Digestion of Selected Foods by Yunnan Snub-Nosed Monkey *Rhinopithecus bieti* (Colobinae)

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KEY WORDS feeding ecology; leaf-eating monkeys; lichen-eating; *Bryoria*; Usneaceae

ABSTRACT Three digestion trials were conducted to quantify aspects of digestive physiology in the Yunnan snub-nosed monkey *Rhinopithecus bieti*, a foregut fermenter that feeds primarily on lichens. Mean retention time (MRT, the average time plastic markers spent in the animal) had a mean estimate of 47 hr (n = 3) with high variability between trials (standard deviation = 17 hr). Recently captured animals, presumably with gut flora and digestive physiology close to wild animals, had a longer retention time than did long-term captives, although lack of standardization across trials (such as in activity level) confounds analysis. Apparent digestibilities for dry matter (71–80%) were in line with other studies of colobine digestion, but fall below those of ruminant ungulates feeding on lichens. Fecal analysis accurately determined the relative proportions of leaves vs. lichens in diets; mature leaves and lichens were not nutritional equivalents but appeared to be physiological equivalents in terms of digest passage. Fecal analysis does not, however, accurately determine the relative proportions of food types with different digestibilities, such as fruit vs. leaves. Am J Phys Anthropol 114:156–162, 2001.

Compartmentalized, foregut fermentation is the digestive adaptation that defines the Colobinae. Compared with the simple-stomached Cercopithecinae, colobine diets are often high in fibrous foods (Struhsaker and Leland, 1987). These differences in diet influence behavior. Relative to cercopithecines, colobines generally have small home ranges and little aggression over food; feeding ecology is strongly implicated as a cause of these behavioral differences (Struhsaker and Leland, 1987; Isbell, 1991). Thus, understanding the foraging decisions of particular populations or species aids in understanding the differences in range use and social behavior among populations or species.

Foraging decisions are directly related to issues of digestion, which are in turn related to plant chemistry (Demment, 1983; Hume, 1989). Fermentative digestion in colobines is analogous to the fermentative digestion of ruminants insofar as, in both groups, microorganisms in the gut decompose foods high in fiber (Parra, 1978; Kay and Davies, 1994). The foregut of many complex-stomached mammals appears to have evolved to maximize retention and digestion of enzyme-resistant polysaccharides as well as to detoxify the harmful secondary compounds found in plant foods. Simple-stomached animals may increase digestion of fibrous foods by retention in the colon, caecum, and large intestine, but in general foods stay longer inside complex-stomached animals. This allows complex-stomached animals to digest food more completely and to select food items from which energy is more difficult to extract (Chivers and Hladik, 1980; Demment, 1983). Retention time and the digestibilities of different foods are key to understanding the foraging decisions of colobines.

The diets of many wild colobines are well documented, as are some nutritional components of those diets (reviewed in Waterman and Kool, 1994), but physiological aspects of colobine digestion remain largely unexplored (Kay and Davies, 1994). The current report details retention times and the apparent digestibilities of diet in the Yunnan snub-nosed monkey *Rhinopithecus bieti*. These issues are of particular interest because lichens, not leaves, are this monkey's primary food (Wu and He, 1989; Kirkpatrick, 1996). Lichens are an uncommon food for mammals, typically used as a winter fallback when foods of other seasons, presumably of higher quality, are unavailable (Richardson and Young, 1977). In this report, we also compare known diets to estimates of diet derived from feces. This was done to see whether fecal analysis is useful in corroborating

Grant sponsor: Wenner-Gren Foundation; Grant sponsor: L.S.B. Leakey Foundation; Grant sponsor: National Science Foundation; Grant sponsor: Freed Foundation of the Wildlife Conservation Society.

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Received 22 March 2000; accepted 20 October 2000.

direct observations of lichen-eating by wild populations of *R. bieti*.

MATERIALS AND METHODS

Study animals

Three intake trials were conducted on a total of five animals. Trials 1 and 2 were conducted at the Kunming Institute of Zoology (KIZ), with one adult female weighing 8.6 kg (trial 1, cage size 12.5 m^3) and one juvenile male weighing 8.4 kg (trial 2, cage size 130 m^3). Both of these animals had been captive about 30 months. Trial 3 was conducted at Baimaxueshan Nature Reserve (BMXS), with three animals housed together in a very small cage (adult male, 13.0 kg; adult female, 5.8 kg; infant, 1.9 kg; cage size, 2.5 m^3). These three animals had been captive about 2 months.

Trial implementation

The nontrial diet of all captives consisted of dicot leaves (primarily of the family Rosaceae), fruit (bananas or apples), and, at KIZ, handmade biscuits of grain (primarily wheat and barley, without vitamin or mineral supplements). In the trials, grasses (Gramineae) and the fruticose lichen *Bryoria* were added to nontrial diets. For trial 3, fruit was eliminated from the diet. Animals were provided about 50 g of *Bryoria* the day before the trials began. This was the first time the animals had eaten lichen since capture. The long-term alteration of diet to a single food type, commonly done in studies of digestion of domestic livestock, was considered inappropriate by captive-care managers; at the time, these five monkeys comprised half of the total captive population of this highly endangered primate, and deaths in captive colobines may result from inappropriate diets (Goltenboth, 1976; Collins and Roberts, 1978).

In each trial, known amounts of food were provided over 3 days. Intake was estimated as food provided minus food remaining at the end of each day, with no correction for transpiration. Hundred-gram samples (n = 3 for each food species) were oven-dried (50–70°C) to constant weight to allow conversion between fresh weight intake and dry weight intake.

Plastic markers placed in the foods identified feces associated with the trial period. (More sophisticated markers were unavailable to us.) Markers were plastic strips about 10 mm long, 1 mm wide, and 4 ml thick. Specific gravity of markers was not noted. In trials 1 and 2, markers were placed in bananas and given in single, pulse doses; red markers were given at the first meal (0700 hr on day 1), and yellow markers at the last (1900 hr on day 3). In trial 3, markers were laced in lichens and given in four doses (0700 hr in the single meal given on day 1, 0700 hr in the single meal given on day 2, and 0700 hr and 1900 hr in the two meals given on day 3).

About 25 markers were given in each of the two doses for trial 1 and 2; about 300 markers in total were given in trial 3 (100 markers each day). In trials 1 and 2, feces were collected for 120 hour (4-hr intervals) after markers first appeared, with 100% of feces collected. In trial 3, feces were collected for 192 hr (12-hr intervals) after markers first appeared; some of the feces, eliminated in the monkeys' seclusion area (about 10% of the total cage space), were not collected. The feces in trial 3 were not identifiable by animal, and therefore feces were combined, resulting in mixed data for these animals. No attempt was made to control for the presence of the unweaned infant.

Analysis of retention times

Following Van Soest (1994), the markers recovered were used to estimate transit time (time from ingestion to first appearance of marker), retention time (range of time for appearance of 5–80% of recovered markers), and mean retention time (MRT, the integrated average of time all recovered markers spent in the gut). Time estimates used the mode of collection interval, e.g., feces collected from the interval of 18–22 hr after ingestion were treated as being evacuated at 20 hr. For example, if 10% of the recovered markers were collected at 20 hr, another 10% were collected at 24 hr, and so on, the weight given these markers in the calculation of MRT would be (0.10 * 20 hr) + (0.10 * 24 hr) and so on. For trial 3, the estimate of MRT assumed that the first 1/3 of recovered markers were from the first dose, the second 1/3 were from the second dose, the next 1/6 were from the third dose, and the final 1/6 was from the final dose; the estimate assumed that the markers in each of the four doses were treated equivalently by the animals' digestive systems.

Analysis of foods and feces

Foods and feces were oven-dried in paper envelopes to constant weight at 50–70°C and analyzed for nutritional components (following Waterman et al., 1988; Van Soest, 1994). Proportions of nutritional components in the diet were calculated from the proportion of each food type ingested (Table 1) and the proportion of each nutritional component in that food type (Table 2). Calculations were made on a daily basis for the 3-day feeding trials, with the 3-day means used for the estimates reported here. The feces analyzed for nutritional components were from the 4-day period holding the highest cumulative percent of markers recovered from the feeding trials. Nutritional components in feces were analyzed on a daily basis, with the 4-day means used for the estimates reported here. Digestibilities for dry matter and for nutritional components were calculated as intake minus defecation, divided by intake (Van Soest, 1994).

Remnants of foods in feces were identified by histological analysis (on contract with the Composition Analysis Laboratory, Colorado State University). Feces were ground through a 1-mm screen and

TABLE 1. Foods ingested on a daily basis in three feeding trials of Rhinopithecus bieti[1]

Trial	Day	Foods ingested (g dry matter)						Feces defecated (g dry matter, total)	Cumulative percent, all markers recovered
		Lichen	Monocot leaves	Dicot leaves	Biscuit	Banana	Total		
Trial 1									
	Day 1	48	6.7	50	63	24	192		
	Day 2	60	13.2	47	126	44	290	55	0
	Day 3	57	0.3	42	103	57	259	44	13
	Day 4							65	44
	Day 5							52	95
	Trial total	165	20.2	140	292	125	742	216	
	Daily mean (g)	55	6.7	47	97	42	247	54	
	Daily mean (%)	22	2.7	19	39	17			
Trial 2									
	Day 1	58	10.3	86	138	50	342		
	Day 2	43	25.7	72	138	36	314	88	14
	Day 3	55	14.8	79	138	31	318	108	18
	Day 4							92	70
	Day 5							93	100
	Trial total	156	50.8	236	413	118	973	382	
	Daily mean (g)	52	16.9	79	138	39	324	95	
	Daily mean (%)	16	5.2	24	42	12			
Trial 3									
	Day 1	281	13.3	21	n.a.	n.a.	315		
	Day 2	123	30.3	24	n.a.	n.a.	178	93	12
	Day 3	151	38.5	78	n.a.	n.a.	267	32	27
	Day 4							29	54
	Day 5							54	81
	Trial total	554	82.2	123	n.a.	n.a.	760	261	
	Daily mean (g)	185	27.4	41			253	52	
	Daily mean (%)	73	10.8	16					

[1] Trial 1 consisted of one adult female (8.6 kg), trial 2 of one juvenile male (8.4 kg), and trial 3 of one adult male, one adult female, and an unweaned infant (total combined weight, 21 kg).

TABLE 2. Dry matter (as percent of fresh weight) and nutritional components (as percent of dry matter) for foods used in three feeding trials of Rhinopithecus bieti

Food type	Species	Dry matter	Crude protein	Water-soluble carbohydrates	Total cell wall (NDF)	Hemicellulose (NDF minus ADF)	Cellulose (ADF minus SAL)	Sulfuric acid lignin (SAL)
Lichen	*Bryoria* spp.	89	4.7	14.3	36	21.5[1]	6.5[2]	7.8
Monocot leaf	*Oryzopsis munroi*	22	27.8	1.4	52	25.1	21.2	5.3
Monocot leaf	*Paspalum comersonii*	32	15.2	4.8	64	30.4	28.8	5.2
Dicot leaf	*Malus* sp.	39	17.6	3.9	32	16.8	6.7	8.3
Dicot leaf	*Prunus pseudocarpus*	14	18.6	5.3	40	14.0	9.9	16.6
Dicot leaf	*Sorbus rehderiana*	26	18.1	4.9	35	16.6	8.8	9.1
Fruit	*Musa* sp.	24	5.7	27.2	23	5.8	3.3	13.7
Biscuit	(home-made, various grains)	46	20.3	23.7	19	13.1	3.1	2.6

[1] Lichenin, a starch-like glucan of high digestibility, is probably the primary component of this fraction.
[2] Chitin, not cellulose, is the primary structural fiber of lichen cell walls and is probably the primary component of this fraction.

placed in suspension on microscope slides. Diet was estimated by the relative density of fragments of each food species in 20 randomly selected grids on each of five slides (i.e., 100 grids total per estimate). This was done on a daily basis for the feces used in nutritional analyses, with the 4-day means used for the estimates reported here.

RESULTS

Across trials, the mean for transit time was 27 hr (n = 3, SD = 7.4, see Fig. 1). For MRT, the mean was 47 hr (n = 3, SD = 17). The two transit time estimates (i.e., from the first and last meals) in trials 1 and 2 were not independent: each trial used one animal, fed the same diet throughout the trial. Thus, it is most appropriate to use the mean estimate from both the first and last meals. The markers for trial 1 had a mean transit time of 33 hr (n = 2) and an MRT of 42 hr (n = 2). Retention time (i.e., interval for 5–80% marker recovery) in trial 1 was 33–49 hr (n = 2). The markers for trial 2 had a mean transit time of 19 hr (n = 2) and an MRT of 33 hr (n = 2). Retention time in trial 2 was 19–45 hr (n = 2). In trial 3, the markers for the first meal had a transit time of 30 hr, and the rough estimate of MRT was 66 hr. (Only five markers were recovered from the first meal in trial 1 (the female manually removed about 80% of markers from her food) and this probably was a factor in the high values in trial 1 relative to trial 2.)

Food remained at the end of each day, and therefore intake was not limited by the amount of food provided. Mean daily intake (dry matter) as a proportion of body weight ranged from 1.2% (trial 3) to 3.8% (trial 2). Intake of lichen varied among trials (from 16% of total diet in trial 2 to 73% in trial 3; see Table 1), as did digestibility of dry matter (DMD, from 71% in trial 2 to 80% in trial 3; see Table 3). Across trials, water-soluble carbohydrates (CHO) were highly digestible (87–93%, Table 3). The apparent digestibility of crude protein (CP) was 49–62%. Microbial protein (CP minus ND-CP (neutral detergent crude protein), which also included a small portion of endogenous protein) comprised about 75% of total fecal CP (Table 3); true digestibility of CP therefore ranged from 83% (trial 1) to 91% (trial 3).

The apparent digestibility of cell wall (neutral detergent fiber, NDF) ranged from 60–81%, while for lignin and/or lignin-like artifacts (sulfuric acid lignin, SAL), it was 41–57%. The trial with the greatest consumption of lichen (trial 3) showed the highest digestibilities for all cell wall components. Lichen cell walls are composed primarily of chitin, and not cellulose or lignin (Allaby, 1992); the "hemicellulose" fraction of *Bryoria* was probably high in lichenin, a starch-like glucan (Van Soest, personal communication). The hemicellulose (NDF minus acid detergent fiber, ADF) and cellulose (ADF minus SAL) fractions of the diets were highly digestible, ranging from 70–95% for hemicellulose and 68–90% for cellulose.

Histological analysis of feces showed variability across trials. In trial 3, with a simple diet of only lichens and leaves, food remnants in feces directly corresponded with actual ingestion (Fig. 2). In trials 1 and 2, the diet was relatively complex, with biscuit and banana in addition to lichens and leaves. In trials 1 and 2, lichens and leaves were overrepresented in the feces, biscuit was underrepresented, and banana was not represented at all. Dicot leaves and lichens both had high NDF and, concomitantly, low CHO, relative to biscuit and banana (Table 2).

DISCUSSION

Differences in experimental diets, cage sizes, and length of captivity of trial animals confound all the analysis of the current study. Further, the gut flora of trial animals had no chance to adjust to the addition of lichen to nontrial diets. Lack of standardization may have caused variability between trials and suggest caution in generalizing across these divergent conditions. The current methods should be adequate, however, if interpreted cautiously.

The estimates of MRT reported here may be of limited utility, for example, due to our use of plastic markers. Radio-opaque or stable rare-earth ele-

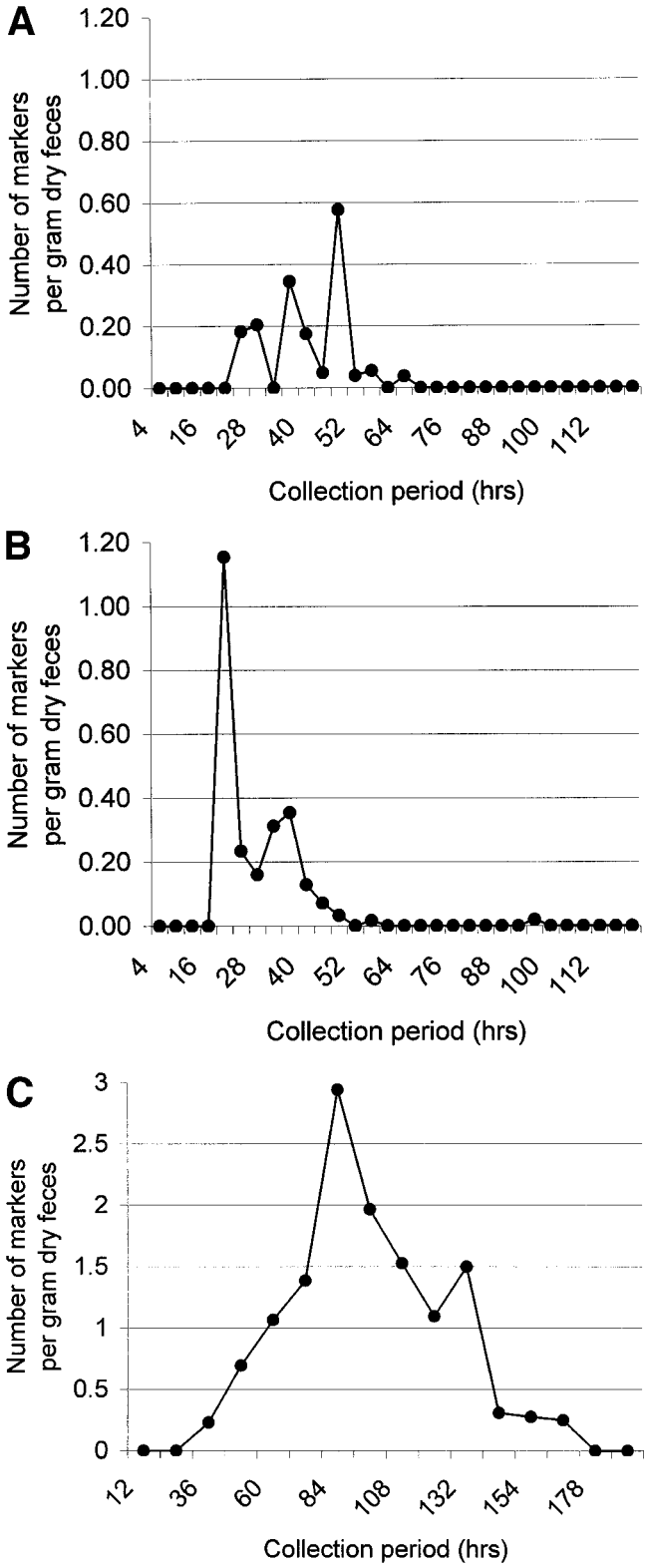

Fig. 1. Passage rates for three digestion trials using *Rhinopithecus bieti*. Marker recovery over time is shown as number of markers per g dry feces for each collection period (every 4 hr in trials 1 and 2; every 12 hr in trial 3). Trials 1 and 2 were conducted with, respectively, an adult female and a juvenile male, both captive about 30 months. Trial 3 was with three animals (adult female, adult male, and infant), captive 2 months. The methods of trial 3 differed substantially from those of trials 1 and 2; see text for detail. **A:** Trial 1. **B:** Trial 2. **C:** Trial 3.

TABLE 3. Apparent digestibility of nutritional components in three feeding trials of Rhinopithecus bieti[1]

	Ingested (g/day)			Defecated (g/day)			Digestibility (%)		
	Trial 1	Trial 2	Trial 3	Trial 1	Trial 2	Trial 3	Trial 1	Trial 2	Trial 3
Dry matter	247	324	253	54.1	95.4	52.0	78	71	80
Crude protein	34	50	25	12.9	25.5	10.2	62	49	58
Neutral detergent crude protein	n.a.	n.a.	n.a.	5.8	7.3	2.2	n.a.	n.a.	n.a.
Water-soluble carbohydrates	44	55	27	3.1	3.7	3.6	93	93	87
Total cell wall (NDF)	71	96	93	21.4	38.3	18.0	70	60	81
Hemicellulose (NDF minus ADF)[2]	35	48	54	3.3	14.5	2.9	91	70	95
Cellulose (ADF minus SAL)[3]	15	22	21	2.2	6.9	2.0	85	68	90
Sulfuric acid lignin (SAL)	21	27	20	11.2	15.8	8.5	46	41	57

[1] Amounts ingested and excreted are calculated from Tables 1 and 2. Digestibility is calculated as ingestion minus defecation, divided by ingestion (Van Soest, 1994). Trial 1 consisted of one adult female (8.6 kg), trial 2 of one juvenile male (8.4 kg), and trial 3 of one adult male, one adult female, and an unweaned infant (total combined weight, 21 kg).
[2] Lichenin, a starch-like glucan of high digestibility, is probably a significant component in this fraction.
[3] Chitin, not cellulose, is the primary structural fiber of lichen cell walls and is probably a significant component in this fraction.

ments are widely considered preferable to plastic markers in feeding trials. The activity of sophisticated markers also depends on diet, however, and at least one study has found that, in colobines, plastic markers provide results comparable to chemical markers (Edwards, 1995). The imperfect markers used in the current trials therefore should provide broadly dependable results, and the wide variation in MRT seen in the three trials here is not completely unexpected, insofar as trials within and between animals often show variance of up to 20% (Warner, 1981). This noted, we would anticipate that relatively larger markers would move more slowly through the digestive tract than small particles or solutes. Since the plastic markers used in these trials were probably large relative to food particles entering the stomach after chewing, they may well have traveled with the indigestible fiber portion of digesta. Although this may bias estimates of retention time, it should not produce marked errors in digestibility estimates, because virtually all feces from the trials were collected.

Dry-matter intake scaled with cage size. Although there are insufficient data for statistical tests, it appears that cage size is a better predictor of dry-matter intake than animal size. Thus, dry-matter intake in this study was probably driven by differences in activity. For the trial with the smallest cage (trial 3), intake as a proportion of body weight (1.2%) was similar to that of captive black-and-white colobus monkey *Colobus guereza* (1.9%, Watkins et al., 1985) housed under similar conditions, and may represent basal intake for colobines (cf. Dasilva, 1992).

Studies of captive colobines, such as *C. guereza* (Kay and Davies, 1994), the silvered langur *Trachypithecus cristatus* (Sakaguchi et al., 1991), and the proboscis monkey *Nasalis larvatus* (Dierenfeld et al., 1992), have found transit times of 14–18 hr, with MRT of 38–47 hr. Transit times in the current trials were longer than the transit times seen in other colobines, although estimates of MRT were similar. Differences in dietary fiber can result in differences in transit times, although this is unlikely to be the causal factor in cross-species variation: *T. cristatus* with a diet of 37% NDF had virtually identical transit times to *N. larvatus* with a diet of 17% NDF. MRT is a more repeatable, accurate measure of fermentation potential than is transit time (Van Soest et al., 1983), and MRT in the colobines reviewed here is generally comparable to that of similar-sized ruminants (Kay, 1987; Conklin-Brittain and Dierenfeld, 1996). In the current trials, the animals in trial 3 had the longest MRT, probably the result of a combination of short time in captivity, small cage, and lack of fruit in diet.

Feeding trials commonly provide the trial diet for days or weeks before beginning collection of feces (Van Soest, 1994); this allows the animal's gut flora to become adapted to the diet. This was not done in the current study. Notwithstanding differences in methods, the apparent digestibilities of *R. bieti*'s dietary constituents, particularly of cell wall components, were similar to the high digestibilities found in other studies of colobines (Watkins et al., 1985; Sakaguchi et al., 1991; Dierenfeld et al., 1992). The animals in this study had not ingested lichens for 2 to 30 months, and gut flora were not expected to be particularly adapted to the digestion of lichens. In ruminants, wild and captive individuals of particular species have qualitatively similar stomach flora (Parra, 1978); this holds for lichen-eating ruminants as well (Aagnes et al., 1995). Colobines potentially adapt to new diets or to seasonal changes in diet by the same method as other foregut fermenters: through rapid changes in proportions of gut microorganisms (Bauchop, 1978).

Using systematic observation of feeding behavior in the wild, Kirkpatrick (1996) estimated that *R. bieti* had a diet of 75% lichens, seasonally varying from 60% in spring to 95% in winter. By analyzing feces collected in the wild, Wu and He (1989) estimated that *R. bieti* had a diet of between 30–40% lichens. Differential digestibility of food types can bias estimates of food intake derived from feces, however. When one food type, such as lichens, dominated the diet, these differences were marginal (trial 3 in Fig. 2). Foods such as biscuit and banana, however, were high in water-soluble carbohydrates

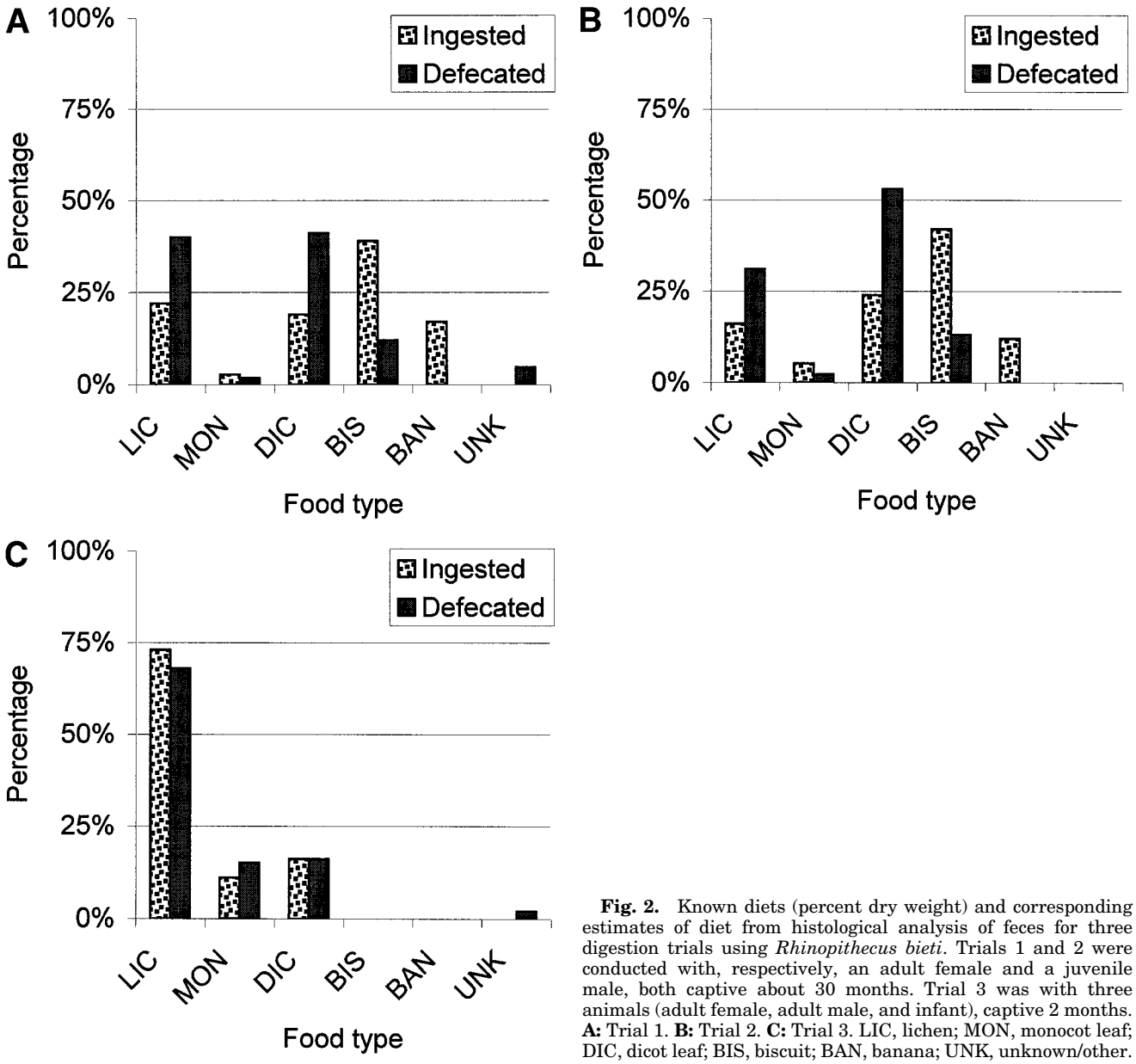

Fig. 2. Known diets (percent dry weight) and corresponding estimates of diet from histological analysis of feces for three digestion trials using *Rhinopithecus bieti*. Trials 1 and 2 were conducted with, respectively, an adult female and a juvenile male, both captive about 30 months. Trial 3 was with three animals (adult female, adult male, and infant), captive 2 months. **A:** Trial 1. **B:** Trial 2. **C:** Trial 3. LIC, lichen; MON, monocot leaf; DIC, dicot leaf; BIS, biscuit; BAN, banana; UNK, unknown/other.

and low in fiber relative to lichens and leaves (Table 2), and were presumably comminuted more finely; this might explain their underrepresentation in feces in trials 1 and 2 (Fig. 2). Lichens were high in CHO relative to dicot leaves, however, and this did not cause differential representation of lichens in feces when compared with leaves. These data, in addition to fiber content (Table 2), suggest that leaves and lichens act as functional equivalents for *R. bieti* in the physiology of passage, though not in nutrition. Estimates from direct observation of the actual and relative proportions of lichens and leaves in diet can therefore be corroborated through fecal analysis; the differences between Kirkpatrick (1996) and Wu and He (1989) may reflect real variation in wild diets rather than differences of methodology. This further implies that fecal analysis will not accurately estimate diets in primates that feed on diverse diets, such as those that combine significant proportions of both fruits and leaves.

Fruticose lichens, such as the *Bryoria* (Usneaceae) eaten by *R. bieti*, are highly digestible. In vitro dry matter disappearance of lichens in the Usneaceae was 89–94% in the rumen fluid of caribou *Rangifer tarandus* (Thomas et al., 1984). *Alectoria sarmentosa* (Usneaceae) fed to mule deer *Odocoileus hemionus* had a dry-matter digestibility (DMD) of 85% and an NDF digestion coefficient of 92% (Robbins, 1987). Lichens contain virtually no cellulose or lignin, although nonstructural phenolics and other compounds can result in lignin-like artifacts in assays (Robbins, 1987). In the current study, *Bryoria* had a cellulose fraction of 6.5% and an SAL fraction of 7.8% (Table 2), but it is improbable that these frac-

tions actually were composed of true cellulose or lignin. This may underlie the high digestibility estimates for lignin found in this study.

The high digestibility of water-soluble carbohydrates (CHO) in this study (median, 93%; Table 3), and the relatively high values of CHO in lichens compared to leaves (Table 2, and also Kirkpatrick, 1996), may indicate that CHO in lichens are a valuable energy source for these primates in the wild. Further, the hemicellulose fraction in the current trials was highly digestible (median, 91%; Table 3). Animals using fermentative digestion generally are anticipated to be better at digesting cellulose than hemicellulose, the opposite being true for animals that do not use fermentative digestion (Milton et al., 1980; Van Soest, 1994), but snub-nosed monkeys appear to digest hemicellulose more fully than cellulose. If indeed the hemicellulose fraction in *R. bieti* diets is high in glucans such as lichenin, this may underlie its high digestibility. The extent to which cellulose is digested, relative to hemicellulose, depends on the physical and chemical composition of cell wall materials. Fermentative digestion, whether in the foregut or in the caecum and colon, allows ready access to storage carbohydrates and the carbohydrates in hemicellulose and hemicellulose-like products, making these nutritional components (in leaves, seeds, and lichens) a crucial factor in colobine food choice.

ACKNOWLEDGMENTS

We thank the Baimaxueshan Nature Reserve (BMXS), and in particular D.F. Dong, for allowing access to the animals used in trial 3; T. Zhong also helped to implement trial 3. M. Norconk, P. Rodman, A. Harcourt, and several anonymous reviewers generously provided comments on the manuscript. Partial funding for implementation of trials came from the Wenner-Gren Foundation, the L.S.B. Leakey Foundation, and the National Science Foundation (to R.C.K.). Funding for nutritional assays came from the Freed Foundation of the Wildlife Conservation Society (to E.S.D. and R.C.K.).

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