Determining the Composition of Herbivore Diets in the Trans-Himalayan Rangelands: A Comparison of Field Methods

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Abstract

In late summer, in a semi-arid mountain range in Nepal, we compared 3 field methods for determining the botanical composition of herbivore diets. Data were collected from the same animals belonging to 1 herd of domestic yak (*Bos grunniens*) and 2 herds of mixed smallstock, consisting of domestic goats (*Capra hircus*) and sheep (*Ovis aries*). Bite count, feeding site examination, and microhistological analysis of feces gave different estimates of forage categories and plant species in both animal groups. Because yaks grazed in other vegetation communities when not observed for bite-counts and feeding signs, the results from the latter methods could not be compared directly with that from fecal analysis. In smallstock, feeding site examination gave higher estimates of graminoids and lower estimates of shrubs than the other 2 methods, probably because all feeding signs on shrubs were not detected. Bite-counts and fecal analysis gave comparable results, except that forbs were underestimated by fecal analysis, presumably due to their more complete digestion. Owing to the difficulty in collecting samples that are representative of the entire grazing period and the problem of recording feeding signs correctly, both feeding site examination and bite-counts are unsuitable methods for studying the food habits of free ranging domestic and wild herbivores. Microhistological analysis of feces appears to be the most appropriate method, but correction factors are needed to adjust for differential digestion. The systematic use of photomicrographs improves the speed and accuracy of the fecal analysis.

Resumen

A fines del verano, en un pastizal semiárido motañoso de Nepal, comparamos 3 métodos de campo para determinar la composición botánica de la dieta de herbívoros. Los datos fueron colectados de los mismos animales perteneciennte a un hato de yaks (*Bos grunniens*) domésticos y dos hatos de rumiantes menores combinados de cabras domésticas (*Capra hircus*) y ovinos (*Ovis aries*). El conteo de bocados, la examinación del sitio de alimentación y el análisis microhistológico de heces dieron diferentes estimaciones de las categorías de forraje y especies de plantas en ambos grupos de animales. Debido a que los yaks apacentaron otras comunidades vegetales, cuando no se observaron para el conteo de bocados y signos de alimentación, los resultados de este método no pudieron ser comparados directamente con los del análisis fecal. El examen del sitio de alimentacion de los ruminates menores produjo estimaciones más altas de las graminoides y más bajas de los arbustos que los otros dos métodos, probablemente porque todos los signos de alimentación en los arbustos no fueron detectados. El conteo de bocados y el análisis fecal produjeron resultados comparables, excepto para las hierbas que fueron subestimadas por el análisis fecal, presumiblemente debido a su más completa digestión. Debido a la dificultad en colectar las muestra que son representatives del periodo completo de apacentamiento y el problema de registrar correctamente los signos de alimentación, tanto el examen del sitio de alimentación como el conteo de bocados son métodos inadecuados para estudiar los hábitos alimenticios de los animales domésticos en libre pastoreo y la fauna silvestre. El análisis microhistológico de las heces parece se el método más apropiado, pero se necesitan factores de correción para ajustar el diferencial de digestión. El uso sistemático de fotomicrográficas mejora la velocidad y certeza del análisis fecal.

Key Words: bite-count, *Bos grunniens*, *Capra hircus*, fecal analysis, feeding site examination, food habits, *Ovis aries*

INTRODUCTION

Knowledge of the food habits of wild and domestic herbivores is a basic requirement for the management of rangeland resources. During the past 60 years, several techniques have been developed to study herbivore food habits (Holechek et al. 1982; Alipayo et al. 1992). Yet, one of the crucial problems confronting range scientists is to select the most practical and reliable method (Barker 1986). The 3 most popular field methods are feeding site examination (Pechanec and Pickford 1937), bite-counts (Hubbard 1952) and microhistological analysis of feces (hereafter fecal analysis) (Baumgartner and Martin 1939). Feeding site examination involves enumeration of feeding signs in sample quadrats where animals have been feeding. The bite-count method is undertaken by observing an animal at close range and recording the number of bites on different plant species. Fecal analysis requires the identification of plant fragments in fecal sample material on the basis of the histological characteristics of specific plants or plant parts.

Although many studies have compared these methods, none have included them in one study. The comparative studies

Research was funded in part by the Norwegian Agency for Development Cooperation (NORAD).

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Manuscript received 24 February 2006; manuscript accepted 12 June 2006.

carried out so far reveal that the consistency among methods is affected primarily by the feeding behavior of the ungulates (Ortega et al. 1995) and the temporal (McInnis et al. 1983; Mohammad et al. 1995) and spatial (Smith and Shandruk 1979; Mofareh et al. 1997) variation in the composition of the available forage species (Free et al. 1971; Bartolome et al. 1995). Therefore, any method that is judged to be appropriate for a given ungulate species in a given habitat may not be suitable for a different species in a different habitat.

Except for the study by Shrestha et al. (2005), to the best of our knowledge no studies have yet been undertaken in the Trans-Himalayan rangelands to evaluate the bite-count technique, the feeding site examination and fecal analysis as methods to estimate the botanical composition of herbivore diets. In order to compare the diets of domestic and wild species, Shrestha et al. (2005) adjusted the results obtained from fecal analysis by comparing them with bite-counts data obtained in domestic goat (*Capra hircus*). However, as their study was not specifically designed to compare the methods, it was difficult to draw any conclusion about their accuracy.

The objective of the present study was to evaluate the suitability of the aforementioned 3 methods for determining the diets of domestic goats and sheep (*Ovis aries*) (henceforth referred to as "smallstock") and domestic yaks (*Bos grunniens*) (henceforth referred to as "yak").

Such an assessment of methods is needed for field studies addressing the controversial issue of competition among wild and domestic ungulates in these marginal lands (Harris and Miller 1995; Miller and Schaller 1996; Mishra et al. 2004; Shrestha et al. 2005).

METHODS

Study Area

The study was conducted in the Phu valley (lat 84°15′ to 84°20′E and, long 28°43′ to 28°50′N) of Manang District of north-central Nepal. It lies in the rain shadow of Annapurna range and shares its northern border with the Tibetan plateau. The area receives annually less than 400 mm of precipitation (ICIMOD 1996) and most of it occurs in the form of snow during winter. The mean maximum and minimum temperatures recorded during this study were 5.8°C and −7.3°C in January and 18°C and 9.5°C in July. The snow and frozen ground start to thaw in March.

Animal husbandry is an age-old strategy of subsistence livelihood in this region (Miller 1987). It is practiced by employing the indigenous grazing management system of rotating livestock herds across different seasonal pastures. The smallstock are usually herded while grazing in the open pastures, and then corralled when they return in the evening. Except for milking yaks and juveniles, other yaks are free-ranging throughout the year.

Three adjacent summer pastures, viz. Tshea, Dhungparpa and Napu, were selected for this study. Data on smallstock were collected from Tshea and Dhungparpa pastures, both of which were located in north-eastern aspects in an altitudinal range of 4 000–4 800 m. Data on yak were collected in the Napu pasture, at 4 400–5 000 m on south-easterly slopes. Vegetation composition is dominated by bunchgrasses and low, densely matted shrubs, which are typical of the semi-arid Tibetan Plateau (Miller 1987). Altitude and aspect appear to govern the distribution of vegetation communities. *Lonicera* spp. L. vegetation community spreads over most of the lower and middle slopes on southern and eastern aspects. Pockets of *Caragana jubata* (Pall.) Poir. are distributed on the northern aspects and the *Artemisia* spp. L.–*Stellera chamaejasme* L. meadow vegetation type is prevalent in the basins. Alpine grasslands dominated by *Carex* spp. L., *Kobresia* spp. Willd. and *Festuca* spp. L. are widespread in the higher slopes.

Fieldwork was conducted during late August and early September. At the onset of data collection, grazing herds of yaks and smallstock were followed for 4 days to familiarize us with the animals and the available vegetation composition and also to identify practical problems associated with the methodology. The feeding site examinations could not be conducted separately for goats and sheep because they were herded together in mixed flocks. We therefore merged our goats and sheep data in the bite-count as well as in the fecal analyses to facilitate comparisons with the feeding site examinations. This was done by weighing the frequencies by the proportion of goats (67%) and sheep (33%) in the smallstock herds. We followed Polunin and Stainton (1987), and Stainton (1988) to identify the forbs and shrubs in field.

Bite-counts

Following Sanders et al. (1980), the bite-count data were spread over 3 periods of the day, viz. morning (06:00–10:00 hours), afternoon (10:00–14:00 hours) and evening (14:00–18:00 hours). A bite was defined as an individual bite taken from a given plant species (Mofareh et al. 1997; Henley et al. 2001). The plant species being eaten every 10^{th} second by a randomly selected feeding individual was recorded on a dictaphone during 15-minute observation periods (Mishra et al. 2004), thereby yielding a maximum of 90 bites per observation period. The animals were observed from a distance of ca. 2 m and a total of 935 and 723 bites were recorded for goats and sheep, respectively, from 2 sites over successive 2 days in Tshea and Dhungparpa pastures. Yaks were observed 1 day in Napu pasture which yielded 715 bites. The locations of the sites were recorded by Global Positioning System (GPS) readings and also marked by using physical features such as boulder outcrops, gullies, scree, etc. as reference points for later feeding site examinations.

Feeding Site Examination

Within hours after completing the bite-count, the feeding site examinations were carried out by a second observer in exactly the same locations where the bite-counts had been recorded. One-m^2 quadrats were placed at 10 m intervals along the feeding routes. Signs, such as exudation of sap, crushed tissue and fresh clippings were used to judge if a plant species had been eaten. A method similar to the Ocular-Estimate-by-Plot method as described by Pechanec and Pickford (1937) and adopted by Laycock et al. (1972) was used in quantifying the consumption. Thirty-eight quadrats from 2 different sites were sampled for smallstock, and 29 quadrats from 1 site were sampled for yaks.

Fecal Analysis

Fecal samples were collected next morning from the same livestock herds, which had been subjected to bite-counts and feeding site examinations the day before. Pellets from 7 and 9 different goats and 7 and 8 different sheep were collected from the 2 different pastures shortly after defecation by observing the animals in their holding pens. Yaks were free-ranging and not corralled at night. Hence, fresh yak dung ($N = 12$) were collected on the pasture. The samples were air dried and stored in paper bags in the field. The reference slides were prepared from 63 plant species that included most of the species judged to be eaten based on field observations and interview of herders.

Preparation of Slides. Two composite samples were prepared for the smallstock and 1 composite sample was prepared for yak. Sample preparation began by randomly selecting 10 pellets and ca. 5 g of dung from each individual smallstock and yak sample, respectively. Five slides from each composite fecal sample were prepared following the method developed by Sparks and Malechek (1968) and later modified by Vavra and Holechek (1980); Jnawali (1995); Shrestha et al. (2005); and Wegge et al. (2006). Also, separate slides for the plant parts such as leaf, stem, flower, seed, and root were prepared.

Preparation of Photomicrographs. The diagnostic features of the plant epidermis such as cells, fibres, trichomes, pores, stomata, vessels, intercellular structures, etc., from each reference slide were photographed using a Leica DFC camera fitted to an optical microscope at 100× and 400× magnification. In order to ensure wide representation, successive photographs were taken until the same type of tissue was encountered repeatedly along a transect. Thus, a reference slide library was made of 2 831 images. These photomicrographs were given specific file names with dichotomous identification keys, describing the general orientation and color, shape, size and type of epidermal tissues (e.g., with cells—cork cells, sponge cells, silica cells, guard cells, etc.), and general texture (density) of each diagnostic feature. This was done in order to facilitate the screening of photomicrographs for the identification of fecal fragments during later analysis. All photomicrographs were organised using Picasa 2 software (Google 2005). Considering the massive number of photomicrographs from the plant reference slides, this method appeared to be efficient and practical both in terms of speed and accuracy.

Slide Reading. The images of fecal fragments were compared with the plant reference photomicrographs at the similar level of magnification (100× and 400×), exposure, brightness, and colour conditions. The first 20 nonoverlapping fragments intercepted by a randomly selected transect line were counted. A total of 5 slides and 2 transects per slide yielded 200 counts per composite sample. Out of the 2 composite samples of smallstock and 1 composite sample of yaks, a total of 400 and 200 fragments were examined, respectively.

Fragments that could not be identified to species or genera, but to forage category were grouped into 'unidentified graminoids', 'unidentified forbs', and 'unidentified shrubs'. A few fragments in smallstock (ca. 5%) and in yak (ca. 2%) were classified as 'unidentified dicots', as they could not be distinguished into shrub or forb categories. The completely unknown fragments, which accounted to ca. 7% in smallstock and ca. 4% in yak, were included in the 'unknown' category.

Data Analysis

Relative frequencies were calculated for each forage category and plant species in bite-count, fecal analysis, and feeding site examination. In feeding site examination, the relative frequencies were calculated by weighting the consumption by production in each quadrat (Smith 1968), as follows:

$$f_i = u_i \times p_i \Big/ \sum_{i=1}^{n} (u_n \times p_n) \qquad [1]$$

where,

f_i = relative frequency of plant species i consumed by an ungulate in the quadrat.

u_i = proportion of total horizontal cover of the plant species i consumed by an ungulate in the quadrat,

p_i = proportion of the plant species i relative to the total vegetative cover in the quadrat.

n = total number of species in the quadrat.

As the unknown dicots and completely unknown proportions made up negligible amounts in the fecal analysis, they were adjusted by distributing them proportionately to the shrubs and forbs, and to all 3 categories, respectively. This was done by assuming that the ratio of identifiable and unidentifiable fragments was proportional to each other for each plant species in the microscopic analysis (Free et al. 1971).

Differences between estimated proportions of forage categories by fecal analysis, bite-count and feeding site examination of smallstock and yak were assessed by Chi-square tests (Alipayo et al. 1992). In doing so, the following null hypotheses were tested:

1. Within each group of herbivores, the estimated proportions of forage categories are the same by *all 3 methods*,
2. Within each group of herbivores, the estimated proportions of *all 3 forage categories* are the same by any given *pair of methods*,
3. Within each group of herbivores, the estimated proportion of *each forage category* is the same by any given *pair of methods*.

The relationships between pair of methods in estimating forage categories were assessed by the Pearson's product moment correlation coefficient (r). The similarity between a pair of methods (Chapuis et al. 2001) was assessed by Schoener's Index (Schoener 1968), which is identical to the percent similarity index as introduced by Renkonen (1938):

$$\text{Schoener's Index} = 1 - 0.5 \sum \left| p_{x_i} - p_{y_i} \right| \qquad [2]$$

where,

p_{xi}: proportion of food item i detected by method x

p_{yi}: proportion of food item i detected by method y.

The index varies from 0.0 for completely dissimilar to 1.0 for completely similar diet compositions as detected by methods.

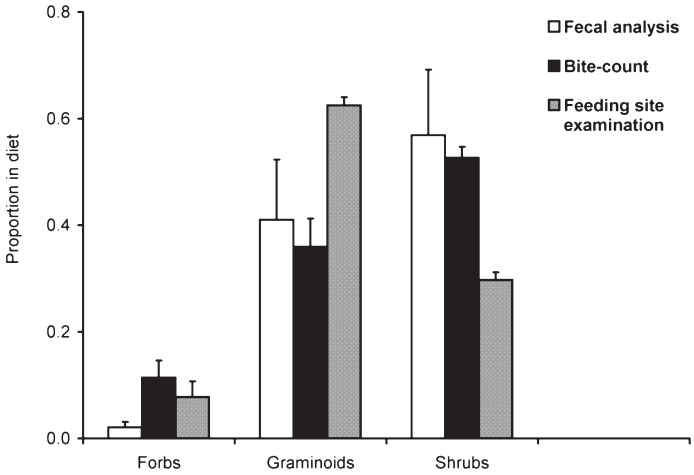

Figure 1. Comparisons between fecal analysis, bite-count, and feeding site examination in estimating the botanical composition of diets of smallstock in the Phu Valley of upper Manang, Nepal. Error bars denote the standard deviation.

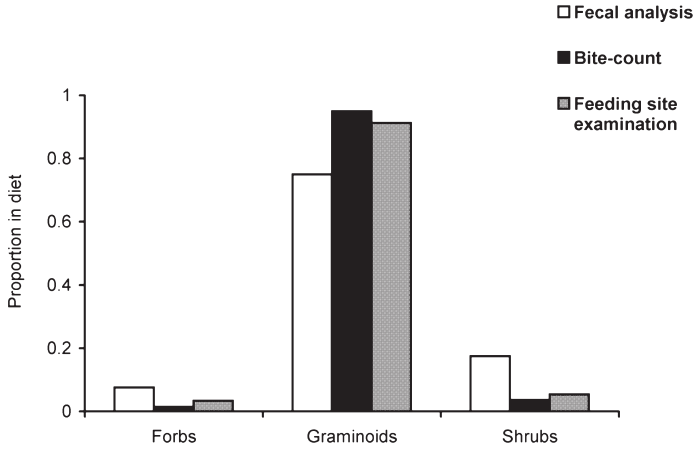

Figure 2. Comparisons between fecal analysis, bite-count, and feeding sites examination in estimating diets of yak in Phu valley of upper Manang, Nepal.

The 3 plant species contributing the highest proportion to the diet by each method were analysed by Chi-square tests to test for differences between pair of methods and between all the 3 methods combined. Pearson correlation coefficient (r) and Schoener's Index were used to determine the relationship and the similarity between the methods in estimating proportions of different plant species.

RESULTS

Comparison at the Level of Forage Categories

The 3 methods differed in estimating forage categories in the diets of both smallstock ($\chi^2 = 23.83$, $P < 0.01$, df = 4; Fig. 1) and yak ($\chi^2 = 21.09$, $P < 0.01$, df = 4; Fig. 2).

Fecal Analysis vs. Bite-count. Fecal analysis and bite-counts differed significantly both in smallstock and in yak (Table 1). In the former, this was mainly due to a lower estimate of forbs by the fecal analysis ($\chi^2 = 6.66$, $P = 0.01$, df = 1; Fig. 1) as there were no significant difference in shrubs ($\chi^2 = 0.32$, $P < 0.57$, df = 1) or in graminoids ($\chi^2 = 0.53$, $P < 0.48$, df = 1).

Fecal Analysis vs. Feeding Site Examination. For both animal groups, fecal analysis also differed from feeding site examination (Table 1) because it gave higher estimates of shrubs and lower estimates of graminoids (Figs. 1 and 2). However, the lower estimate of forbs by fecal analysis was significant only in the smallstock ($\chi^2 = 3.726$, $P = 0.05$, df = 1).

Bite-count vs. Feeding Sites. Bite-counts and feeding site examination differed only in smallstock (Table 1); the feeding site examination gave lower estimates of shrubs ($\chi^2 = 11.25$, $P < 0.01$, df = 1) and higher estimates of graminoids ($\chi^2 = 13.986$, $P < 0.01$, df = 1). In yak, no differences were detected in any of the forage categories by the two methods.

Similarities and Relationships. In smallstock, the bite-count was most similar (Table 2) and closely related (Table 3) to the fecal analysis. In yak, the bite-count was more similar to the feeding site examination than to the fecal analysis (Table 2). As the data were collected for only one day from a single site, we were unable to use correlation test on data in yaks.

Comparison at the Level of Plant Species

Fecal analysis consistently identified the highest number of plant species both in smallstock and yak (Table 4). In smallstock, feeding site examination detected the least number of plant species, but the 3 methods varied less in total number identified relative to yak. In yak, bite-count and feeding site examination detected only one-fourth, and one-half of the species, respectively, than that identified by fecal analysis.

As with the forage categories, the 3 methods differed in estimating the proportions of the 3 most important food species in both smallstock ($\chi^2 = 25.44$, $P < 0.01$, df = 6) and yaks ($\chi^2 = 89.29$, $P < 0.01$, df = 10). Pair-wise comparisons revealed that feeding site examination differed from bite-count and fecal analysis in both animal groups, but the difference between the latter 2 methods was not significant in the smallstock (Table 1). The ranking of the important food species in smallstock further attests to this, as the bite-count and fecal analysis gave consistently higher ranks to the 2 important food species *Poa pagophila* (Bor.) Kew Bull. and *C. jubata* than that by the feeding site examination (Table 5). In the case of yak, no methods were in agreement in estimating the 3 most important plant species (Table 1).

Further analysis based on Schoener's Index and Pearson's product moment correlation coefficient showed a pattern consistent with the previous results on forage categories. They showed that in smallstock, fecal analysis was most similar (Table 2) and more closely related (Table 3) to bite-count than to feeding site examination.

DISCUSSION

The 3 methods differed in estimating the diets of smallstock and yak both at the forage category and at the plant species level. In smallstock, feeding site examination gave higher estimates of graminoids and lower estimates of forbs and shrubs than the

Table 1. Pair-wise comparisons of methods in estimating the proportions of forage categories and the 3 most important plant species in smallstock and yak.

	Forage category						Plant species[1]					
	Smallstock			Yak			Smallstock			Yak		
	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df
Fecal analysis vs. bite-count	6.7	0.03	2	15.85	< 0.01	2	2.08	0.56	3	56.37	< 0.01	5
Fecal analysis vs. feeding site examination	16.63	< 0.01	2	10.36	0.01	2	10.32	< 0.02	3	38.29	< 0.01	5
Feeding site examination vs. bite-count	14.21	< 0.01	2	1.19	0.55	2	23.63	< 0.01	3	31.31	< 0.01	4

[1]Average proportions of the 3 plant species with the highest contribution in each sample collection.

other two methods. Furthermore, fecal analysis underestimated the proportion forbs compared with bite-count. In yak, bite-count and feeding site examination gave similar results, with consistently higher estimates of graminoids and lower estimates of forbs and shrubs than fecal analysis.

The daytime sampling period in yak for both bite-count and feeding site examination probably explains the observed discrepancy between fecal analysis and these 2 methods. Although not studied systematically, we observed that yaks shifted to lower slopes during nighttime. The vegetation in these low-lying areas was dominated by dicots with higher species richness than the upper alpine grasslands. Hence, it is likely that yaks consumed more dicots when we did not collect data on bite-count and feeding site examination.

Unlike yak, the smallstock were kept in an enclosure when they returned from the pasture. Also they were confined to the same pasture for more than 5 days during the data collection period, and the vegetation community was relatively homogeneous where the smallstock foraged. Hence under these conditions, the asynchronous sampling period between fecal analysis and the other two methods can not account for the observed discrepancy in smallstock (Smith and Shandruk 1979). In the following section, we discuss the possible biasing factors in each studied method.

Feeding Site Examination

Feeding signs are known to get readily obscured in plants which are susceptible to disarticulation (Smith 1968; Smith and Shandruk 1979). Shrubs are more likely to be disarticulated because of the prevalence of nodes. For this reason, feeding site examination probably overlooked some of the feeding signs on shrubs. In addition, the method employed in quantifying the consumption of forage species might also have contributed to underestimation of shrubs in the feeding site examination. Owing to the difficulty in estimating consumption on the basis of counting all feeding signs on individual plants, we estimated utilization by cover values, similar to the Ocular-Estimate-by-Plot method (Pechanec and Pickford 1937; Laycock et al. 1972). This method restricted our observation mainly to the horizontal part of the shrub canopy.

Table 2. Similarity (Schoener's Index) between pairs of methods in estimating the proportions of forage categories and the 3 most important plant species in smallstock and yak.

	Smallstock		Yak	
Method pairs	Forage category	Plant species	Forage category	Plant species
Bite-count vs. fecal analysis	0.89	0.83	0.80	0.53
Bite-count vs. feeding site examination	0.73	0.65	0.96	0.74
Fecal analysis vs. feeding site examination	0.72	0.69	0.84	0.62

Bite-count Technique

Inaccurate identification of plants and differential bite size are the major factors affecting the accuracy of the bite-count data. Identification of plants is influenced by the forage category (Henley et al. 2001), terrain conditions (Sanders et al. 1980), and the training of the observer (Free et al. 1971). The bias due to these factors per se was minimized in the present study because the bites were recorded by approaching the domestic animals within a distance as close as 2 m by an observer, who had nearly 1 year of experience with the local flora.

The bite size is reported to vary according to season (Free et al. 1971), size of the leaves (Mofareh et al. 1997; Henley et al. 2001), and mouth morphology of the ungulate (Ortega et al. 1995; Mofareh et al. 1997). Free et al. (1971) showed that bite weight was roughly constant in spring and summer, but variable during autumn when the forage began to mature and leaves began to dry and curl. If this is the case, our bite-count data were less biased due to variation in bite size because they were collected in summer. Henley et al. (2001) concluded that bite-counts tend to underestimate the dietary contribution of large-leaved plants (e.g., forbs). However, in the dry trans-Himalayan rangelands, leaves of forbs and shrubs are small and rather similar in size. Lastly, Mofareh et al.'s (1997) conclusion of more uniform bite sizes in narrow-muzzled ungulates such as deer and small bovids compared to cattle seems to correctly explain our results of similar proportion of shrubs and graminoids by bite-counts and fecal analysis.

Therefore, our bite-count data in smallstock probably gave rather accurate results. It is likely that the reason for the discrepancy between this method and fecal analysis in estimating forbs has more to do with the fecal analysis method than with the bite-count method.

Fecal Analysis

The fecal analysis consistently gave lower proportions of forbs than bite-count also when tested separately for goats ($\chi^2 = 11.33$, $P < 0.01$, df = 1) and sheep ($\chi^2 = 18.54$, $P < 0.01$, df = 1). These findings closely agree with the study undertaken in summer in domestic goats in an area adjacent to the present study area (Shrestha et al. 2005) and elsewhere (Smith and Shandruk 1979; McInnis et al. 1983; Alipayo et al. 1992;

Table 3. Relationships (Pearson's product moment correlation coefficient, *r*) between pairs of method in estimating the proportions of forage categories and the 3 most important plant species in smallstock and yak.

	Forage category			Plant species[1]					
	Smallstock			Smallstock			Yak		
	r	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*
Fecal analysis vs. bite-count	0.97	< 0.01	6	0.84	< 0.02	7	0.78	0.07	6
Fecal analysis vs. feeding site examination	0.57	0.23	6	0.80	0.03	7	0.65	0.17	6
Feeding site examination vs. bite-count	0.48	0.33	6	0.45	0.31	7	0.95	< 0.01	4

[1]Average proportion of plant species with the highest contribution in each sample collection.

Bartolome et al. 1995). Considering the authors' previous experience with the fecal analysis method and knowledge of the local flora, the bias was not due to incorrect identification of plant species, which is often the case with untrained observers (Free et al. 1971; Holechek and Gross 1982; Alipayo et al. 1992). Besides, detailed collection of reference specimens comprising plant tissues from flower, seed, stem, leaf, and root, and the use of photomicrographs improved the accuracy, as evidenced by the low proportions of completely unknown fragments in the present study.

Instead, the bias most likely was due to differential digestion of ingested plant material. Persistence of plant material after passage through the gut varies according to the digestibility of the plant species (Pulliam 1978). Digestibility depends to a large extent on the lignification of epidermal tissue. Many perennial species (e.g., shrubs) have highly lignified epidermal tissue, and proportionally more of such plants will therefore "survive" digestion compared with annuals, including forbs (Storr 1961). Moreover, the epidermal tissue in xeric shrubs is known to be more cutinized than forbs, thereby further reducing the extent of their digestion. For these reasons, forbs are more susceptible to digestion (Vavra et al. 1978; Bartolome et al. 1995) relative to shrubs (Holechek and Gross 1982), and this is especially true in semi-arid environments like ours (Long et al. 1999). This appears to be the most obvious reason why fecal analysis gave lower estimates of forbs compared to bite-count in our study.

Precision is expected to increase during winter (Vavra et al. 1978; Chapuis et al. 2001) when digestibility (Long et al. 1999) and/or abundance of forbs are low. Fecal analysis is also found to be more precise in grazers like sheep and cattle (Vavra et al. 1978; Alipayo et al. 1992; Bartolome et al. 1995; Mohammad et al. 1995; Mofareh et al. 1997) than in browsers such as deer (Holisova et al. 1986; Lewis 1994). This supports the report that fecal analysis is less accurate when the diet consists more of shrubs and forbs than of monocots (Slater and Jones 1971). Our results suggest that it is not the amount of shrubs but probably the amount of forbs, which give rise to a bias in the fecal analysis.

Table 4. Total number of plant species identified by fecal analysis, bite-count and feeding site examination in smallstock and yak.

Ungulates	Smallstock	Yak
Fecal analysis	26	29
Bite counts	22	8
Feeding site examination	18	13

CONCLUSION AND MANAGEMENT IMPLICATIONS

Both the feeding site examination and the bite-count method gave biased estimates of the diet of the free-ranging yaks because the data from these methods did not cover the late evening and night feeding bouts. Apart from this, the former method did not detect all the feeding signs in shrubs and is also unsuitable when more than one herbivore uses the range. Although rather precise, the bite-count method can only be used for tame animals, which are not free-ranging. Considering this, the fecal analysis appears to be the most appropriate method for comparing food habits of wild and domestic ungulates in the Trans-Himalayan rangelands. However, this method is quite time-consuming and demands a great deal of skill in identifying the plant species in the fecal samples. Using high definition photomicrographs together with the development of dichotomous identification keys of reference plant species and their parts can mitigate these problems. Also, the problem of differential digestion in the fecal analysis can be addressed by developing appropriate correction factors (Brand 1978; Barker 1986). In doing so, the phenological stage of the plants and type of ungulate should be taken into consideration.

ACKNOWLEDGMENTS

The authors are grateful to Annapurna Conservation Area Project of the King Mahendra Trust for Nature Conservation for support during fieldwork. We thank G. S. Rawat and C. Richard for their help in identifying plant specimens, and N. M. B. Pradhan, A. K. Shrestha, and S. Mathema for assistance in the laboratory work.

Table 5. Ranking of the 3 most important food species[1] by 3 different methods in smallstock. The ranking is based on the average of 2 composite fecal samples and 2 days of observations of bite-counts and feeding site examinations.

	Fecal analysis		Bite-count		Feeding site examination	
Plant species	Percent of diet	Rank	Percent of diet	Rank	Percent of diet	Rank
Carex sp.	11.46	1	16.23	2	47.15	1
Lonicera spinosa	8.11	2	19.34	1	14.12	2
Poa pagophila	4.58	4	14.16	3	1.52	11
Caragana jubata	4.17	6	9.11	4	1.08	12
Spiraea sp.	5.65	3	6.79	5	8.51	3
Agrostis sp.	1.49	11	0.15	18	4.70	5
Danthonia jacquemontii	0.67	15	1.68	11	8.25	4

[1]Species with the highest contribution in each sample collection.

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