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RESEARCH ARTICLES

Small Ruminants: Digestive Capacity Differences Among Four Species Weighing Less Than 20 Kg

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Small ruminants are generally classified as either browsers or frugivores. We compared intake and digestion in one browsing species, the pudu *(Pudu pudu),* body weight 9 kg, and three frugivorous species, the red brocket *(Mazama americana),* 20kg, the bay duiker *(Cephalophus dorsalis),* 12kg, and Maxwell's duiker *(C. maxwellii),* 9 kg. Rations comprised: a commercial grain and alfalfa pellet, a small amount of vegetables, and mixed hay. Across species, neutral-detergent fiber (insoluble fiber) consumed averaged 34.2 ± 2.6% of dry matter (DM) while the crude protein consumed averaged 16.1 ± 0.5% DM. Apparent DM digestion was similar in pudu (75.2 ± 4.7%), brocket (73.2 ± 1.1%), and Maxwell's duikers (73.0 ± 2.8%), and significantly lower *(P* = 0.0167) in bay duikers (67.1 ± 4.3%). There were significant differences among species in digestibilities of neutral-detergent fiber, hemicellulose, and cellulose, but they did not follow body size differences, since larger species were expected to show higher digestion coefficients for fiber compared to smaller species. The type of fiber fed may have influenced these results. Frugivores may be adapted to a diet of soluble fibers, as might be found in wild fruits, instead of the insoluble fibers in the diet fed. Passage trials were conducted on the two smallest species. The mean transit time for pudu was 29.9 ± 0.8 hr, and for the Maxwell's duiker was 42.2 ± 6.4 hr.

Key words: pudu, red brocket, Maxwell's duiker, bay or black-backed duiker, nutrition

INTRODUCTION

In discussions comparing ruminants, their digestive capacities, and their feeding system stratification, debate has centered around whether body size was the primary adaptive factor in ruminant digestive evolution ~Robbins et al., 1995; Gordon and Illius, 1994], or whether feeding ecology and diet were primary and body weight

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differences were secondary [Hofmann, 1989]. Based on stomach structure differences, Hofmann [1989] theorized that browsers (and frugivores) had evolved a lower digestive capacity for fiber, compared to grazers, irrespective of body size. Gordon and Illius [1994] presented data in support of the primacy of body weight, while Robbins et al. [1995] presented results refuting the theory that concentrate selectors (browsers) and intermediate feeders digested fiber less well than did grazers.

This study compared one small browsing South American temperate deer, the pudu *(Pudu pudu),* body weight 9 kg, to three frugivorous species, the South American rainforest deer, red brocket *(Mazama americana),* 20 kg, and two African rainforest duikers or antelopes, Maxwell's duiker *(Cephalophus maxwellii),* 9 kg, and bay duiker *(C. dorsalis),* 12 kg. Free-ranging bay duikers, however, were reported to weigh 20—23 kg [Hart, 1986; Karesh et al., 1995].

Pudu and red brocket are both diminutive members of the *Cervidae* family native to Latin America. The pudu is found in temperate rain forests of Chile and Argentina [MacNamara, 1981]. It is considered a vulnerable species [IUCN, 1990], with 90% of its historic habitat disrupted. Its feeding ecology is that of a browser [Eldridge et al., 1987], eating succulent leaves like *Fuchsia* spp. The brocket inhabits tropical, lowland areas throughout South and Central America [Robinson and Redford, 1991]. It is an important game animal to subsistence hunters [Aranda, 1991]. This diurnal animal feeds primarily on fruits, as well as fallen flowers, fungus, and some succulent leaves [Branan and Marchinton, 1985; Branan et al., 1985; Bodmer, 1989, 1990].

Duikers are native to Africa and constitute important sources of protein to local people. Maxwell's duiker is native to west Africa while the bay duiker is native to west and central Africa [Macdonald, 1984]. They occur sympatrically in west Africa. Free-ranging bay duikers consume diets comprising 80—89% fruit [Feer, l989a,b; Dubost, 1984]. Hofmann and Stewart [1972] classify duikers in general as selectors of juicy, concentrated herbage, especially fruit and dicot foliage. They are ruminants in the *Bovidae* family, but the rumen is small and simple, adapted to a quick turnover of food and a high fermentation rate. The omasum is reduced compared to larger antelope and cattle, with few leaflets but with a horny papillation suggesting a straining function [Hofmann and Stewart, 1972]. No investigations have been reported on the digestive capacity of Maxwell's duiker; one has been performed on the bay duiker, a nocturnal animal [Hart, 1986].

The purpose of this study was to compare digestive capacities among ruminants of differing body weights but all smaller than the animals used in the previous comparisons [Gordon and Illius, 1994; Robbins et al., 1995]. We also compared digestion coefficients between two subcategories within Hofmann and Stewart's [1972] "concentrate selector" category: browsers vs. frugivores.

MATERIALS AND METHODS

Intake and Digestibility Trial

All feeding trials were performed in the animals' home pens at the Wildlife Conservation Park (WCP), Bronx, New York. Diet digestibility trials on the Maxwell's duikers were performed during November 1991, using nine mature animals, housed singly or in mixed-sex pairs or trios. The trials on the bay duikers were performed concurrently and included seven mature animals, housed as one trio and four

TABLE 1. Diets consumed by four species of small ruminants at the Wildlife Conservation Park, Bronx, NY

Food item	*Pudu pudu* (n=6) DW g[a]	*Mazama Americana* (n=3) DW g	*Cephalophus maxwellii* (n=6) DW g	*C. dorsal is* (n=5) DW g
Grain pellet	216	326	253	175
Kale	5	3	-	-
Yam	8	11	8	8
Hay	70	82	44	121
Total, g	299	422	305	304
Body weight, kg	9	20	9	12

[a]Dry weight, grams.

singles. Data from each pen were averaged and treated as one animal; consequently, for statistical purposes the Maxwell's had an 'n' of 6 and the bays had an 'n' of 5.

Trials on the pudus were performed during December 1991, using 10 mature animals, also housed singly or in mixed-sex pairs or trios. The trials on the brockets were concurrent and included six mature animals, housed as one trio, one pair, and one single. Data were averaged as described above, and for statistical purposes the pudus had an 'n' of 6 and the brockets an 'n' of 3. There was no sexual dimorphism in weight between males and females of any species (WCP veterinary records), so problems were not anticipated by these groupings.

Pens housing the animals varied from 1.9 m to 3.3 m wide by 3 - 3.3 m long by 2.7 - 3.3 m high with cement floors, covered by woodchip bedding. Weighed amounts of grain pellets, hay, and vegetables were provided daily in large rubber basins over a 6 day acclimation and a 6 day collection period. The pellet and mixed hay were offered in excess. Almost identical diets were offered to the four species in this study; established diets were not altered for the study. Duikers were not offered kale, which was considered a treat to be used at the discretion of the keeper. Water was supplied in rubber buckets and each pen contained a mineralized salt block. A powdered vitamin E supplement was added to the diet to provide a total dietary concentration of 200 lU/kg dry matter. Duikers were fed at 1200 hr, pudus and brockets at 1400 hr. Diets consumed are shown in Table 1.

Total orts (remaining food) per pen were collected each day, dried, and weighed. Total feces per pen were collected once daily just before feeding. When necessary, feces were separated from wood chips by hand and all were dried at 600C. Urine was not collected separately, thus some contamination of feces may have occurred; urine remaining following evaporation during drying was not corrected for in subsequent calculations.

For analysis, the vegetable food items were freeze dried, and all feed items (vegetables, pellets, and hay) and pooled fecal samples were ground to pass a 2 mm screen. All feed and fecal samples were analyzed for crude protein (CP) (total N x 6.25), ash [Williams, 1984], total cell wall or fiber (NDF), cellulose, hemicellulose, and lignin [Goering and Van Soest, 1970, as modified by Robertson and Van Soest, 1981]. Metabolic fecal dry matter and metabolic fecal nitrogen losses were determined as described by Van Soest [1994].

To determine interspecific differences, we used ANOVA and Fisher LSD multiple comparison statistics [StatView SE ± Graphics software, 1991]. The accepted a-level was 0.05.

Passage Trial

Chromium-mordanted fiber was prepared according to Uden et al. [1980]. Passage trials were performed on one female pudu (9.1 kg BW) and one female Maxwell's duiker (9.5 kg BW), housed separately; two trials per animal were performed. We were constrained to use so few animals because the trials were conducted in the Wildlife Health Center, which had limited space. The animals were fed the same diet as that fed during digestibility trials (Table 1).

Porous rubber mats covered the 3 x 6 m cement pen floors. Both the pudu and duiker were fed Cr-mordanted fiber mixed into 5 g mashed bananas, which they consumed immediately. All feces were collected and weighed fresh every 4 hr for 4 days, and every 6 hr for the last 2 days of each trial. A 1 week clearance period was allowed between marker trials. After drying (600C) and weighing, each fecal sample was ground to pass a 2 mm screen, and 1 g subsamples were prepared for Cr analysis by atomic absorption spectrophotometry on a model 2280 instrument equipped with a Cr lamp using analytical-grade acetylene and standard methodology [Perkin-Elmer, 1982].

Mean transit time (MTT) in hours was quantified as the integrated average of the marker excretion curve. The equation was:

$$\text{MTT} = \sum_{i=1}^{n} \frac{t_i M_i}{M_i}$$

where t_1 was the time between marker administration and the ith defecation, the Mi was the amount of marker in the *i*th defecation [Wrick et al., 1983; Van Soest et al., 1983].

RESULTS

Intake and Digestibility Trial

Level of dry matter intake (as a percentage of body mass) was about 36% lower in the brockets compared with the pudus, and 26% lower in bay duikers compared with Maxwell's duikers (Table 1). While the quantities of each food item consumed were different, the chemical composition of the diets was similar across species (Table 2). Total cell wall or NDF consumption did not differ significantly *(P* = 0.0727), nor did protein consumption *(P*= 0.0918), among the four species.

The amounts of cellulose (Cs) and hemicellulose (HC) consumed were significantly different among species interspecifically (up and down comparisons in Table 2) and between the amounts of HC and Cs consumed intraspecifically (left and right comparisons in Table 2). The bay duikers consumed significantly more Cs than the other animals. The pudu, brocket, and Maxwell's duiker consumed significantly more HC than Cs *(P*= 0.001, F= 7.128), while the bay duiker consumed equal amounts.

There were significant differences among the digestion coefficients for various

TABLE 2. Chemical fractions as a percent of dry matter (DM) consumed by four species of small ruminants at the Wildlife Conservation Park, Bronx, NY (mean ± SD)

Species	n	CP[a]	NDF	HC	Cs	Ls
Pudupudu	6	15.8 ± 1.2	36.0 ± 5.8	18.2 ± 2.5a*[d]	14.2 ± 2.9ab*	3.6 ± 0.5a
Mazama americana	3	16.2 ± 0.4	34.0 ± 2.1	17.5 ± 0.9ac*	13.0 ± 1.1ab*	3.3 ± 0.2a
Cephalophus maxwellii	6	16.8 ± 0.6	30.5 ± 2.4	15.2 ± 0.3b*	11.9 ± 1.7a*	3.4 ± 0.5a
Cephalophus dorsalis	5	15.7 ± 0.6	36.2 ± 2.6	15.9 ± 0.3bc	15.8 ± 1.8b	4.5 ± 0.5b
Mean		16.1 ± 0.5	34.2 ± 2.6	16.7 ± 1.4	13.7 ± 1.7	3.7 ± 0.5
P		0.0918	0.0727	0.0095	0.0452	0.0032
F		2.555	2.812	5.359	3.357	7.021

[a]CP = crude protein; NDF neutral-detergent fiber or total cell wall; HC = hemicellulose; Cs = cellulose; Ls = sulfuric acid lignin.
dLetters = = significant at 95% level, up/down; * significantly different, 95%, left/right.

chemical fractions interspecifically (up and down comparisons in Table 3). The bay duikers were significantly lower than the rest in fiber fractions and dry matter digestibility. Only the brocket digested hemicellulose significantly more than cellulose *(P* < 0.05) (left and right comparisons in Table 3).

Metabolic fecal losses of dry matter were moderate and not significantly different (Table 4). Metabolic fecal nitrogen losses were significantly different only between the pudu and Maxwell's duiker *(P*= 0.01), two animals similar in size, but the pudu lost less nitrogen.

Passage Trial

The excretion curve for pudu showed a quick rise, a slight plateau, and a sharp drop (Fig. 1). The peak excretion time for the pudu was 26.6 ± 3.3 hr, the mean transit time (MTT) was 29.9 ± 0.8 hr, and the retention time (5 - 95% excretion time) was 32.8 ± 5.5 hr. The Maxwell's duiker's curve, however, while going up quickly, descended much more gradually (Fig. 2). In addition, the Maxwell's curve had more than one peak; the primary (first) peak excretion time was 21.1 ± 4.4 hr, M'TT was 42.2 ± 6.4 hr, and retention time 70.1 ± 5.8 hr.

DISCUSSION

In contrast to the results reported by Gordon and Illius [1994], larger size did not confer improved fiber-digesting capabilities among the ruminants in this study. It was also unclear why the brockets ate only 64% of the pudus' intake level or why the bay duikers ate only 74% of the Maxwell's duikers intake. Future research examining different fiber levels and fiber types should closely monitor for intake changes as diets change.

Hart [1986] compared blue duikers *(C. monticola,* a 4.7 kg animal) to bay duikers (20 kg) in digestion trials performed in the field, utilizing native fruits and leaves in Zaire. He predicted that the larger species would digest a low-quality diet (36.6—39.4% NDF) more completely than the smaller species would, and that both would digest a high-quality diet (14.7—16.0% NDF) more completely than a low-quality one, with the digestion of the high-quality diet equally complete in both species. However, his results showed both species digested both diets equally well (about 77% of DM for both species on low quality and 83% of DM for both on high).

TABLE 3. Digestion coefficients on a dry matter basis from four species of small ruminants at the Wildlife Conservation Park, Bronx, NY (mean ± SD)

Species	n	DM[a]	CP	NDF	HC	Cs	Ls
Pudu pudu	6	75.2 ± 4.7a[d]	77.4 ± 5.1	58.8 ± 8.2a	67.2 ± 6.3a	61.6 ± 14.0a	14.1 ± 12.6a
Mazama americana	3	73.2 ± 1.1a	75.0 ± 0.8	54.3 ± 4.1a	66.8 ± 3.0a*	49.7 ± 4.8ab*	5.2 ± 7.9ab
Cephalophus maxwellii	6	73.0 ± 2.8a	74.8 ± 3.1	49.4 ± 7.1b	55.0 ± 5.5b	53.2 ± 9.6a	7.7 ± 16.2a
Cephalophus dorsalis	5	67.1 ± 4.3b	70.1 ± 6.5	38.9 ± 4.7e	48.8 ± 5.4b	39.5 ± 9.1b	-14.9 ± 11.1b
Mean		72.1 ± 3.5	74.3 ± 3.0	50.4 ± 8.5	59.4 ± 9.1	51.0 ± 9.1	3.0 ± 12.5
P		0.0167	0.1161	0.0013	0.0001	0.0271	0.0136
F		4.592	2.302	8.529	13.225	3.976	4.866

[a]DM = dry matter; CP = crude protein; NDF = neutral-detergent fiber or total cell wall; HC = hemicellulose; Cs = cellulose; Ls = sulfuric acid lignin.
[d]Letters = significant at 95% level, up/down; * significantly different, 95%, left/right.

TABLE 4. Metabolic fecal losses from four species of small ruminants at the Wildlife Conservation Park, Bronx, NY (mean ± SD)

Species	n	%DM[a]	%N
Pudupudu	6	9.9 ± 1.0	0.41 ± 0.1 a[c]
Mazama americana	3	11.3 ± 0.3	0.5 ± 0.02 ab
Cephalophus ma.xwellii	6	11.0 ± 2.0	0.58 ± 0.1 b
Cephalophusdorsalis	5	11.7 ± 1.7	0.53 ± 0.1 ab
Mean		11.0 ± 0.8	0.50 ± 0.1
P		0.276	0.0414
F		1.411	3.517

[a]DM = dry matter; N = nitrogen.
[c]Letters = significant at 95% level.

Differing fiber levels did not change either species' abilities to digest NDF, but bay duikers digested the NDF fraction significantly better than blue duikers only on the high-quality diet. In spite of a larger body size, the bay duikers could not digest the high-fiber (low-quality) natural diet better than could the blue duikers, corroborating our results. Hart did not compare hemicellulose to cellulose digestibilities.

Hemicellulose and cellulose are insoluble fibers requiring a retention time long enough to allow extensive fermentation. Domestic cattle digest cellulose better than hemicellulose [Van Soest, 1994]. Hemicellulose digestion dynamics differ from cellulose in monogastrics, however, in that the sugars and hemicellulose fragments resulting from hydrolysis in the acid stomach allow for more extensive fermentation of hemicellulose than cellulose in the hindgut [Keys et al., 1970]. Cellulose is not affected by acid hydrolysis. Simple-stomached animals, like humans and chimpanzees, have been shown to digest hemicellulose as completely or more completely than cellulose [Milton and Demmet, 1988].

The higher or equal hemicellulose digestion in these small ruminants compared to domestic ruminants may indicate rumen bypass of some fiber or some types of fiber, allowing the acid stomach to prepare the hemicellulose for digestion/fermentation further down the tract. This bypass may be the result of reduced complexity of the omasum structure in small ruminants compared to large ones, documented by

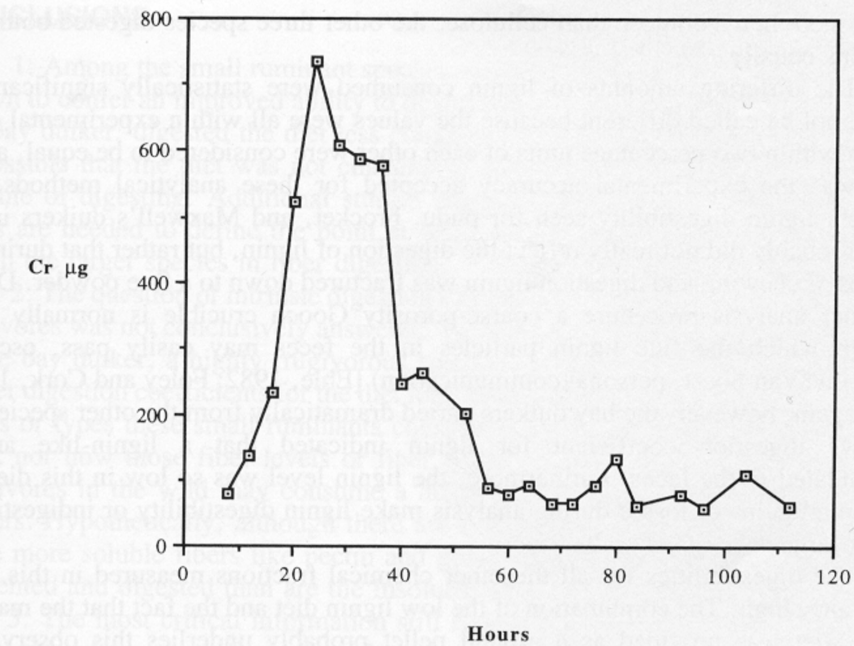

Fig. 1. Chromium excretion curve for *Pudu pudu*. The curve represents the average of two trials.

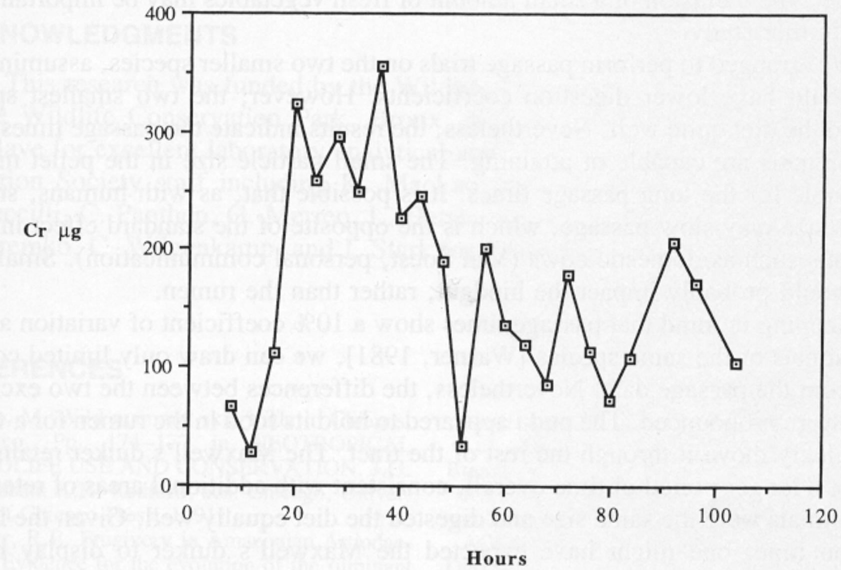

Fig. 2. Chromium excretion curve for *Cephalophus maxwellii*. The curve represents the average of two trials.

Hofmann [1989]. Food would then pass through the rumen faster and the acid stomach would have more influence on the hemicellulose than it does in larger ruminants [Ehle et al., 1982; Keys et al., 1970]. Although only the brockets digested significantly more hemicellulose than cellulose, the other three species digested both fiber fractions equally.

more hemicellulose than cellulose, the other three species digested both fiber fractions equally.

The differing amounts of lignin consumed were statistically significant but should not be called different because the values were all within experimental error. Values within two percentage units of each other were considered to be equal, as this level was the experimental accuracy accepted for these analytical methods. The apparent lignin digestibility seen for pudu, brocket, and Maxwell's duikers in this study probably did not really reflect the digestion of lignin, but rather that during the process of chewing and digestion lignin was fractured down to a fine powder. During the fiber analysis procedure a coarse-porosity Gooch crucible is normally used, through which the fine lignin particles in the feces may easily pass, escaping detection (Van Soest, personal communication) [Ehle, 1982; Foley and Cork, 1992]. Once again, however, the bay duikers varied dramatically from the other species; the negative digestion coefficient for lignin indicated that a lignin-like artifact accumulated in the feces. Furthermore, the lignin level was so low in this diet that very small gains or losses during analysis make lignin digestibility or indigestibility appear large.

The digestibilities for all the other chemical fractions measured in this study were fairly high. The combination of the low lignin diet and the fact that the majority of the diet was provided as a ground pellet probably underlies this observation. Grinding of low-lignin feeds improves their digestibility [Van Soest et al., in press]. As a diet to be fed small ruminants in captivity, the diet fed in this study seems adequate. The inclusion of a small amount of fresh vegetables may be important, and merits further study. We arranged to perform passage trials on the two smaller species, assuming that they would have lower digestion coefficients. However, the two smallest species digested the diet quite well. Nevertheless, the results indicate the passage times these small animals are capable of attaining. The small particle size in the pellet may be responsible for the long passage times. It is possible that, as with humans, smaller particle size may slow passage, which is the opposite of the standard effect in large ruminants such as domestic cows (Van Soest, personal communication). Small particles would probably impact the hindgut, rather than the rumen.

Keeping in mind that passage times show a 10% coefficient of variation among wild animals of the same species [Warner, 1981], we can draw only limited conclusions from the passage data. Nevertheless, the differences between the two excretion curves were pronounced. The pudu appeared to hold its food in the rumen for a while, then quickly move it through the rest of the tract. The Maxwell's duiker retained its food for a longer period of time overall, consistent with additional areas of retention. Both animals were the same size and digested the diet equally well. Given the longer retention time, one might have expected the Maxwell's duiker to display higher digestion coefficients.

Theoretically each digestive compartment is capable of selective retention. Pigs produce a distinct secondary peak that has been shown to be the result of cecal emptying [Ehle et al., 1982]. The Maxwell's duiker's higher metabolic fecal nitrogen (MFN) losses may come from microbes active in the lower tract, in the secondary points of retention, which therefore escape digestion and are lost in the feces. Swine, with their secondary excretion peak from cecal emptying, show MFN losses of 0.66% N.

CONCLUSIONS

1. Among the small ruminant species studied here, body size or weight was not shown to confer an improved ability to digest fiber. In fact, one of the larger species, the bay duiker, digested the diet less completely than did the other three species. It is possible that the diet was not challenging enough to show what the animals are capable of digesting. Additional studies comparing different fiber levels and fiber types are needed to define the point at which the smaller species, perhaps, cannot match the larger species in fiber digestion.
2. The question of intrinsic digestion capacity differences between browsers and frugivores was not conclusively answered. However, comparing the pudu, a browser, to the bay duiker, a highly frugivorous species, the browser did show significantly higher digestion coefficients for the diet fed. There are no reports of what overall fiber levels or types these small ruminants consume on a daily, free-ranging basis in the wild, nor how those fiber levels or fiber types might change throughout the year. Frugivores in the wild may consume a different type of fiber than do browsers or grazers. Hypothetically, although there are few data on wild fruits, frugivores consume more soluble fibers like pectin and gums, which are more easily and quickly fermented and digested than are the insoluble fibers fed in this trial.
3. The most critical information still lacking for these species is the chemical composition of natural diets. Knowledge of seasonal variations in requirements or foods selected in the wild would also help in the formulation of captive diets.

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