

Determination of bamboo-diet digestibility and fecal output by giant pandas

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Abstract: The goals of this study were to determine digestibility of a bamboo diet by giant pandas (*Ailuropoda melanoleuca*) and to evaluate potential internal markers (naturally occurring markers in their diet) for their ability to estimate fecal output and digestibility. Digestibility predictions using internal markers were based on either feed offered or feed consumed. Two giant pandas were used in 1-, 2-, and 3-day digestibility trials with total collection of feces. In the 3-day trial, animals were fed 100% bamboo with no dietary supplements. In all other trials, supplements were included in addition to bamboo. The 3 internal markers chosen for evaluation were acid insoluble ash (AIA), acid detergent lignin (ADL), and acid detergent insoluble nitrogen (ADIN). Results from digestibility trials indicated that apparent nutrient digestibility could be determined with no differences ($P > 0.05$) between pandas. Six apparent dry matter (DM) digestibility values ranged from 6.9 to 38.5%. Apparent DM digestibility for the male and female panda in the unsupplemented (3-day) trial were 6.9 and 12.4%, respectively. Among the 3 potential internal markers evaluated, AIA more accurately predicted fecal output ($r = 0.99$; $P < 0.01$) than ADL ($r = 0.84$; $P < 0.02$) or ADIN ($r = 0.85$; $P < 0.02$). Calculations using AIA and feed consumed more accurately predicted nutrient digestibility than did feed offered calculations for all 3 internal markers. Apparent crude protein (CP) digestibility was 33.8% and was predicted by AIA and feed consumed calculations to be 35.5% ($r = 0.88$; $P = 0.009$). Acid insoluble ash and feed consumed calculations predicted fiber digestibility to be 35.1% compared to apparent fiber digestibility (31.8%; $r = 0.97$, $P < 0.001$). Methods and data presented in this study may be used to predict nutrient digestibility in wild pandas in their native habitat.

Key words: *Ailuropoda melanoleuca*, digestibility, fecal output, giant panda, internal markers

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Giant pandas (*Ailuropoda melanoleuca*) are phylogenetically classified as carnivores (Chorn and Hoffman 1978, Gittleman 1999); however, their diet is primarily herbivorous, composed almost entirely of bamboo (95 to 99% of their diet; Schaller et al. 1985, Reid and Hu 1991, Long et al. 2004), with the remainder of the diet from a number of potential sources. Villagers in China have reported finding remains of small rodents (e.g., bamboo rats [*Rhizomys* spp.], golden monkeys [*Pygathrix roxellana*], and musk deer [*Moschus* spp.]) in the feces of wild pandas (Schaller et al. 1985). Dierenfeld et al. (1995) reported that captive pandas consume supplements

such as rice gruel, high-fiber biscuits, and food such as fruits and vegetables.

Nutritionally, the giant panda is considered monogastric, with the digestive tract of a typical carnivore such as a bear. Bears have a simple stomach, and if any anaerobic fermentation occurs, it is farther along the gastrointestinal tract. Compared to other carnivorous animals, bears generally have a longer small intestine (Li 1986). However, pandas are an exception in that they have a relatively short small intestine (Li 1986). The reduced length of the panda small intestine contributes to less complete digestion, forcing them to consume large amounts of bamboo to meet nutrient and energy requirements.

Bamboo is classified as a grass (family Poaceae, subfamily Bambusoideae; McClure 1993). Golden

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bamboo (*Phyllostachys aurea*) was reported to be 63.4% culm (central stalk), 20.6% branch, and 16.0% leaf as a percent of the total plant (Mainka et al. 1989). Because a majority of the plant is made up of culm and branches, one would presume that bamboo is composed primarily of structural carbohydrates (cellulose, hemicellulose, and lignin). This highly indigestible structure poses a challenge to pandas, because they have limited ability to digest structural carbohydrates. A slower passage rate could limit intake but allow for better utilization of nutrients in bamboo; however, the passage rate of giant pandas is very rapid (5 to 11 hours; Dierenfeld 1997, Edwards et al. 2006, H.A. Bissell unpublished data). The well-developed masseter muscles, molars, and pre-molars of pandas provide sufficient power to easily crush bamboo (Chorn and Hoffman 1978). Mastication increases nutrient availability, particularly of plant cell contents (Dierenfeld et al. 1982), and increases surface area to allow better digestion.

Analyzing fecal samples is an integral component in determining digestibility; however, obtaining total fecal output from pandas, both in the wild and in captivity, is problematic. Therefore, alternatives to total fecal collection for this species need to be investigated. One such alternative may be the use of an internal marker. An internal marker is an indicator that occurs naturally in a diet that must be non-absorbable and non-metabolizable in the gastrointestinal tract (Faichney 1975, Merchen 1993). An effective internal marker must: (1) not affect or be affected by the digestive process, (2) be physically similar to or associated with the material it is to mark, and (3) be estimated in digested samples through a specific and sensitive method (Faichney 1975).

Faichney (1975), Fahey and Jung (1983), and Merchen (1993) reported that using an internal marker for determination of digestibility confers advantages in terms of convenience and cost compared to total fecal collection. Merchen (1993) found this to be especially true for grazing animals and stated that the use of internal markers was more accurate than total fecal collection for grazing animals. These findings could have implications for the use of natural markers in bamboo to determine fecal output and nutrient digestibility. Although pandas are not considered grazing animals in captivity, they could be classified as such in their natural habitat because their diet consists almost entirely of a grass.

Block et al. (1981) reported that the use of acid insoluble ash (AIA) as a natural marker for determining apparent dry matter (DM) digestibility in ruminants allowed free access to feed. They found that digestibility calculations using AIA as a marker for only the diet offered (not taking into account refused feed) underestimated digestibility, compared to calculations that also accounted for AIA content of the refused diet. Van Keulen and Young (1977) concluded that the use of AIA as a marker is satisfactory for estimating DM digestibility. McCarthy et al. (1974, 1977) used total fecal collection and HCl insoluble ash to calculate digestibility of a diet with 0.5% celite (diatomaceous earth) by domestic pigs (*Sus scrofa*) at 2 stages of growth. Apparent digestibility of energy and nitrogen by pigs of both growth stages was less when using HCl insoluble ash as an internal marker compared to total fecal collection. Also, the addition of celite to the diet did not improve accuracy for determination of digestibility when using HCl insoluble ash. Thonney et al. (1985) attempted to use fecal grab samples to validate DM digestibility estimates using AIA when feeding silage and obtained similar estimates comparing total fecal collection to AIA. They concluded that in diets containing $\geq 0.75\%$ AIA (DM basis), the use of AIA for determination of digestibility in ruminants appears to be accurate.

No enzymes for lignin degradation appear to exist in mammals or in anaerobic bacteria (Van Soest 1982); therefore, lignin is considered indigestible and has been evaluated as a potential internal marker. Merchen (1993) reported that underestimation of digestibility when using acid detergent lignin (ADL) as an internal marker resulted from incomplete recovery of lignin, with an amplification in magnitude of error as the extent of loss increased. Incomplete recovery of lignin is more problematic as dietary lignin concentration decreases. Sunvold and Cochran (1991) limit fed alfalfa, bromegrass, or prairie hay diets to steers, performed total fecal collection, and evaluated ADL as an internal marker to estimate organic matter (OM) digestibility. Their results showed that when feeding alfalfa hay diets, the OM digestibility estimates using ADL as an internal marker were numerically similar to those using total fecal collection. These findings were upheld for bromegrass and prairie hay diets. Merchen (1993) reported that use of lignin as a marker should be limited to research trials in

Table 1. Digestibility trials from the Memphis Zoo, Aug 2003 through Feb 2004 for captive male (466) and female (507) giant pandas.

Trial date	Duration, hr	Animal	Initial mass, kg	Final mass, kg	Bamboo spp. ^a	Supplement ^b	Total supplement fed ^c
Aug 2003	24	507	80.6	79.5	PLLAU, PLLGL	PF, LE, RA, SM	3.8%
Oct 2003	24	466	76.7	77.6	PLLAU, PLLGL, PLLAR, PLLRU	PF, BL, RA	1.6%
Nov 2003	24	507	82.4	82.0	PLLAU, PLLGL, PLLRU	PF, BL, RA, SC	3.9%
Dec 2003	72	466/507	77.4/79.0	77.6/79.2	PLLGL	N/A ^d	0.5%/0.6%
Feb 2004	48	507	84.7	85.4	PLLAU	PF, BL, RA	1.9%

^aPLLAU = *Phyllostachys aureosulcata*, PLLGL = *P. glauca*, PLLAR = *P. aurea*, PLLRU = *P. rubromarginata*.

^bPF = Eukanuba® Low-Residue™ Puppy Dry Formula (The Iams Company, Dayton, Ohio, USA); LE = Marion Leaf Eater biscuit (Marion Zoological, Plymouth, Minnesota, USA); BL = shredded bamboo leaves; RA = red apples; SC = sugarcane; SM = powdered skim milk.

^cAs percent of diet.

^dMinimal amount of dog food was provided with corn kernels.

which total fecal recovery of lignin can be guaranteed. Substantial loss of lignin may occur in certain instances, thereby increasing the error associated with estimation of digestibility.

Empirical data regarding panda digestion are rare, due to small numbers of animals and difficulties with sample collection from this elusive species. Therefore, methods for remotely detecting digestibility in this species should be investigated. We evaluated apparent nutrient digestibility of bamboo by giant pandas with and without dietary supplementation. We also tested the efficacy of virtually indigestible compounds in bamboo as internal markers for determining apparent nutrient digestibility and fecal output. Our intent was to identify a marker that would facilitate nutrition studies with wild panda populations, in which diet and intake data are often unavailable.

Methods

Digestibility trials

We conducted 6 digestibility trials (Table 1) at the Memphis Zoo using 2 giant pandas, a 3-year-old female (international studbook 507) and a 5-year-old male (466). To lend variation to data and to ensure that fecal output equations generated would be valid for a wide range of diets, we used a number of bamboo species and conducted feeding trials with and without non-bamboo dietary supplements. This approach also facilitated comparisons of diet digestibility between bamboo-only and mixed diets. During the trials, pandas had free access to drinking water and were housed individually in temperature-regulated rooms (19 to 24°C). Prior to each trial, bamboo was harvested, transported to the Memphis

Zoo, and stored in a 16°C cooler equipped with water misters. For all trials, pandas were allowed free access to bamboo and were offered fresh bamboo periodically, according to keeper schedules and animal behavior (between 20 and 50 kg/day for the female and 30 and 60 kg/day for the male; as-fed basis).

Prior to feeding, bamboo was removed from the storage cooler and separated into 2 equal bundles based on approximate leaf and culm percentage and weight. One randomly selected bundle was rinsed and fed to the pandas, whereas the other bundle was separated into leaf, branch, and culm portions for sample collection and analysis. Samples were stored in a -20°C freezer until removed for further processing. Prior to laboratory analysis, leaf, branch, and culm samples were dried to constant mass in a 60°C forced-air oven and ground to pass a 2-mm screen in a Wiley mill (Thomas Scientific, Swedesboro, New Jersey, USA).

At the initiation and conclusion of each digestibility trial the animals consumed 20, 25, or 30 kernels of corn along with supplement (to encourage ingestion). We used this technique to determine rate of passage and to mark excretion of feces formed from bamboo consumed during the trial. Fecal collection began when corn first appeared in the feces following the initiation of a trial (4 to 6 hours after feeding corn, depending on passage rate), and ended when corn consumed at the end of a trial first appeared in the feces. During all digestibility trials, total collection of orts (refusals) and feces was performed. Orts were broken into respective parts, stored, and processed as described previously for feed samples.

Digestibility trials with bamboo and supplements. We conducted 4 digestibility trials (Table 1)

with no alteration to zoo diets; thus, dietary supplements were provided to the pandas in addition to bamboo. Pandas consumed experimental diets for a minimum 3-day adaptation period prior to trial initiation. Of the 4 trials evaluating digestibility of bamboo and supplement, 3 were conducted for 24 hours. We used 4 bamboo species of the same genus: *Phyllostachys aureosulcata*, *P. glauca*, *P. aurea*, and *P. rubromarginata*. The supplements for each 24-hour trial consisted of a combination of Eukanuba® Low-Residue Puppy Formula, Marion Leaf eater biscuits, red apples, shredded bamboo leaves, sugar-cane, and powdered skim milk (Table 1).

We used the female giant panda in an additional 48-hour feeding trial to investigate the digestibility of *P. sulcata* and dietary supplements. Supplements consisted of a low-residue puppy formula, Eukanuba® Low-Residue™ Puppy Dry Formula, red apples, and shredded bamboo leaves. All other aspects of the trial were similar to methods described for 24-hour trials.

Bamboo-only digestibility trial. We used both pandas in a 72-hour feeding trial (Table 1) to investigate the digestibility of bamboo (*P. glauca*) without supplement. Adaptation to bamboo-only diets began 3 days before initiation of the trial. No supplements were fed as part of the diet during the adaptation period or the trial itself. Minimal amounts of Eukanuba® Low-Residue™ Puppy Dry Formula were provided to the animals only at the beginning and the end of the trials to facilitate consumption of corn kernels to monitor fecal output for collection. The pandas were fed red apples throughout the day (approx 150 g/day; as-fed basis) during operant conditioning and enrichment training exercises.

Evaluation of internal markers

We selected 3 virtually indigestible components of bamboo (AIA, ADL, and ADIN) as candidates for predicting nutrient digestibility and fecal output. Total fecal collection was performed as described previously, using whole-kernel corn as an indicator of feces formation from bamboo fed during digestibility trials. Feces collected during each trial were composited over the entire trial period. We used total collection of feed and orts to determine quantity of nutrients consumed and to evaluate internal markers for digestibility and fecal output predictions. We used 2 calculations to estimate nutrient digestibility based on feed offered or feed consumed. The first method calculated digestibility

based on concentrations of nutrients and markers in the diet offered to the animals, without accounting for orts. The second method calculated digestibility based on concentrations of nutrients and markers actually consumed, by subtracting amounts in orts from amounts in the diet. Equations used for the 2 methods were as follows:

$$\text{Feed Offered} = 100 - 100 \times \frac{\% \text{marker in feed}}{\% \text{marker in feces}} \times \frac{\% \text{nutrient in feces}}{\% \text{nutrient in feed}}$$

$$\text{Feed Consumed} = 100 - 100 \times \frac{\% \text{marker consumed}}{\% \text{marker in feces}} \times \frac{\% \text{nutrient in feces}}{\% \text{nutrient consumed}}$$

Laboratory analysis

We analyzed feed, orts, and feces for DM, ash, CP, neutral detergent fiber (NDF), acid detergent fiber (ADF), ADL, crude fiber (CF), and ether extract (EE) according to the Association of Official Analytical Chemists (2003). Analyses of AIA and ADIN were performed according to Van Keulen and Young (1977) and Goering and Van Soest (1970), respectively.

Statistical analysis

We analyzed all data for digestibility trials using general linear model procedures (SAS Institute 2002). When significant differences were detected, means were separated using least square means. We analyzed data for prediction of digestibility and fecal output using internal markers via correlation and regression procedures, with comparison of correlation coefficients and regression models to determine the best predictors (SAS Institute 2002).

Results

Digestibility trials

There were no between-animal differences ($P > 0.05$) in apparent digestibilities of any nutrient except hemicellulose ($P = 0.014$; Table 2).

Evaluation of internal markers

Fecal output. Predictive regression equations determined for each internal marker were as follows:

Table 2. Digestibility (% dry matter basis) of nutrients in 4 bamboo species for a captive male (466) and female (507) giant panda consuming a diet of bamboo and supplements or bamboo only at the Memphis Zoo, Aug 2003–Feb 2004. DM = Dry matter, OM = organic matter; CP = crude protein; CF = crude fiber; NDF = neutral detergent fiber; ADF = acid detergent fiber; HC = hemicellulose; EE = ether extract.

Animal	Number of trials	DM intake (kg/d)	DM	Ash	OM	CP	CF	NDF	ADF	HC	EE
466	2	6.2	11.5	5.9	12.0	30.2	14.3	10.0	13.0	5.4	6.8
507	4	3.1	26.7	3.5	28.9	36.5	27.3	24.1	18.4	29.1	-16.3
SEM ^a		0.40	7.78	6.62	8.31	8.41	15.76	4.26	8.54	4.61	61.05
P		0.007	0.185	0.783	0.172	0.573	0.536	0.055	0.630	0.014	0.773

^aSEM = Standard error of the mean.

for AIA, Fecal output = 1.04(AIA) - 0.44; for ADL, Fecal output = 1.00(ADL) + 3.58; and for ADIN, Fecal output = 1.77(ADIN) + 0.17; Table 3; Fig. 1).

Digestibility. Apparent nutrient digestibility was predicted based on feed offered or feed consumed and internal marker estimations (Table 4). Apparent nutrient digestibility was more accurately predicted using the equation for feed consumed and AIA as the internal marker, whereas ADL and ADIN over- or under-predicted digestibility.

Discussion

Digestibility study

Mainka et al. (1989) reported DM digestibility of diets consumed by a younger and older panda as 19.0 and 15.2% respectively, which more closely resembled values determined by Dierenfeld et al. (1982; 19.6%, SE = 0.12%) than values in the present study. Mainka et al. (1989) calculated bamboo and sugarcane digestibility, assuming gruel

supplement digestibility as 100.0% and apple digestibility as 82.0%. Digestibility calculations by Dierenfeld et al. (1982) were based on 100% gruel digestibility, 82% for apples, and 75% for carrots and feline diets. In the present study, apparent digestibility of the diet was determined from total fecal output without assuming individual dietary component digestibility. Differences in apparent DM digestibility may have resulted from differences in diet and assumptions made in calculations. The current study did not rely on estimates of supplement digestibility; rather, we measured total diet digestibility, and in one feeding trial, directly quantified digestibility of bamboo only.

Another source of potential variation was loss of water from plant tissues and consequent effects on bamboo mass estimates. Mainka et al. (1989) used a 10% correction factor that accounted for water loss when determining DM digestibility. In our study,

Table 3. Evaluation of internal markers to predict fecal output by captive giant pandas consuming a diet of bamboo and supplements or bamboo only at the Memphis Zoo, Aug 2003–Feb 2004.

	Actual fecal output	Predictions of fecal output ^a		
		AIA	ADL	ADIN
Mean output, kg	5.5	5.3	9.1	10.0
Range of output, kg				
minimum	1.2	1.3	2.3	-2.1
maximum	16.7	17.3	22.1	30.4
r		0.9909	0.8392	0.8483
P		<0.001	0.018	0.016
Slope of regression		1.04	1.00	1.77
Intercept		-0.44	3.58	0.17

^aAIA = acid insoluble ash; ADL = acid detergent lignin; ADIN = acid detergent insoluble nitrogen.

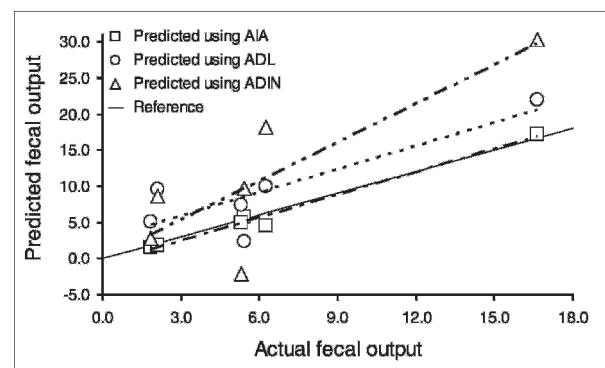


Fig. 1. Evaluation of three internal markers to predict fecal output by giant pandas, compared to a reference line (intercept = 0; slope = 1): acid insoluble ash (AIA; $Y = 1.04x - 0.44$; $r = 0.9909$; $P < 0.001$), acid detergent lignin (ADL; $Y = 1.00x + 3.58$; $r = 0.8392$; $P = 0.019$), and acid detergent insoluble nitrogen (ADIN; $Y = 1.77x + 0.17$; $r = 0.85$; $P = 0.016$).

Table 4. Evaluation of internal markers to predict digestibility by giant pandas consuming a diet of bamboo and supplements or bamboo only at the Memphis Zoo, Aug 2003–Feb 2004, using calculations based on feed offered and nutrients consumed. Consumed predicted digestibility regression equations ($r > 0.85$) using acid insoluble ash (AIA) are as follows: organic matter (OM), $Y = 0.97x + -1.18$; crude protein (CP), $Y = 0.91x + 2.31$; crude fiber (CF), $Y = 1.00x + -2.62$; neutral detergent fiber (NDF), $Y = 0.96x + -1.15$; acid detergent fiber (ADF), $Y = 0.96x + -1.64$; hemicellulose (HC), $Y = 0.98x + -1.25$; ether extract (EE), $Y = 1.06x + -3.69$.

Nutrient (apparent digestibility) ^a	Offered predicted digestibility ^{bc}			Consumed predicted digestibility ^{cd}		
	AIA	ADL	ADIN	AIA ^a	ADL	ADIN
Ash (9.2%)	4.0	-211.4	-79.7	13.2	-113.8	-92.2
<i>r</i>	0.35	0.11	0.34	0.76	0.40	0.28
<i>P</i>	0.442	0.822	0.461	0.049	0.38	0.541
OM (31.2%)	50.1	-54.1	10.4	34.2	-36.5	-35.5
<i>r</i>	0.06	0.16	0.23	0.96	0.29	0.15
<i>P</i>	0.903	0.726	0.616	0.001	0.528	0.750
CP (33.8%)	13.7	-172.9	-56.5	35.5	-62.7	-30.1
<i>r</i>	0.24	0.76	0.90	0.88	0.13	0.67
<i>P</i>	0.612	0.050	0.006	0.009	0.775	0.098
CF (31.8%)	61.9	-15.8	33.3	35.1	-40.2	-29.2
<i>r</i>	0.17	0.31	0.44	0.97	0.31	0.24
<i>P</i>	0.708	0.492	0.324	<0.001	0.5	0.602
NDF (28.3%)	53.4	-43.4	16.3	31.7	-43.6	-44.2
<i>r</i>	0.05	0.08	0.46	0.96	0.13	0.25
<i>P</i>	0.909	0.856	0.304	0.001	0.787	0.593
ADF (26.3%)	60.6	-20.8	29.9	30.2	-43.1	-46.6
<i>r</i>	0.07	0.18	0.42	0.96	0.04	0.27
<i>P</i>	0.886	0.703	0.353	0.001	0.924	0.554
HC (28.9%)	41.2	-82.8	-6.9	31.8	-48.5	-45.3
<i>r</i>	0.11	0.01	0.48	0.96	0.14	0.31
<i>P</i>	0.808	0.989	0.273	0.001	0.759	0.504
EE (1.3%)	35.0	-95.8	-16.2	5.8	-89.4	-36.6
<i>r</i>	0.10	0.25	0.36	0.99	0.53	0.74
<i>P</i>	0.832	0.592	0.433	<0.001	0.220	0.058

^aBased on total fecal collection.

^bBased on feed offered to the animal.

^cAIA = acid insoluble ash; ADL = acid detergent lignin; ADIN = acid detergent insoluble nitrogen.

^dBased on feed offered minusorts.

bamboo was stored in coolers fitted with water misters and was rinsed prior to feeding. These procedures appeared to introduce a considerable amount of variability due to water loss, not only from within plant tissues but also from surface water.

Individual digestibility trials. In the present study, 6 apparent DM digestibility values ranged between 6.9% and 38.5%. Apparent DM digestibility was greater during the 24-hour trials, ranging from 16.0% to 38.5% (38.5% and 34.9% for the female, and 16.0% for the male). In the 48-hour trial, apparent DM digestibility of the female was 21.0%. Apparent DM digestibilities of the male and female from the unsupplemented trial were 6.9% and

12.4%, respectively. At these reduced rates of nutrient absorption, pandas on bamboo-only diets must substantially increase dry matter intake to satisfy daily nutrient requirements. Data are lacking regarding the ability of giant pandas to consume enough bamboo to meet their nutrient needs during certain stages of their life (e.g., lactation). For both pandas, the smallest apparent DM digestibility value came from the bamboo-only trial. Although overall DM digestibility of supplemented diets may be greater, the digestibility of bamboo itself in such a diet may be reduced. Furthermore, a permanent diet of bamboo only or bamboo with minimal supplement better reflects the diet of pandas in the wild.

Fecal output and digestibility predictions

We selected 3 internal markers to calculate fecal output and digestibility based upon the assumption that because they are indigestible they may be totally recovered in the feces. Acid insoluble ash as an internal marker was more highly correlated with actual fecal output than ADL or ADIN. Prior studies have shown fecal AIA recovery to be greater than 100% in ruminants (Van Keulen and Young 1977, Block et al. 1981); recovery of AIA in panda feces should be close to 100% of that in the diet as well. Furthermore, grasses typically contain smaller quantities of lignin and ADIN than other feedstuffs, whereas concentrations of silica (the major constituent of AIA) are greater in bamboo compared to other plant species (Greenway 1999). Thus, AIA serves as a good marker for estimating fecal output from this forage in particular, with important implications for estimating nutrient digestibility in wild panda populations.

Kilmer et al. (1979) and Block and Muller (1979) found that AIA marker digestibility for sheep and cattle after accounting for ors was more similar to digestibility calculated from total fecal collection than when ors were disregarded. We found the same to be true in this study: digestibility estimates using AIA were more highly correlated with actual nutrient digestibility when they were based on feed consumed equations, as opposed to feed offered calculations. The only case in which AIA and feed consumed estimations failed to produce a highly significant correlation with actual digestibility was in the case of ash ($r = 0.76$, $P = 0.049$). However, predictive power in this instance was still stronger than that based on AIA and feed offered, as well as any calculations using ADL or ADIN. Long et al. (2004) used lignin to calculate hemicellulose digestibility of pandas in the Qinling Mountains of China. These researchers reported hemicellulose digestibility of 18.1%, which more closely resembles our predicted digestibility using AIA (31.8%) than ADL (-48.5%). The difference may be attributed to several factors such as species of bamboo, seasonal affects of digestibility, captive versus non-captive pandas, and variation of the concentration of these markers in bamboo. With the information we have presented, it is possible for research on the nutrition of wild panda populations to deviate from tracking individual animals to simply identifying recent panda foraging sites. Once such sites are located, AIA analyses of field samples (feces, standing

bamboo, and bamboo that has been clipped but not consumed) may be used to make inferences regarding nutrient digestibility in giant pandas in their native habitat.

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