackback	Subadult	Adult	Juvenile	Juvenile	Infant
Sex	Male	Male	Male	Female	Female	M/F	M/F
Age (years)	>12	8–12	5–7	>6	5	3–4	1–2
Food allowance ratio	2	1.5	1	1	0.75	0.50	0.25

TABLE 3. Nutritional composition of baseline and treatment diets, per food allowance, for Phase 1

As fed	Weight (g)	Dry matter (g)	Water (g)	Crude protein (g)	Crude fiber (g)	ADF (g)	Fat (g)	ME (kcal)
Baseline Phase 1								
Milk	826.3	122.3	714.0	34.6	2.5	1.6	2.5	444.4
Biscuit	480.0	442.3	37.7	124.9	22.9	37.2	14.3	1,750.6
Fruit	598.9	80.0	513.0	3.8	4.8	6.3	1.0	289.4
Vegetables	984.0	137.4	847.0	23.0	11.2	17.4	1.6	443.1
Forage mix	58.4	54.6	3.8	6.0	1.0	2.6	0.9	207.2
Totals	2,957.6	836.6	2,115.5	192.3	42.4	65.1	20.3	3,134.7
Treatment Phase 1								
Milk	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Biscuit	480.0	442.3	37.7	124.9	22.9	37.2	14.3	1,750.6
Fruit	397.0	53.0	344.0	2.5	3.1	4.2	0.6	191.7
Fruit juice	246.7	29.6	217.1	0.3	0.6	1.5	0.8	114.8
Water to dilute	589.6	0.0	589.6	0.0	0.0	0.0	0.0	0.0
Vegetables	1,507.0	211.0	1,296.0	35.3	17.3	26.7	2.4	680.5
Forage mix	58.4	54.6	3.8	6.0	1.0	2.6	0.9	207.2
Totals	3,278.7	790.5	2,488.2	169.0	44.9	72.2	19.0	2,944.8
Difference from baseline	321.1	–46.1	372.7	–23.3	2.5	7.1	–1.3	–189.9

ADF, acid detergent fiber; ME, metabolizable energy (extrapolated from human studies).

TABLE 4. Nutritional composition of baseline and treatment diets, per food allowance, for Phase 2

As fed	Weight (g)	Dry matter (g)	Water (g)	Crude protein (g)	Crude fiber (g)	ADF (g)	Fat (g)	ME (kcal)
Baseline Phase 2								
Milk	836.3	122.3	714.0	34.6	2.5	1.6	2.5	444.4
Biscuit	480.0	442.3	37.7	124.9	22.9	37.2	14.3	1,750.6
Fruit	602.5	80.4	522.1	4.1	4.7	6.4	1.0	290.8
Vegetables	1,001.1	140.2	860.9	23.5	11.5	17.7	1.6	452.1
Forage mix	58.4	54.6	3.8	6.0	1.0	2.6	0.9	207.2
Totals	2,978.3	839.8	2,138.5	193.1	42.6	65.5	20.3	3,145.1
Treatment Phase 2								
Milk	0.0	0.0	0.0	0.0	0.0	0	0	0.0
Biscuit	480.0	442.3	37.7	124.9	22.9	37.2	14.3	1,750.6
Fruit	781.8	104.4	677.4	5.0	6.1	8.3	1.3	377.6
Fruit juice	246.7	29.6	217.1	0.3	0.6	1.5	0.8	114.8
Water to dilute	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0
Vegetables	831.3	116.4	714.9	19.5	9.5	14.7	1.3	375.4
Forage mix	58.4	54.6	3.8	6.0	1.0	2.6	0.9	207.2
Totals	2,398.2	747.3	1,650.9	155.7	40.1	64.3	18.6	2,825.6
Difference from baseline	–580.1	–92.5	–487.6	–37.4	–2.5	–1.2	–1.7	–319.5

ADF, acid detergent fiber; ME, metabolizable energy (extrapolated from human studies).

Data Collection

Subjects were observed during the hourly post-prandial period of the evening indoor meal. Short (5-minute) focal sessions were conducted with instantaneous point sampling at 15-second intervals. In addition, all occurrences of R/R attempts, R/R bouts, stealing regurgitant from another, and staring within close range at a regurgitating gorilla were recorded for the focal animal. All occurrences of agonistic behavior within the focal animal's social group were also recorded.

Data Analysis

A multiple ANOVA (MANOVA) for repeated measures was used to compare baseline and treatment levels of behavior in nine behavioral categories: R/R, feeding on hay, drinking water, other undesirable behavior, self-directed behavior, other active behavior, inactivity, affiliative social behavior, and agonistic social behavior. Probability of £0.05 was considered statistically significant. If the overall MANOVA was significant, planned, post hoc hypothesis testing was conducted to determine whether there were significant behavioral differences between the baseline and treatment conditions and between the two baseline conditions within each phase.

A repeated-measures MANOVA was used to determine whether there were significant behavioral differences in baseline conditions between the two phases. An analysis of covariance (ANCOVA) was then used to determine whether there were significant behavioral differences in treatment conditions between the two phases. The baseline data served as a covariate in determining whether differences in behavior between treatment conditions were related to dietary or seasonal variations. All analyses were performed using Systat© 7.0.

RESULTS

The overall MANOVA was significant for Phase 1 ($F = 14.779$, $P < 0.0001$). Specific hypothesis testing results are presented in Table 5. Replacing milk with an equal volume of diluted fruit juice resulted in a 28% decrease in R/R and a doubling of the percentage of time gorillas spent eating hay. In addition, decreases in inactivity, drinking water, and affiliative social behaviors were observed during the treatment period. There were no changes in other undesirable behaviors such as eating or manipulating feces, self-clasping, or hair-plucking, and there were no changes in self-directed behavior, agonistic social behavior, or other active behaviors such as nest-building or object examination. There were no differences between the two baseline periods in any of these behaviors.

The overall MANOVA was also significant for Phase 2 ($F = 38.373$, $P < 0.0001$). Specific hypothesis testing results are presented in Table 6. In contrast to Phase 1, R/R was the only behavior that changed after the removal of milk in Phase 2. Replacing milk with a decreased volume of fruit juice resulted in a 37% decrease in R/R. There were no other changes in behavior during the treatment period and there were no differences between the two baseline periods for any of the behaviors within this study.

A repeated-measures MANOVA revealed seasonal differences in baseline gorilla behavior. Although the baseline diet was the same in both Phase 1 and Phase 2 of this study, differences in behavior were apparent between winter baseline periods (Phase 1) and summer baseline periods (Phase 2). These results are presented in Table 7.

TABLE 5. Comparisons of gorilla behavior between conditions in Phase 1

	Baseline (32 oz milk)	Treatment 32 oz diluted (fruit juice)	Baseline (32 oz milk)	Hypothesis test: baselines vs. treatment	Probability (α = 0.05)
Scan data (percentage of time)					
R/R	10.6%	7.6%	9.7%	F = 5.042	$P = 0.038$
Eat hay	10.4%	22.2%	11.5%	F = 8.960	$P = 0.008$
Inactive	37.2%	28.8%	35.2%	F = 6.067	$P = 0.024$
Drink water	2.3%	1.2%	2.8%	F = 5.763	$P = 0.027$
Social (affiliative)	4.9%	2.2%	4.5%	F = 6.067	$P = 0.024$
Other undesirable	3.3%	2.5%	3.6%	F = 1.808	ns
Self-directed behavior	6.6%	8.1%	9.9%	F = 0.018	ns
Social (agonistic)	0.4%	0.1%	0.2%	F = 3.185	ns
Other active behavior	17.6%	20.7%	21.0%	F = 0.332	ns
All-occurrence data (no. per 5 - min)					
R/R attempts	0.035	0.060	0.045	F = 0.431	ns
R/R bouts	0.509	0.353	0.519	F = 2.720	ns
Feed on another's regurgitant	0.240	0.120	0.090	F = 0.304	ns
Examine another engaging in R/R	0.047	0.053	0.038	F = 0.149	ns
Agonistic behavior	0.135	0.158	0.113	F = 0.468	ns

ns, no significance.

Gorillas were more active during the winter baseline periods than in the summer ones, consuming more hay and engaging in more R/R, other undesirable behavior, and other active behavior. Gorillas were more inactive during the hot summer, engaging in more affiliative social behavior and self-directed behavior than in the win-

TABLE 6. Comparisons of gorilla behavior between conditions in Phase 2

	Baseline (32 oz milk)	Treatment 32 oz diluted (fruit juice)	Baseline (32 oz milk)	Hypothesis test: baselines vs. treatment	Probability (α = 0.05)
Scan data (percentage of time)					
R/R	5.9%	3.7%	6.3%	F = 8.508	$P = 0.010$
Eat hay	1.3%	1.6%	0.3%	F = 0.767	ns
Inactive	45.5%	46.6%	46.3%	F = 0.115	ns
Drink water	3.4%	3.3%	2.9%	F = 0.011	ns
Social (affiliative)	8.4%	8.0%	11.7%	F = 1.221	ns
Other undesirable	1.0%	1.2%	2.0%	F = 0.594	ns
Self-directed behavior	17.1%	17.5%	13.9%	F = 1.681	ns
Social (agonistic)	0.1%	0.3%	0.4%	F = 0.136	ns
Other active behavior	16.0%	16.7%	15.0%	F = 0.605	ns
All-occurrence data (no. per 5 - min)					
R/R attempts	0.022	0.017	0.011	F = 0.000	ns
R/R bouts	0.428	0.256	0.422	F = 4.684	$P = 0.045$
Feed on another's regurgitant	0.061	0.061	0.072	F = 0.239	ns
Examine another engaging in R/R	0.056	0.056	0.072	F = 0.221	ns
Agonistic behavior	0.089	0.111	0.233	F = 1.342	ns

ns, no significance.

TABLE 7. Comparisons of gorilla behavior between baseline conditions in Phase 1 and Phase 2

Baseline	Phase 1 winter	Phase 2 summer	Repeated measures MANOVA	Probability ($\alpha = 0.05$)
Scan data (percentage of time)				
R/R	10.2%	5.8%	F = 116.507	*P* = 0.001
Eat hay	10.9%	0.8%	F = 13.938	*P* = 0.002
Inactive	36.3%	45.9%	F = 13.307	*P* = 0.002
Drink water	2.5%	3.0%	F = 2.888	ns
Social (affiliative)	4.8%	9.5%	F = 13.958	*P* = 0.002
Other undesirable	3.5%	1.4%	F = 24.494	*P* = 0.001
Self-directed behavior	8.1%	15.0%	F = 14.716	*P* = 0.001
Social (agonistic)	0.3%	0.3%	F = 1.597	ns
Other active behavior	19.1%	15.7%	F = 19.468	*P* < 0.001
All-occurrence data (no. per 5 min)				
R/R attempts	0.039	0.016	F = 1.065	ns
R/R bouts	0.513	0.403	F = 9.474	*P* = 0.007
Feed on another's R/R	0.174	0.063	F = 2.223	ns
Examine another's R/R	0.043	0.061	F = 0.201	ns
Agonistic behavior	0.125	0.161	F = 0.026	ns

ns, no significance.

ter. There were no differences in the amount of time gorillas spent drinking water or engaging in agonistic social behavior between summer and winter baseline periods.

Differences in behavior were also observed between treatment periods of Phase 1 and Phase 2. To account for the seasonal differences in behavior, the two treatment phases were compared with baseline data as a covariate. Results showed that there were no significant behavioral differences between the two treatment conditions that could not be attributed to season (Table 8).

Scan data from both phases of this study were combined to describe qualitative aspects of gorilla R/R. The regurgitation cycle consisted of three components: behaviors that consistently occurred just before regurgitation (pre-R/R), actual regurgitation, and reingestion. The majority of the regurgitation cycle was spent on reingestion (77%) compared with pre-R/R behaviors (17%), with actual regurgitation taking up the least amount of time (5%). Pre-R/R behaviors most often consisted of bending over (34%), massaging or poking at the stomach (33%), clearing a spot on the floor (26%), and other behaviors such as head shaking and rocking (7%). During the regurgitation phase of the cycle, food was most often regurgitated onto the floor (65%), into the hand (27%), or within a closed mouth (8%). The regurgitant was then reconsumed using the hand (47%), by licking it directly off the floor (38%), or chewed within the mouth (15%).

When analyzed separately, there were no differences in pre-R/R or regurgitation behaviors between baseline and treatment in either phase of the study. However, there was a significant decline in the percentage of time spent reingesting regurgitant during the treatment conditions compared with baseline in both Phase 1 (F = 7.237, *P* = 0.015) and Phase 2 (F = 6.442, *P* = 0.021). When summarized across both phases, all occurrence data revealed that the hourly rate at which gorillas stole regurgitant from one another was 1.06. Of the 89 times this behavior was observed (in 83.5 hours of data), 55 were an infant male

TABLE 8. Comparisons of gorilla behavior between treatment periods of Phase 1 and Phase 2 with baseline data as covariate

	Treatment	
	Phase 1 winter	Phase 2 summer
Scan data (percentage of time)		
R/R	7.6%	3.5%
Eat hay	22.2%	1.5%
Inactive	28.8%	47.0%
Drink water	1.2%	3.1%
Social (affiliative)	2.2%	7.6%
Other undesirable	2.5%	1.1%
Self-directed behavior	8.1%	16.8%
Social (agonistic)	0.1%	0.3%
Other active behavior	20.7%	17.0%
All occurrence data (no. per 5 min)		
R/R attempts	0.060	0.016
R/R bouts	0.353	0.242
Feed on another's R/R	0.120	0.058
Examine another's R/R	0.053	0.053

None of the values was statistically different (a = 0.05) when the covariate was controlled.

stealing from a tolerant silverback, 21 were an adult female stealing from the same silverback, and 10 were infants or juveniles stealing from adult females. The hourly rate at which gorillas were observed staring at a regurgitating gorilla was 0.5. Of the 46 times this behavior occurred, 31 were infants or juveniles observing a regurgitating adult.

DISCUSSION

Results of the milk removal study suggest that milk was indeed a contributing factor to the performance of R/R in the post-prandial period of the evening meal. Several points may be concluded from this study. First, replacement of milk with an equal volume of diluted fruit juice demonstrated that milk has properties beyond those of this alternative liquid that may contribute to the performance of R/R. Although R/R still occurred when an equal volume of diluted fruit juice was consumed, it was reduced by 28%. Milk may contribute to R/R because its thick, coating properties facilitate the regurgitation of food or because it is a favored food item that gorillas prefer to consume again and again.

Second, when an equal volume of diluted fruit juice replaced milk as the evening beverage, gorillas doubled their consumption of hay in the post-prandial period of the evening meal. Removing milk from the diet may have actually further decreased satiety after the evening meal, resulting in increased feeding in the post-meal period. Determining why gorillas increased feeding rather than R/R in this condition deserves further investigation.

Third, seasonal differences in behavior were observed. Gorillas were less active during the summer than winter as indicated by time spent inactive and time spent engaging in self-directed behavior in the post-prandial period of the evening meal. In addition, gorillas spent significantly less time engaging in R/R during the summer than winter. Seasonal differences in behavior alone accounted for a 44% decrease in R/R between the winter and summer baseline periods.

Fourth, replacing milk with a lesser volume of undiluted fruit juice during the summer led to an additional 37% decrease in R/R. Unlike during the winter phase, no other behaviors were affected by the treatment, perhaps due to the general malaise of gorillas during the hot climatic conditions.

Finally, a number of observations can be made regarding the morphology and ontogeny of R/R behavior. For example, the majority of the R/R cycle was spent reconsuming regurgitant, which supports the suggestion that gorillas engage in R/R to prolong time spent feeding [Loeffler, 1982; Lukas, 1999]. Removal of milk from the gorilla diet did not affect time spent engaging in pre-R/R or regurgitation behavior but did reduce time spent reconsuming regurgitant. If removal of milk can further increase the amount of time gorillas spend feeding on appropriate forage items, zoos can optimize exhibition of natural behavior for this species by discontinuing the provision of milk.

Replacing R/R with appropriate foraging behavior is particularly important if youngsters are learning this behavior through social observation. The results of this study suggest that infant and juvenile gorillas do observe adults while they regurgitate and further consume regurgitant they obtain from a regurgitating adult. On several occasions, infant and juvenile gorillas were observed watching an adult engage in R/R and subsequently assuming similar body postures and movements while expectorating and reconsuming what appeared to be saliva. Further research is needed to confirm anecdotal observations that suggest the behavior might be socially enhanced, if not learned. Given that possibility, it is important for managers of captive gorillas to provide an abundance of species-appropriate feeding opportunities to minimize the performance of R/R by all social group members.

Overall, the results from this study suggest that removing milk from the gorilla diet at Zoo Atlanta significantly reduced R/R in the indoor holding facility after the evening meal and, in the winter, additionally increased the amount of time gorillas spent feeding at that time. These findings have implications for the nearly 30% of zoos surveyed in 1995 that continue to feed milk to gorillas on a daily basis [Popovich and Dierenfeld, 1997]. Although R/R may occur throughout the day, removing milk from the diet would at least reduce the incidence of this behavior by some animals at certain times in the day and may even promote alternate and more appropriate feeding behavior. This suggests that given the opportunity, gorillas may transfer the expression of frustrated feeding motivation from a post-prandial stereotypic behavior such as R/R [Lukas, 1999] to a more species-typical activity such as feeding on foraging materials. Such a change requires that managers of captive gorillas provide items on which gorillas may feed or from which they might otherwise increase their behavioral repertoire.

In the captive gorilla husbandry manual, Popovich and Dierenfeld suggested that “no animal or dairy products should be in the formulation of diets provided to gorillas” [1997, p. 144]. They further endorsed a high-fiber, low-fat diet composed of vegetables, dark green leafy produce or browse, dry high-fiber, low-fat diet composed of vegetables, dark green leafy produce or browse, dry high-fiber primate biscuits, fruit, and occupational forage material such as grains, nuts, or seeds. The current study provides evidence that the removal of milk from the captive gorilla diet has the potential to reduce R/R and may be a step toward better approximating the natural diet for captive gorillas. Further research should be conducted to develop a practical diet that zoos can administer that would aggressively reduce or eliminate R/R from the captive gorilla behavioral repertoire.

CONCLUSIONS

1. Removing milk from a gorilla diet led to a decrease in R/R in the postprandial period. Milk has properties beyond those of an alternative liquid that may contribute to the performance of R/R.

2. During the winter months, removing milk from the diet also led to increased consumption of high-fiber forage after the usual evening meal.

3. Seasonal differences in baseline behavior were observed. Overall, gorillas were more active during the winter than summer. Specifically, gorillas ate more hay and engaged in more R/R during the winter than summer.

4. The majority of the R/R cycle is spent reconsuming regurgitated food items, which supports the idea that gorillas engage in R/R to prolong the feeding period.

5. Infant and juvenile gorillas spend time observing adults while they engage in R/R and consume regurgitant they obtain from regurgitating adults. Further research is needed to confirm anecdotal observations that suggest the behavior might be socially enhanced, if not learned.

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APPENDIX. Amounts of specific fruits and vegetables (in grams) in one food allowance for baseline and treatment diets in Phase 1 and Phase 2

	Phase 1		Phase 2	
Food	Baseline	Treatment	Baseline	Treatment
Fruits				
Apple	180.0	119.4	181.2	181.2
Orange	150.0	99.6	150.8	150.8
Banana	84.1	55.5	84.3	198.5
Grapefruit	68.9	45.6	69.3	134.4
Plum	75.9	50.4	*	*
Peach	*	*	76.6	76.6
Lime	40.0	26.6	*	*
Lemon	*	*	40.3	40.3
Leafy greens				
Collards	66.5	102.0	59.8	59.8
Kale	50	76.7	45.3	25.0
Parsley	40.8	62.5	36.7	36.7
Vegetables				
Green beans	100.0	153.1	115.1	0.0
Cabbage	80.0	122.4	92.0	92.0
Broccoli	75.3	115.2	86.5	60
Carrot	65.0	99.5	74.8	74.8
Celery	80.0	122.4	92.0	92.0
Green peppers	59.0	90.3	67.8	67.8
Yellow squash	62.4	95.8	72.0	72.0
Starch				
Sweet potato	97.0	148.6	82.5	168.8
Acorn squash	111.1	170.1	94.2	0.0
Corn on the cob	97.0	148.6	82.5	82.5