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Foods, macronutrients and fibre in the diet of blue sheep (*Psuedois nayaur*) in the Annapurna Conservation Area of Nepal

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Abstract

Food resources are often critical regulating factors affecting individual fitness and population densities. In the Himalayan Mountains, Bharal "blue sheep" (*Pseudois nayaur*) are the main food resource for the endangered snow leopard (*Panthera uncia*), as well as being preyed upon by other predators. Blue sheep, however, may face a number of challenges including food resource competition with other wild and domestic ungulates, and hunting pressure. Here, we characterized the diet of blue sheep in the Annapurna Conservation Area (ACA) of Nepal and conducted proximate nutritional analysis on a limited number of plants identified as foods. Furthermore, we investigated the macronutrient and fiber balance of these plants using nutritional geometry which is a state-space approach to modeling multidimensional and interactive nutritional aspects of foraging. A total of 19 plant species/genera were identified in blue sheep pellets using microhistological analysis. On average, across seasons and regions of the study area, the two most frequently occurring plants in pellets were graminoids: *Kobressia* sp. and *Carex* spp. The macronutrient balance of *Kobresia* sp. was relatively high in carbohydrate and low in protein, while other plants in the diet were generally higher in protein and lipid content. Analysis of fiber balance showed that the two most consumed plants of blue sheep (*i.e.*, *Kobresia* spp. and *Carex* spp.) contained the highest concentration of hemicellulose, which is likely digestible by blue sheep. The hemicellulose and lignin balance of plants ranged relatively widely, yet their cellulose contents showed less variation. Foraging by blue sheep may therefore be a balance between consuming highly digestible high-carbohydrate plants and plants less-digestible but higher in protein and/or lipid.

Introduction

Food resources are often critical regulating factors affecting individual growth and population densities (Miyashita 1992; Raubenheimer and Simpson 1997; Carbone and Gittleman 2002; Simpson et al. 2004; Brasher et al. 2007). This includes large ungulate prey species, as ungulate biomass has been shown to depend upon regional food availability (Fritz and Duncan 1994). Herbivores, however, face numerous challenges related to food resources and nutrition, including nutritionally imbalanced foods (Wehi et al. 2013; Nie et al. 2014), plant toxins (Rosenthal and Berenbaum 1991), and incompletely digestible fiber (Milton 1979).

In the Himalayan mountains, native blue sheep (also known as naur and bharal; *Pseudois nayaur*) are the main prey species of the endangered snow leopard (*Panthera uncia*; >60% of their diet) and are also prey of other

predators (Aryal et al. 2013, 2014a,b). The blue sheep is widely distributed, being found in mountainous areas of China, Nepal, Pakistan, and India (Aryal et al. 2013; Harris 2014), with highest abundance occurring in the Himalayan region of Nepal (Oli et al. 1993; Aryal et al. 2014a). Within Nepal, maintaining healthy blue sheep populations is considered important in reducing livestock depredation by snow leopard, thereby reducing human-wildlife conflict (Oli et al. 1994; Aryal et al. 2014a,b,c). Factors influencing the distribution and abundance of blue sheep in Nepal include trophy hunting, which may be unsustainable (Aryal et al. 2010), and habitat preferences (Aryal et al. 2013). Blue sheep may also face competition with domestic sheep and goats due to dietary overlap, which will likely become more of a problem as pastoral use increases (Mishra et al. 2004; Shrestha et al. 2005; Raubenheimer 2011).

An increasing body of research has been devoted to blue sheep, including studies of: diet and ecology (Mishra et al. 2004, Shrestha et al. 2005; Shrestha and Wegge 2008); population dynamics (Oli and Rogers 1991; Aryal et al. 2014a); and general species information and habitat preferences (Cincotta et al. 1991; Schaller and Gu 1994; Harris and Miller 1995; Miller and Schaller 1998; Namgail et al. 2004; Namgail 2006). Yet despite these advances, there is a lack of information regarding the diet and nutritional ecology of blue sheep, especially the nutrient composition and balance of foods.

Studies utilizing nutritional geometry, a state-space approach to modeling the multidimensional and interactive effects of nutrients, have demonstrated that the balance of macronutrients (protein, carbohydrate, and fat) in foods is a driving force behind animal foraging behavior across several taxa (Felton et al. 2009; Rothman et al. 2011; Simpson and Raubenheimer 2012; Johnson et al. 2013) rather than simply energy or single nutrient (e.g., protein) intake *per se* (Erlenbach et al. 2014; Solon-Biet et al. 2014; Kohl et al. 2015; Simpson et al. 2015). These physiological and behavioral preferences have ecological effects, for example, the macronutrient balance of foods has been shown to strongly influence the body composition (e.g., lean vs. fat mass) of the consumer (Solon-Biet et al. 2014), and predator body composition can be directly related to that of its prey (Hawlena and Schmitz 2010; Hawley et al. 2014). In fact, predation risk can influence the macronutrient selection of herbivores, which can result in changes in their body composition and ecosystem nutrient transfer (Hawlena and Schmitz 2010). Furthermore, macronutrient regulation can be used to inform the nutritional ecology of wild animals (Kearney et al. 2010; Coogan et al. 2014), and also their conservation (Raubenheimer and Simpson 2006; Raubenheimer et al. 2012). Studies incorporating the concept of macronutrient balance can, therefore, be extremely useful in understanding the habitat requirements, temporal nutrient dynamics, and nutritional constraints faced by wild animals by, for example, providing predictive models of foraging behavior based on the nutrient content of foods (Coogan et al. 2014). Such studies are of importance for large ungulate prey species that support populations of predators, such as the blue sheep.

The objective of this paper was to investigate the diet of blue sheep in the Annapurna Conservation Area (ACA) of Nepal. Our study focused on the diet of blue sheep in the Mustang and Manang regions of the ACA, with an emphasis on the remote Mustang region for which there is a lack of information due to its relatively isolated location (Aryal et al. 2014a). To that end, we identified plants found in blue sheep pellets using microhistological analysis. In addition, we conducted proximate nutritional analysis on a limited (due to logistical constraints) number of plants consumed by blue sheep and investigated the macronutrient and fiber balance of these plants using the right-angled mixture triangle (RMT) which is a geometric analysis used to investigate the proportions of nutrients in foods or mixtures (Raubenheimer 2011; Raubenheimer et al. 2014).

Material and Methods

Study area

The study was carried out from January 2010 to June 2011 in the Yak Kharka region of the Manang district, as well as the Upper and Nammu regions of the Mustang districts of the ACA, which is located in the Trans-Himalayan region of Nepal (Fig. 1). The Yak Kharka region experiences diverse climatic conditions due to a wide range in elevation (1600 m–8156 m), and a large portion (>1000 km^2) of land is used for grazing by livestock (Aryal et al. 2014a). The upper Mustang region lies in the subalpine zone and experiences intense winds and solar radiation, and the entire area remains snow covered from approximately November to March (Aryal et al. 2014d). A more detailed description of the Yak Kharka and upper Mustang regions is given in Aryal et al. (2014a). The Nammu area of the Mustang district lies northeast of the district headquarters of Mustang district (i.e., approximate 20 km east from Jomsom; Fig. 1). In general, the study areas represent grassland habitat typical of the Trans-Himalayan landscape. A human population of >30,000 resides in the study area and livestock farming was the main source of income in both districts (Manang and Mustang districts). Elevation in both study areas ranges from 2800 m to 6000 m and experiences low precipitation (<1000 mm/year; Aryal et al. 2014a,b,c). Preda-

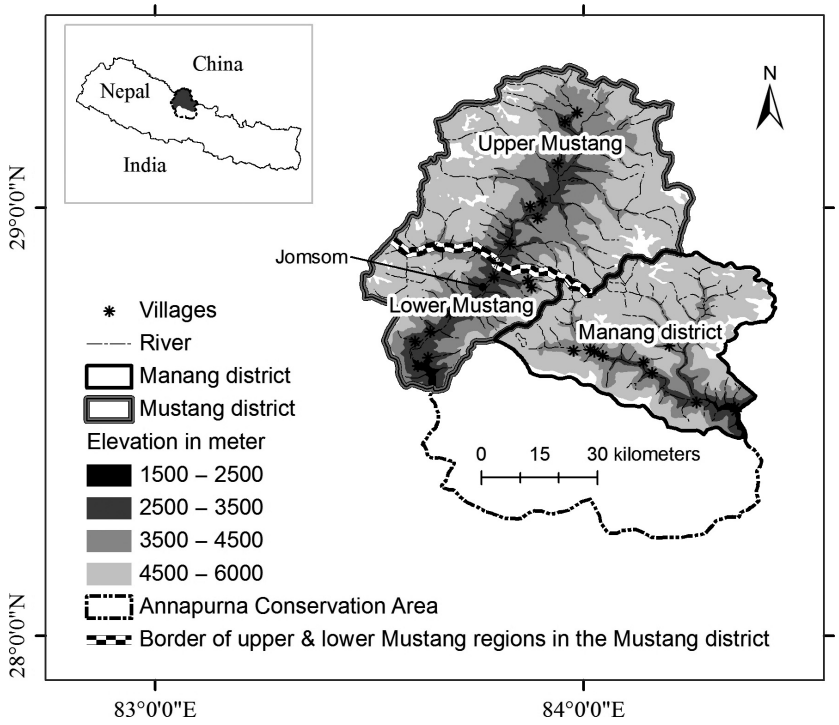

Figure 1. Map of the study area showing location within Nepal (upper) and the Manang and Mustang districts within Annapurna Conservation Area.

tors in the study area include snow leopard, brown bear (*Ursus arctos*), wolf (*Canis lupus*), and jackal (*Canis aureus*; Aryal et al. 2014a,b). Other prey species in the study area include Tibetan argali (*Ovis ammon hodgonii*), Tibetan gazelle (*Procapra picticaudata*), and wild ass (*Equus kiang*) among others (Aryal et al. 2012b).

Diet composition of blue sheep

Due to logistical constraints and the patterns of distribution of the blue sheep, fecal pellets were collected in different regions of the study area at different times, including: January–February 2010 in the Yak Kharka, Manang ($n = 48$); February–March 2010 in the Upper Mustang ($n = 61$); May 2011 in the Upper Mustang ($n = 58$); and June–July 2011 in the Nammu area, Mustang ($n = 43$). Fecal pellets of blue sheep were collected after following blue sheep herds. Herds were located by direct observation, as they are relatively easy to sight in the study area. Once we located a herd, we followed the group and collected fresh pellet samples. Pellet samples were collected in plastic bags (one sample per bag), and later transferred to the Institute of Forestry, Pokhara, Nepal, for fecal laboratory analysis. Pellet samples were processed using microhistological diet analysis (Sparks and Malechek 1968; Shrestha et al. 2005; Aryal et al. 2012b,c). First, samples were oven-dried at 40°C overnight (12 h) and then ground using a grind. Samples were then processed following established techniques for garments slide preparation (Sparks and Malechek 1968; Holechek and Gross 1982; Aryal et al. 2012c, 2014b). After grading the samples, fragments were washed with 2% ethanol (C_2H_6O) in order to keep them dry and sieved (1–0.3 mm). Samples were washed in 5% potassium hydroxide (KOH) to remove black colors from plant fragments and then passed through ethanol and finally xylene (C_8H_{10}) to remove moisture remains inside the fragments (Sparks and Malechek 1968; Holechek and Gross 1982; Aryal et al. 2012c, 2014b). We followed similar methods in preparing reference slides of plant species, which we used to identify plant fragments in fecal samples available. A total of 38 plant species were collected from the field and prepared as reference slides. Samples were selected based on a previous diet study of blue sheep (Shrestha et al. 2005) and availability of species in this region. For each permanent slide, 20 fecal plant fragments were randomly selected and identified to species using the reference species slides, and unidentified plant fragments were categorized as "unidentified" (Sparks and Malechek 1968; Holechek and Gross 1982; Aryal et al. 2012c, 2014b). After identifying plant species, we estimated the relative frequency (RF; %) of each species (Sparks and Malechek 1968; Aryal et al. 2012a; Panthi et al. 2012; Aryal et al. 2014b).

There are some limitations to microhistological analysis, as plants may not appear in scat in the proportion they were consumed depending upon digestibility; however, the method has been used successfully to rank plant species

eaten by animals (Mcinnis et al. 1983). In order to correct for differential digestibly of plant material, we used conversion factors (CF) developed by Shrestha et al. (2005), which were based on bite counts and micro-histological analysis of a similar species (domestic goat; *Capra hircus*), from the upper Mustang region and used to evaluate the diet of blue sheep and Tibetan argali. Specifically, we multiplied food items RF by the appropriate CF: 1.208 for graminoids; 5.311 for forbs; and 0.850 for woody browse (Shrestha et.al. 2005). We then summed the corrected RF estimates and calculated the % corrected RF of each food item. As unidentified species were not included in the correction, corrected food items were given as a percentage of the identified portion of the diet. We present both corrected and uncorrected RF data in order to facilitate comparison between studies where either approach has been used.

Plant sample collection and nutritional analysis

We collected a limited selection of plant samples from the Manang and Mustang districts of the ACA after following grazing herds of blue sheep. In grazing areas of blue sheep, we collected 200–400 g grass samples from available grasses for analysis. Samples were transferred to the Institute of Forestry, Pokhara, Nepal, where they were oven-dried in the laboratory at 40°C for 24 h. The dry plant samples were analyzed for nutritional content following standard analysis methods used in Rothman et al. (2012). First, samples were ground in a Wiley Mill through a 1-mm screen. Neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) content of food items were measured via sequential analysis using an A200 fiber analyzer (ANKOM, Macedon, NY). Samples were analyzed for NDF both with and without residual ash (with α-amylase), then for ADF with residual ash, and finally for acid detergent lignin (Goering and Van Soest 1970; Van Soest et al. 1991). Total nitrogen (N) was estimated by combustion (AOAC 1990) using a Leco TruSpec (Leco, St. Joseph, MI). Crude fat (CF) was estimated using a XT15 Fat Analyzer (ANKOM, Macedon, NY), where samples were placed in filter bags and boiled in petroleum ether at 90°C for 120 min. Crude protein (CP) was estimated by multiplying %N by 6.25. Ash was measured by incinerating samples at 550°C. As blue sheep likely digest fiber as an energy source, the majority of which is likely hemicellulose, we estimated hemicellulose content of plants by subtracting ADF from NDF (NDF includes hemicellulose + cellulose + lignin, and ADF includes cellulose + lignin). We also estimated cellulose content of plants by subtracting ADL from ADF. Percent total nonstructural carbohydrates (TNC) were estimated by subtraction, where the sum of the percentage of ADF (for the reasons given above), EE, CP, and Ash were subtracted from 100%.

Geometric analysis of blue sheep forage

After performing nutritional analysis, we used right-angled mixture triangle (RMT; Raubenheimer 2011) analysis to examine the balance of macronutrients and fiber in plant samples. The RMT is a geometric approach used to investigate multidimensional data on the ratios (or balance) of food components in individual foods or food mixtures and is especially relevant to field-based nutritional ecology studies where proportional compositions (as opposed to accurate intake amounts) are the only metric available (Raubenheimer 2011; Raubenheimer et al. 2014). We used a 3-dimensional RMT, where macronutrients were expressed as percentage of total macronutrients (i.e., crude protein + crude fat + TNC) on a dry matter basis, where protein was shown on the implicit *z*-axis, the value of which is inversely related with distance from the origin. For fiber analyses, we modeled hemicellulose, cellulose, and lignin which were expressed as percentage of the sum of the three fiber types (i.e., hemicellulose + cellulose + lignin) on a dry matter basis. Cellulose was shown on the implicit *z*-axis for the RMT analysis of fiber balance. We also used an RMT to examine the relationship between the macronutrient concentration and digestible fiber in plants sampled, where protein and nonprotein (fat + TNC) macronutrients were shown on the *x*- and *y*-axes, hemicellulose on the implicit axis, and expressed as a percentage of the sum of macronutrients plus hemicellulose.

Statistical analysis

We used an ANOVA to test for significant differences in the concentration and balance of macronutrients and fiber in plant samples between months of collection. We used a Kruskal-Wallis test for data that were not normally distributed and/or heteroskedastic. We used a Shapiro–Wilk test to assess normality, and a Bartlett test to assess heterogeneity of variances. We used Pearson correlation test to examine the relationship between macronutrient and fiber concentration. All tests were conducted using the program R version 3.0.3 (R Core Team 2014).

Results

Diet composition of blue sheep

A total of 19 plant species/genera were recorded in blue sheep pellets, as well as unidentified fragments (Table 1).

Table 1. Relative frequency (RF; %) of plants fragments found in blue sheep (*Pseudois nayaur*) pellets in the Manang and Mustang districts of the Annapurna Conservation Area of Nepal. RF is given both without and with applying the following correction factors (CF) from Shrestha et al. (2005): 1.208 for graminoids; 5.311 for forbs; and 0.850 for browse. Corrected estimates are given as a percentage of the identified portion of scats. Plants are listed in order of highest to lowest RF corrected.

Study area and sampling period		Yak Kharka, Manang Jan-Feb 2010 (pellet, *n* = 48)		Upper Mustang Feb -March 2010 (pellet, *n* = 61)		Upper Mustang May 2011 (pellet, n = 58)		Nammu area, Mustang June-July 2011 (pellet, *n* = 43)		Average	
Vegetation	Class	% RF	Corrected %RF	% RF	Corrected %RF	% RF	Corrected %RF	% RF	Corrected %RF	% RF	Corrected %RF
Kobresia sp.	Graminoid	23.1	21.2	29.2	32.0	16.0	15.1	14.7	15.2	20.4	20.8
Carex sp.	Graminoid	17.6	16.2	14.2	15.5	7.5	7.1	16.4	16.9	13.5	13.7
Anaphalis sp	Forb	3.0	12.0	0.1	0.5	4.5	18.6	1.8	8.2	2.3	10.3
Chesneya sp.	Forb	3.5	14.2	0.0	0.0	2.8	11.5	2.0	8.9	2.0	9.0
Oxytropis sp.	Forb	2.5	10.2	3.0	14.6	1.0	4.0	0.0	0.0	1.6	7.3
Artemisia spp.	Browse	8.8	5.7	10.1	7.8	12.2	8.1	9.8	7.1	10.0	7.1
Elymus spp.	Graminoid	3.3	3.0	5.7	6.3	9.8	9.3	6.5	6.8	6.2	6.3
Sedum sp.	Forb	0.0	0.0	0.0	0.0	1.4	5.8	3.4	15.6	1.1	5.0
Agrostis sp.	Graminoid	4.4	4.0	3.5	3.8	2.3	2.1	3.4	3.6	3.3	3.4
Lonicera spinosa	Browse	3.1	2.0	1.2	1.0	8.7	5.7	6.1	4.4	4.6	3.3
Caragana spp.	Browse	4.4	2.8	10.1	7.8	2.3	1.5	0.2	0.1	4.2	3.0
Potentilla fruticosa	Browse	0.8	0.5	2.7	2.1	5.6	3.7	2.6	1.9	2.9	2.0
Pennisetum flaccidium	Graminoid	1.1	1.0	0.8	0.9	1.0	0.9	4.9	5.1	1.8	1.9
Ephedra spp.	Browse	0.8	0.5	4.7	3.6	0.0	0.0	5.1	3.7	2.5	1.8
Astragalus spp.	Forb	0.2	0.9	0.0	0.0	1.3	5.3	0.0	0.0	0.4	1.7
Stipa sp.	Graminoid	3.3	3.0	2.7	3.0	0.0	0.0	0.0	0.0	1.5	1.5
Aster albescens	Browse	1.8	1.1	0.3	0.3	1.3	0.8	3.4	2.5	1.6	1.2
Clematis sp.	Browse	2.3	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.4
Salsola nepalensis	Browse	0.0	0.0	1.0	0.8	0.6	0.4	0.0	0.0	0.4	0.3
Unidentified	NA	16.2		10.6		21.9		19.6		19.0	

On average across seasons and study areas, the two most frequently occurring plants in blue sheep pellets (both with and without applying CF) were the graminoids *Kobressia* sp.(20.8% with CF) and *Carex* spp. (13.7% with CF; Table 1). Other species found at relatively high frequencies were *Artemisia* spp. (browse), and, after applying CF, *Anaphalis* sp., and *Chesnaya* sp. (Table 1). On average, graminoids made up 47%, forbs 13%, and browse 22% of identified fragments in blue sheep pellets, while 19% of plants fragments were unidentified. After applying CF, graminoids contributed 48%, forbs 37%, and browse 16% of the identified portion of diet. *Kobresia* sp. seemed to decrease in the diet from January to July, as well as other plants such as *Oxytropis* sp. (Table 1). *Carex* spp. seemed to decrease in the diet from January to May, but increased again during June–July in the Nammu area (Table 1). Conversely, *Sedum* sp. tended to increase in the diet from May to July. Some species occurred in the diet seemingly erratically, such as *Chesneya* sp., *Anaphalis* spp., and *Ephedra* spp. (Table 1).

Nutritional content, macronutrient, and fiber balance of plants

We performed nutritional analysis on a limited number of plants collected from the Mustang and Manang districts in January, March, June/July, and November (macronutrients in Table 2; and fiber in Table 3) and were thus limited in the ability to make comparisons with diet RF and between seasons and regions of the study area; however, patterns emerged in our RMT analysis of macronutrients (Fig. 2) and fiber (Fig. 3) despite these limitations. For example, the macronutrient balance of *Kobresia* spp., the most consumed (i.e., highest relative frequency) plant food, was relatively high in carbohydrate and low in protein content compared to other plants found in the diet of blue sheep, and the macronutrient balance changed little between November and January samples (Fig. 2A and B). The second most frequently consumed plant, *Carex* spp., was relatively similar to *Kobresia* spp. in protein content but lower in lipid during March, but a sample of

Table 2. Proximate nutritional composition of plants consumed by blue sheep in the Mustang and Manang districts of the Annapurna Conservation Area of Nepal, including month of collection. All estimates are given as a percentage of dry matter, with the exception of dry matter (g/g wet weight). Total nonstructural carbohydrate (TNC) was estimated by subtraction [i.e., TNC = 100% − (acid detergent fiber + fat + crude protein + ash)].

Name	Area	Month-year	Dry matter	Crude protein	Fat	Ash	TNC
Anaphalis contorta	Manang	January-10	0.94	6.56	1.31	9.74	34.08
Anaphalis sp.	Mustang	June/July 10	0.95	12.05	–	–	–
Anaphalis triplinervis	Mustang	June/July 10	0.93	9.96	–	22.31	–
Artemisia biennis	Mustang	November-09	0.93	11.18	1.64	14.64	40.41
Artemisia sp.	Manang	January-10	0.93	6.13	2.22	–	–
Artemisia sp.	Mustang	November-09	0.90	10.10	4.19	12.10	35.19
Artemisia sp.	Mustang	November-10	0.93	11.59	2.01	–	–
Artemisia sp.	Mustang	March-10	0.92	5.92	2.10	4.41	27.13
Artemisia sp.	Mustang	November-10	0.94	15.19	3.34	11.21	43.18
Artemisia sp.	Mustang	June/July 10	0.94	15.63	–	8.35	–
Artemisia sp.	Mustang	June/July 10	0.93	14.87	–	9.84	–
Artemisia sp.	Mustang	June/July 10	0.93	15.23	–	11.43	–
Artemisia sp.	Mustang	June/July 10	0.92	7.08	–	8.20	–
Artemisia varnica	Mustang	March-10	0.95	7.10	0.69	5.11	32.41
Aster sp.	Mustang	November-10	0.96	15.80	3.39	15.71	46.75
Aster sp.	Manang	January-10	0.93	6.08	3.27	6.46	50.26
Astragalus sp.	Manang	January-10	0.95	8.47	1.87	3.84	29.20
Astragalus sp.	Mustang	March-10	0.95	6.41	2.86	8.01	26.45
Caragana gerardiana	Manang	January-10	0.94	6.98	4.00	13.31	20.15
Caragana sp.	Mustang	November-09	0.92	10.66	2.01	19.33	25.27
Caragana sp.	Mustang	March-10	0.93	9.82	2.30	4.96	34.17
Caragana sp.	Mustang	March-10	0.94	8.80	2.13	–	–
Caragana sp.	Mustang	June/July 10	0.91	10.00	–	18.63	–
Caragana sp	Mustang	June/July 10	0.92	10.53	–	3.51	–
Carex sp.	Mustang	November-09	0.93	27.14	3.15	8.08	49.85
Carex sp.	Mustang	March-10	0.92	5.50	1.65	4.62	49.81
Carex sp.	Mustang	June/July 10	0.94	11.85	–	10.27	–
Carex sp.	Mustang	June/July 10	0.92	6.99	–	4.95	–
Clematis tibetana	Mustang	November-10	0.94	18.05	2.56	14.35	48.47
Ephedra gerardiana	Mustang	March-10	0.96	9.63	3.16	19.61	14.80
Ephedra gerardiana	Manang	January-10	0.95	8.36	3.89	10.52	36.46
Ephedra sp.	Mustang	June/July 10	0.90	14.90	–	8.46	–
Ephedra sp.	Mustang	June/July 10	0.91	14.61	–	10.43	–
Kobresia sp.	Manang	January-10	0.94	4.29	4.11	4.35	50.66
Kobresia sp.	Mustang	November-10	0.93	5.64	2.50	4.33	50.60
Kobresia sp.	Mustang	June/July 10	0.92	12.67	–	10.49	–
Kobresia sp.	Mustang	June/July 10	0.97	6.36	–	–	–
Lonicera sp.	Mustang	March-10	0.95	4.37	1.64	3.98	33.53
Lonicera sp.	Manang	January-10	0.94	4.80	5.22	3.62	28.49
Lonicera sp.	Mustang	June/July 10	0.92	5.21	–	4.34	–
Oxytropis sp.	Mustang	June/July 10	0.91	15.85	–	24.96	–
Oxytropis williamsis	Manang	January-10	0.93	11.66	3.43	11.67	26.04
Potentilla fruticosa	Manang	January-10	0.95	8.43	3.53	4.38	32.92
Potentilla sp.	Mustang	November-10	0.95	12.86	3.77	17.48	46.40

Carex spp. from November showed a much higher protein balance (Figure 2a,b). The RMT analysis of fiber balance showed that the two most consumed plants of blue sheep, *Kobresia* spp. and *Carex* spp. (which together had a relative frequency of 34.5 with CF) contained the highest amounts of hemicellulose, which was relatively constant across sampling periods (Fig. 3A and B). The hemicellulose and lignin balance of plants ranged relatively widely, yet the cellulose content of plants showed less variation, being more tightly aligned along the *z*-axis at approximately 40% cellulose content (Fig. 3A and B). The hemicellulose balance of plant samples varied inversely with macronutrient balance (Fig. 4): plants that were higher in macronutrients

Table 3. Neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), hemicellulose, and cellulose content of plants consumed by blue sheep in the Mustang and Manang districts of the Annapurna Conservation Area of Nepal, including month of collection. Estimates are given on a dry matter basis.

Name	Area	Month-year	NDF	ADF	ADL	Hemicellulose	Cellulose
Anaphalis contorta	Manang	January-10	60.78	48.31	19.49	12.48	28.82
Anaphalis sp.	Mustang	June/July 10	59.90	48.43	30.91	11.47	17.52
Anaphalis triplinervis	Mustang	June/July 10	58.99	43.41	16.64	15.59	26.76
Artemisia biennis	Mustang	November-09	45.57	32.12	14.07	13.45	18.04
Artemisia sp.	Manang	January-10	65.68	47.24	16.49	18.44	30.75
Artemisia sp.	Mustang	November-09	62.17	38.41	11.70	23.76	26.71
Artemisia sp.	Mustang	November-10	57.08	32.36	12.37	24.72	19.99
Artemisia sp.	Mustang	March-10	81.12	60.44	25.87	20.68	34.57
Artemisia sp.	Mustang	November-10	40.43	27.08	10.37	13.35	16.70
Artemisia sp.	Mustang	June/July 10	46.74	36.73	19.41	10.00	17.32
Artemisia sp.	Mustang	June/July 10	47.69	38.75	21.04	8.94	17.71
Artemisia sp.	Mustang	June/July 10	65.89	36.88	10.05	29.00	26.83
Artemisia sp.	Mustang	June/July 10	72.63	49.62	22.87	23.02	26.75
Artemisia varnica	Mustang	March-10	80.05	54.69	25.43	25.36	29.26
Aster sp.	Mustang	November-10	28.45	18.34	5.89	10.11	12.45
Aster sp.	Manang	January-10	49.55	33.92	10.87	15.63	23.06
Astragalus sp.	Manang	January-10	72.60	56.61	24.72	15.99	31.90
Astragalus sp.	Mustang	March-10	73.44	56.28	26.41	17.16	29.87
Caragana gerardiana	Manang	January-10	71.11	55.56	20.24	15.55	35.32
Caragana sp.	Mustang	November-09	54.35	42.73	25.23	11.62	17.50
Caragana sp.	Mustang	March-10	63.22	48.75	23.57	14.47	25.18
Caragana sp.	Mustang	March-10	57.65	44.11	29.19	13.54	14.92
Caragana sp.	Mustang	June/July 10	60.04	49.33	29.78	10.72	19.54
Caragana sp	Mustang	June/July 10	70.62	52.82	25.08	17.79	27.75
Carex sp.	Mustang	November-09	21.65	11.80	4.73	9.85	7.06
Carex sp.	Mustang	March-10	75.50	38.42	4.85	37.08	33.57
Carex sp.	Mustang	June/July 10	76.68	39.33	13.45	37.35	25.88
Carex sp.	Mustang	June/July 10	75.66	35.73	5.57	39.94	30.16
Clematis tibetana	Mustang	November-10	28.12	16.57	6.84	11.55	9.73
Ephedra gerardiana	Mustang	March-10	63.01	52.80	36.55	10.21	16.25
Ephedra gerardiana	Manang	January-10	48.96	40.78	22.20	8.18	18.58
Ephedra sp.	Mustang	June/July 10	56.32	53.59	36.55	2.73	17.04
Ephedra sp.	Mustang	June/July 10	55.31	50.27	32.60	5.04	17.67
Kobresia sp.	Manang	January-10	73.70	36.59	4.96	37.11	31.62
Kobresia sp.	Mustang	November-10	75.10	36.93	4.90	38.17	32.03
Kobresia sp.	Mustang	June/July 10	64.79	31.13	10.39	33.66	20.74
Kobresia sp.	Mustang	June/July 10	70.28	31.98		38.29	
Lonicera sp.	Mustang	March-10	73.13	56.49	27.68	16.65	28.81
Lonicera sp.	Manang	January-10	75.11	57.87	26.96	17.24	30.91
Lonicera sp.	Mustang	June/July 10	71.72	53.50	23.57	18.23	29.93
Oxytropis sp.	Mustang	June/July 10	49.20	37.42	21.16	11.78	16.26
Oxytropis williamsis	Manang	January-10	61.47	47.20	14.32	14.27	32.88
Potentilla fruticosa	Manang	January-10	64.83	50.73	23.57	14.10	27.16
Potentilla fruticosa	Mustang	March-10	69.42	54.59	24.90	14.84	29.69
Potentilla sp.	Mustang	November-10	31.26	19.49	5.66	11.78	13.82

(protein, fat, and carbohydrates) balance had lower hemicellulose balance, while plants that were lower in macronutrient balance had higher hemicellulose balance.

The results of statistical tests indicated that the protein: nonprotein (ANOVA, $P = 0.21$) and the hemicellulose:-cellulose + lignin (Kruskal-Wallis, $P = 0.07$) balance of plant samples was not significantly different between monthly sampling periods; however, the concentration of total macronutrients (ANOVA, $P = 0.002$) and NDF (Kruskal-Wallis, $P = 0.003$) on a dry matter basis were significantly different between months. Fiber (NDF) and total macronutrient concentration (% dry matter) of plants were negatively correlated ($r = -0.73$), yet

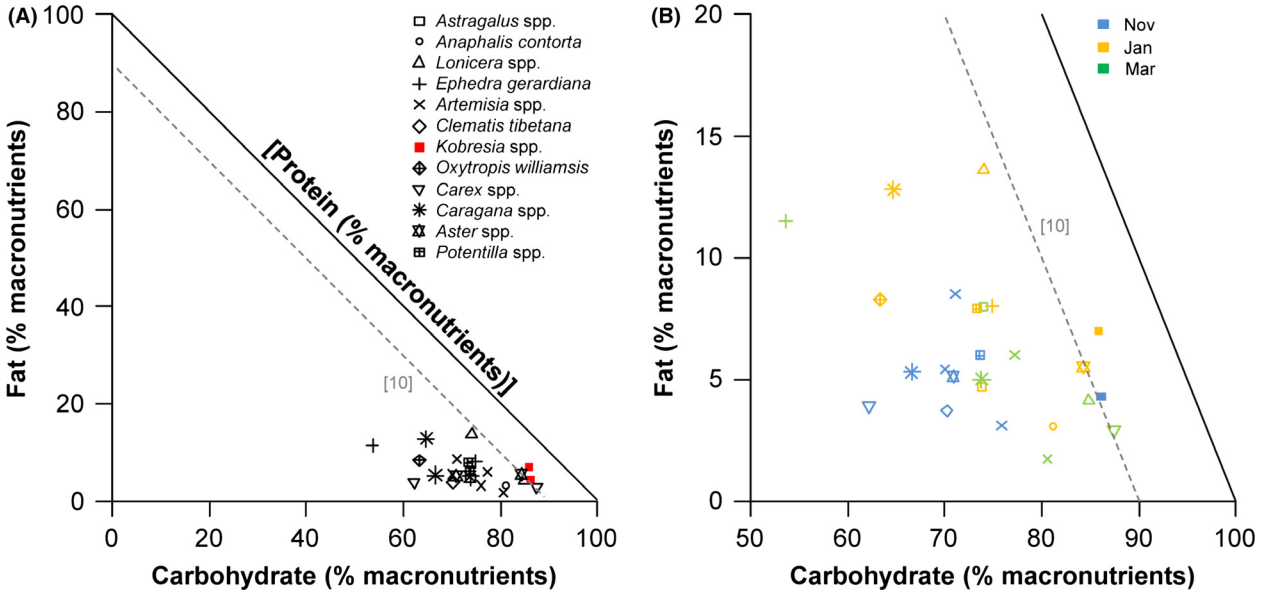

Figure 2. (A) Right-angled mixture triangle (Raubenheimer 2011) showing the macronutrient balance of plants consumed by blue sheep (*Pseudois nayaur*). Macronutrients are expressed as percentage of total macronutrients (i.e.,. protein + fat + carbohydrate). Protein is shown on the implicit *z*-axis, the value of which is inversely related with distance from the origin. A dashed gray line indicating 10% protein is shown for reference. The plant genus found most frequently in the diet of blue sheep (*Kobresia* spp.) is shown as a red symbol; (B) A close-up of the region of nutrient space occupied by plants consumed by blue sheep [legend provided in panel (A)]. Macronutrient estimates are color-coded to match the month in which the sample was collected. All data points represent a single sample.

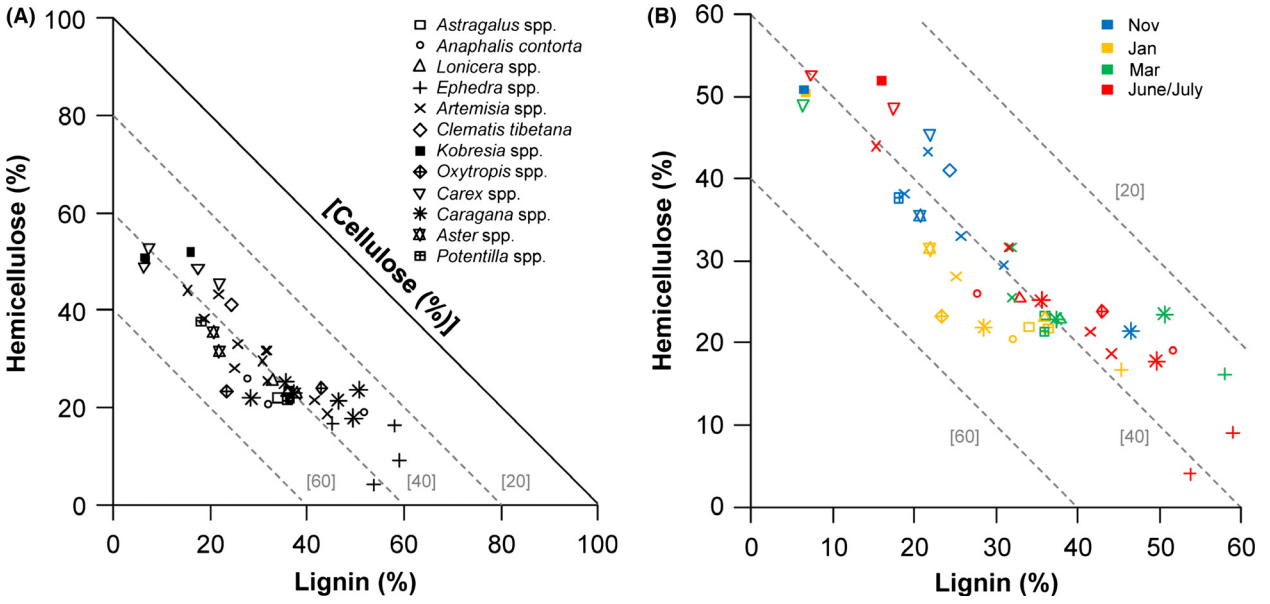

Figure 3. (A) Right-angled mixture triangle (Raubenheimer 2011) showing the fiber (hemicellulose, cellulose, and lignin) balance of plants consumed by blue sheep (*Pseudois nayaur*) as a percentage of the sum of each (hemicellulose + cellulose + lignin). Cellulose is shown on the implicit *z*-axis, the value of which is inversely related to the distance from the origin. Dashed gray lines indicating 20%, 40%, and 60% cellulose are shown for reference; (B) A close-up of the region of the fiber nutrient space occupied by plants consumed by blue sheep. Fiber estimates are color-coded to match the month in which the sample was collected.

hemicellulose concentration and total macronutrient content were not correlated ($r = 0.06$). Additional nutritional estimates for nonfood plants species are given in the Online Supplemental Information (Tables S1 and S2) to aid nutritional ecology studies of other species for which data may be limited.

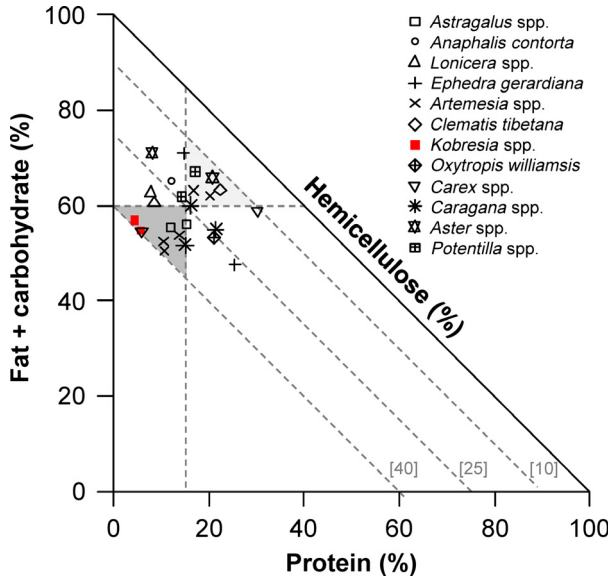

Figure 4. Right-angled mixture triangle (Raubenheimer 2011) showing the balance of protein and nonprotein (fat + carbohydrate) macronutrients to digestible fiber (hemicellulose) of plants consumed by blue sheep (*Pseudois nayaur*) as a percentage of the sum of each (protein + nonprotein macronutrients + hemicellulose) on a dry matter basis. Hemicellulose is shown on the implicit *z*-axis which is inversely related to the distance from the origin. Dashed gray lines indicating 40%, 25%, and 10% hemicellulose balance, as well as lines indicating 60% nonprotein macronutrient and 15% protein, are shown for reference. Light gray shading indicates plants that have higher macronutrient and lower hemicellulose balance, while dark gray shading indicated plants that have higher hemicellulose and lower macronutrient balance. The plants found most frequently in the blue sheep diet (*Kobresia* spp.) are shown as red squares.

Discussion

Our analysis indicated that *Kobresia* spp. and *Carex* spp. graminoids were the dominant foods of blue sheep within the Mustang and Manang districts of the ACA. In a previous study investigating the habitat use and resource availability of blue sheep (Aryal et al. 2013, 2014a), *Kobresia pygmea* was the most important plant species found in blue sheep habitat in both the Yak Kharka and upper Mustang regions, which in light of our results suggests the food resources are a strong determinant of habitat use. While a previous study found that graminoids were the main plant type consumed by blue sheep (followed by browse and forbs) in the Damodar Kunda area of the Mustang region during summer, *Kobresia* spp. were reportedly absent in blue sheep habitat, and were, accordingly, not found in their diet (Shrestha et al. 2005). *Kobresia pygmea* was, however, found in the diet of Argali in the Damodar Kunda region (Shrestha et al. 2005), suggesting that the two ungulate species may compete for these resources if present in regions where they are sympatric. Negali are rare in Nepal, however, and may only occur in the Damodar area (Shrestha et al. 2005). Other species of graminoids consumed by blue sheep were similar between the above-mentioned studies, including *Carex* sp., *Elymus* spp., *Stipa* sp. and *Agrostis* sp. While *Agrostis* sp. was the most important species consumed by blue sheep in the Damodar Kunda (Shrestha et al. 2005), it was a relatively minor part of blue sheep diet in the Mustang and Manang. Among forbs, both *Chesneya* sp. and *Oxytropis* sp. were found in the diet of blue sheep in the Mustang/Manang and the Damodar Kunda; however, *Sedum* sp., which was not found in blue sheep habitat in the Damodar Kunda, was noticeable in the diet of blue sheep of the mustang region from May to July. Among browse, *Potentilla fruticosa* was an important browse species in the Damodar Kunda, yet was a relatively minor part of blue sheep diet in the Manang and Mustang regions of the study area. Overall, in the Damodar Kunda blue sheep were reported to consume 54% graminoids, 6% forbs, and 40% browse (uncorrected), and 51%, 22%, and 27%, respectively (corrected; Shrestha et al. 2005). Our analysis suggests that blue sheep in the Manang and Mustang districts similarly consumed a diet high in graminoids; however, forbs seemed to be consumed more by blue sheep, and browse consumed less, than in the Damodar Kunda.

Our RMT analysis of the macronutrient balance of blue sheep plant foods suggests that plants other than *Kobresia* spp. are complementary to high-carbohydrate *Kobresia* spp. in the sense that they provide more protein and/or fat than *Kobresia* spp. alone. Our RMT analysis of the fiber balance of plants consumed by blue sheep, indicated that the two most consumed foods (*Kobresia* spp. and *Carex* spp.) were highest in hemicellulose content, which is likely digestible by blue sheep. Our results suggest that forage selection by blue sheep may be a balance between consuming easily digestible high-carbohydrate foods and less-digestible high protein and/or lipid forage. Blue sheep also seem to forage on plants either high in total macronutrient balance or high in digestible fiber (hemicellulose) balance. Total macronutrient concentration on a dry matter basis varied inversely with the NDF content of plants, but there was no correlation between the total dry matter concentration of macronutrients in plants and hemicellulose content due to the variability in the lignin and cellulose concentrations. Interestingly, however, the balance of the ratios of hemicellulose to protein and nonprotein macronutrients in plant foods of blue sheep indicated that there was an inverse relationship between the balance of macronutrients and digestible fiber.

As our analysis was based on a limited number of samples collected in different areas and seasons, we caution

that future research is necessary to gain a complete picture of blue sheep nutritional ecology. One example would be an examination of seasonal changes in the nutritional content of foods and the relationship to the RF of plants in blue sheep diet. While our analysis detected differences in nutrient concentration between in plants sampled during different months, differences in species collected between periods confounds robust phenological comparisons and should be examined further. As well, differences in the nutritional content of plants across an elevation gradient likely influences the timing of plant nutrition (Coogan et al. 2012), and therefore diet of blue sheep across different areas. Furthermore, a more complete nutritional profile of available vs. consumed foods will help determine whether blue sheep are actively foraging for a balance of nutrients different from what they would consume if they simply foraged (proportional to availability). The toxic components of plants should also be included in future geometric analysis.

Despite the limitations, our study contributes important information on the nutritional ecology of blue sheep for which relatively limited information is available, and which may be used to inform conservation and management strategies of blue sheep in the wild. For example, habitat conserved for blue sheep should include some of the key species (*Kobresia* spp. and *Carex* spp.) identified in the study; however, if not available plants with similar macronutrient and fiber balance may provide a suitable alternative. It might also be that agricultural plants with similar nutrient balance to *Kobresia* spp. and *Carex* spp. may be more prone to crop depredation by blue sheep. Further understanding the nutritional preferences of blue sheep and the nutritional characteristics of available foods will provide information that may help reduce human–wildlife conflict and aid the management and conservation of both prey and predator alike.

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Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Proximate analysis of plants not found in blue sheep diet.

Table S2. Fiber content of plants not found in blue sheep diet.

