

## **FORAGING ECOLOGY OF LIVESTOCK ON THE TIBETAN CHANGTANG: A COMPARISON OF THREE ADJACENT GRAZING AREAS**

RICHARD P. CINCOTTA

*Department of Range Science, Utah State University  
Logan, Utah 84322-5230, U.S.A.*

PETER J. VAN SOEST AND JAMES B. ROBERTSON  
*Animal Science Department, Cornell University  
Ithaca, New York 14853, U.S.A.*

CYNTHIA M. BEALL AND MELVYN C. GOLDSTEIN  
*Department of Anthropology, Case Western Reserve University  
Cleveland, Ohio 44106, U.S.A.*

### **ABSTRACT**

In a high-altitude (above 4860 m), semiarid grazing ecosystem in western Tibet, only 28% of summer grazing areas supported aboveground net primary productivity greater than  $10 \text{ g m}^{-2}$ . The frequencies of vegetation types selected for grazing were unique for each herd type (yak, small ruminant) in each area. Herd type and grazing area were both significant factors in daily horizontal and vertical displacement of herds from encampments.

Yak were versatile foragers, consuming coarse forages when encountered, but adept at grazing small (<3 cm high) sedges. Whereas browse was a minor component of yak diets (4.1%), it was heavily selected by goats (31.2%) and sheep (17.9%). All ruminant livestock readily consumed spinulose forbs when encountered. Statistical differences in dietary quality were attributed to grazing area effects.

The overriding determinant of grazing behavior appeared to be the vegetational characteristics of the area within which livestock producers held grazing rights. Differentiating factors in these areas were (1) the availability of "low risk" vegetation (forage demonstrating predictable emergence and growth) in riparian areas watered by glacier-fed springs, versus more unpredictable nonriparian forage sources fed by monsoonal rainfall; and (2) the topographic situation of forage-yielding vegetation types.

### **INTRODUCTION**

Western Tibetan pastoralists use livestock to convert plant material to milk, animal fiber, and meat on high-altitude, semiarid rangelands. Because the nature, distribution, and utilization of forage appear to underlie the patterns of pastoral strategies (Dyson-Hudson and Dyson-Hudson, 1969), quantifying these factors and their variability among western Tibetan populations may

improve our understanding of high-altitude pastoralism. Thus, our objectives were to compare grazing among adjacent pastoral populations on the basis of (1) the selection of vegetation types as foraging habitat, and patterns of herd movement; (2) the botanical composition of livestock diets; and (3) the forage quality of these diets. Due to logistic and political constraints encountered in the

Tibetan Autonomous Region, People's Republic of China, at the time of this study, research was limited to the summer monsoon season, within the period of plant growth. In environments with extreme seasonal differences (the situation for most pastoralists), grazing activities during the growing season represent a specialized part of an annual cycle, and should be set in context.

During foliar emergence and early growth, forages are highly digestible and at peak nitrogen (N) concentrations (cf. Pratt and Gwynne, 1977; cf. Squires, 1981). Pastoralists have been observed moving herds opportunistically (Coughenour et al., 1986) to facilitate the consumption of early growth forage, thus obtaining energy beyond levels needed for livestock weight maintenance and lac-

tation, and encouraging the deposition of metabolizable energy in fatty tissues of their stock. Eventually vegetation matures and dries, resulting in a decrease in forage quality and subsequent inhibition of animal production (milk production and weight gains). In western Tibet, livestock fat reserves are reclaimed in the winter as (1) catabolic energy in livestock for basal metabolism, expenditures of movement, and fetal metabolism; and (2) fatty meats for human consumption (for a review of the significance of fatty meat consumption, see Speth and Spielmann, 1983). Thus, nutritional quality of livestock diets during the monsoons is a mediator of livestock and human survival during the remainder of the year.

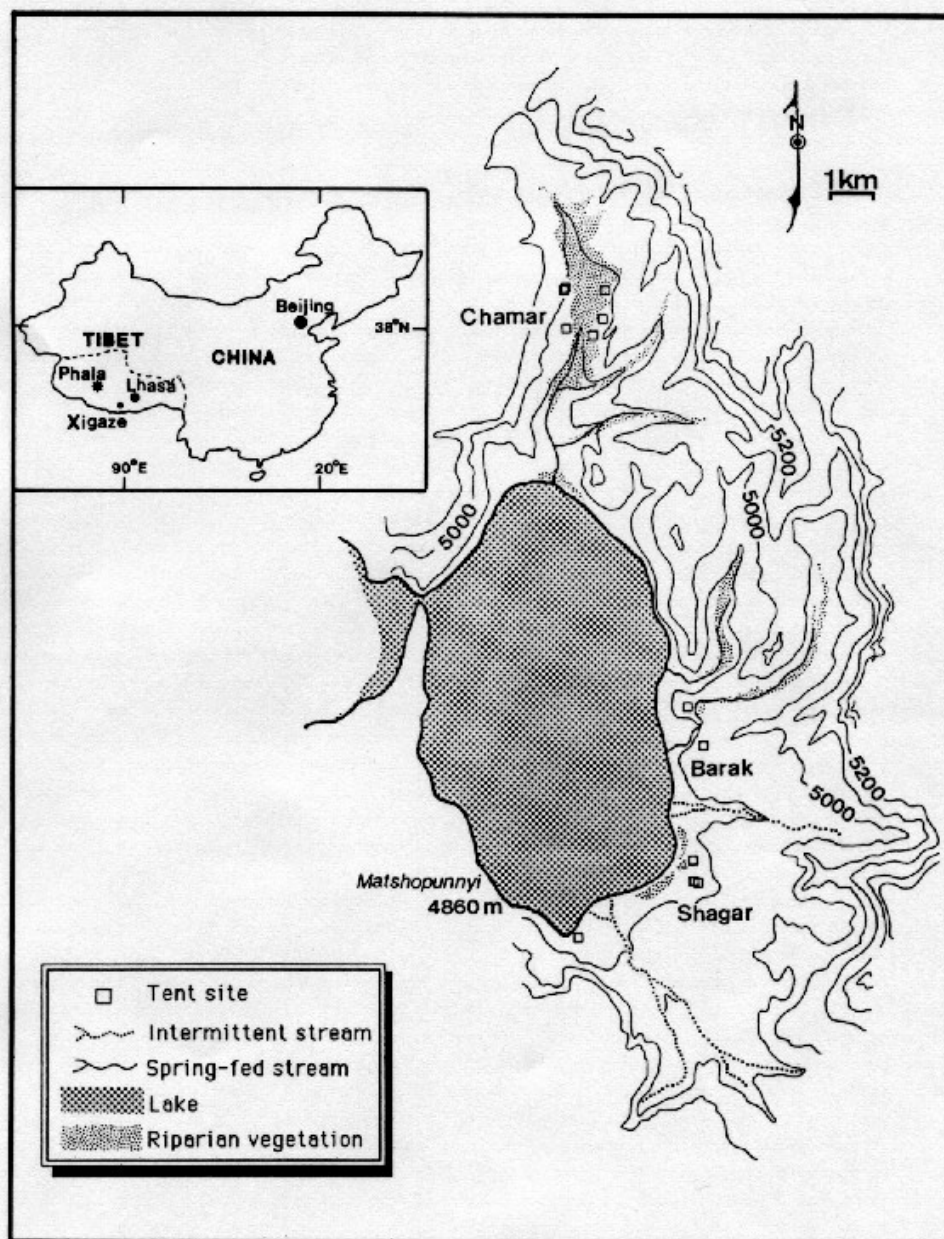


FIGURE 1. Maps of the People's Republic of China showing the location of Phala within Tibet and the pastoralist encampments within Phala. In the latter, heavily stippled areas around streams and near the lake shore denote spring-fed riparian vegetation types.



## STUDY AREA

Research was conducted in three administrative subunits composed of pastoral encampments and associated grazing areas: (1) Shagar and Lomamayo (research pertains only to the Shagar encampment of this subunit), (2) Chamar, and (3) Berak. These encampments are situated in Phala Xiang, which borders a saline lake, Matshopunnyi (30°30'N, 86°30'E), on the western Tibetan Plateau (Figure 1). In 1987, 28 people lived in Shagar-Lomamayo, 51 in Chamar, and 30 in Berak (see Table 1 for resident herd sizes). Families were assigned to encampments by the government at the time of dissolution of a commune in 1981 (Goldstein et al., 1990).

In 1987, summer grazing in Shagar-Lomamayo, Chamar, and Berak covered an area of roughly 80 km<sup>2</sup>, encompassing three vegetated landscape features: (1) steep mountain slopes up to 5500 m in elevation; (2) hilly wet meadows in spring-fed valley bottoms; and (3) broad sandy semiarid valleys that descend to the lake at 4860 m. The surrounding mountains are of sedimentary origin, bearing sandy-clay to sandy-silt loam soils. Pockets of sandy loess impinge upon some of the exposed lower slopes. Glacial deposition has left sand and gravel ridges on valley floors.

Precipitation is monsoonal, with an annual average between 200 and 250 mm (Geeland and Twitchet, 1974). About 75% of precipitation occurs in June, July, and August. However, the distribution of precipitation during that period is spatially and temporally erratic. Temperatures average 15°C in summer and -15°C in winter, with extreme diurnal ranges, frequently exceeding 30°C. Winter snowfall is infrequent and snow accumulation is reportedly of short duration. The plant growing season lasts from late April to mid-September, during which

frost occurs frequently, and snowfall without accumulation is not unusual.

The topography of Phala is overlaid with a patchwork of vegetation types, each distinct in aboveground net primary productivity (AGNPP) and phenological timing. Vegetation types can be placed into two major groups based upon their source of water: nonriparian and glacier-fed riparian types (Figure 2).

Nonriparian types reside in the semiarid valleys and on slopes (Figure 3) where plant species composition, emergence, and growth are related to local precipitation, altitude, and aspect. Their productivity appears to rely on direct monsoonal rains, runoff from rainfall and snow accumulation, and interseasonal soil water storage. Thus, most vegetation of semiarid valleys and slopes emerges only after the onset of the monsoon. However, changes in AGNPP in this vegetation are not as rapid or dramatic as in tropical systems driven by monsoons. In semiarid vegetation of Phala, AGNPP is restricted by three interrelated factors: (1) low soil temperatures and resultant constraints on N mineralization and uptake; (2) high root to shoot biomass ratio; and (3) the adaptive dwarf form (probably adapted to wind; cf. Jones, 1986) of aboveground structures of resident plants (Mani, 1978).

TABLE 1  
*Abundance of livestock in three administrative subunits in Phala, 1987*

Subunit	Goats	Sheep	Yak	Horse
Shagar and Lomamayo	589	474	179	3
Chamar	780	1170	206	8
Berak	865	1071	156	5



FIGURE 2. An inundated riparian area (center of photo) fed by glacial-melt springs, and surrounded by nonriparian vegetation types of which the montane sedge type is most prevalent. This valley is grazed by herds from the Berak encampment.





In contrast, riparian vegetation types are largely uncoupled from monsoonal precipitation. Soils are saturated with moisture from glacial melt springs (Figure 4), which begin to supply premonsoonal moisture to wet meadow vegetation in late April and early May, thus initiating the earliest sequence of plant emergence and growth in Phala.

Herbaceous perennials are the most abundant plant life form throughout Phala; sedges (cyperaceous species of the genera *Kobresia* and *Carex*), and grasses (graminaceous species, primarily *Stipa*, and accompanied in lower abundance by species of *Poa*, *Calamagrostis*, and *Koeleria*) are major constituents of most vegetation types. There is only one locally abundant truly woody species, a rosaceous shrub, *Potentilla parvifolia* Fisch. ap. Lehm. (nomenclature according to Wu, 1987; for the family Morinaceae, according to Cannon and Cannon, 1984). This species grows at the edge of wet meadows and on other sites availed with deep soil moisture. *Artemisia welbyi* Hemsl. & Pearson ex Deasy, a xeric half-shrub (a woody base supporting herbaceous stems), is abundant on sandy alluvial fans. Phala's vegetation supports a variety of wild herbivores, including antelope (*Pantholops hodgsoni*), gazelle (*Procapra picticandata*), blue sheep (*Pseudois nayaur*), wild ass (*Equus hemionus*), and black-lipped pika (*Ochotona curzoniae*).

Phala pastoralists maintain milking and nonmilking herds of yak (*Bos grunniens*), sheep (*Ovis aries*), and goats (*Capra hirtus*), that are herded by day, and returned to the encampment for the night. Female yak weigh approximately 225 to 300 kg and stand about 1.2 m high at the shoulder. Adult female sheep weigh about 30 to 35 kg, and stand about 59 cm. Adult female goats are smaller, weighing 20 to 25 kg, and standing about 52 cm at the shoulders. Milk is used to make yogurt, butter, and cheese. In addition, pastoralists harvest animal fiber and meat for domestic consumption. They export yak butter, sheep's wool, cashmere (from goats), animal skins, and live animals, for which they obtain barley, tea, and trade items through cash or barter (Goldstein and Beall, 1989; for other Tibetan pastoral areas see Ekvall, 1968; Clarke, 1987). About 25% of the households own locally bred horses, which they ride. Yak are also ridden and used as pack animals.

Phala pastoralists rotate among pastures (all above 4860 m) on a seasonal basis. Each of the three home encampment grazing areas that we studied are winter-spring-summer (January to September) pastures for sheep and goat herds. These small stock spend the fall (September to December) in a pasture that has been deferred



FIGURE 3. An edge of the semiarid valley floor and adjacent alpine slope in the summer grazing area of Shagar pastoralists. The female herder (foreground) is standing amidst vegetation composed of a mixture of forbs, *Stipa* spp., and sedges. On the hillside (background), yak are feeding on *Kobresia pygmaea* (montane sedge type), a small sedge that often forms "mats" in which live individuals of this species grow amidst a thick sod composed of the roots and crowns of dead conspecifics.

from grazing during the growing season. Rather than return to the home encampment for winter, female yak are taken to other ungrazed pastures on mountain slopes (Goldstein et al., 1990) where they feed principally on a small upland sedge, *Kobresia pygmaea* (C.B. Clarke). C.B. Clarke, Goldstein et al. (1990) found that herd owners employ complex strategies of seasonal herd division, redistribution, and relocation in distant "satellite camps." In addition, wage labor, supplied by other pastoralists, is often important to large herd owners.

## METHODS

### SAMPLING PERIOD

Observations of livestock vegetation type selection, botanical composition of dietary forage, forage collection, and vegetation mapping were conducted in the grazing areas between 25 June and 6 August 1987 (6 wk

during the monsoonal rainy season). Sampling was conducted for 19 d in Shagar, 14 d in Chamar, and 10 d in Berak.

A format was used similar to that introduced by Coppock et al. (1986a, 1986b), with which they detailed



FIGURE 4. *Kobresia* hillock vegetation in a riparian site near the Chamar encampment. The crowns of hillocks appear to be stabilized by the thick roots of large sedges, especially *Kobresia royleana*. In this sedge-dominated type, each plant is knotted within a thick spongy mat of vegetation. Therefore, uprooting during grazing is rare.

the seasonal livestock ecology of Turkana pastoralists. For comparisons with Turkana wet season diets, this article retains most of the basic nutritional parameters and standards of comparison in their analysis.

#### VEGETATION TYPE SELECTION

The surface area of summer pastures was determined by field mapping and satellite imagery (SPOT 1 satellite image obtained on 4 June 1988). A ground survey was conducted using a pocket altimeter, pace-meter, and hand-compass to set stone monuments at 0.5-km intervals along transects.

Vegetation types were divided into major and minor pastures based upon observation of herd behavior and estimates of AGNPP. Major pastures were defined as portions of the landscape on which herders allowed livestock to graze freely for extended periods. These pastures consisted of vegetation types with  $AGNPP \geq 10 \text{ g m}^{-2}$  ( $100 \text{ kg ha}^{-1}$ ). In contrast, we defined minor pastures as the remaining areas ( $AGNPP < 10 \text{ g m}^{-2}$ ). While traversing minor pastures, livestock either grazed rapidly or did not graze. Minor pastures generally consisted of sandy southerly exposures, gravelly soils, and boulder fields. The standing crop biomass of major pastures (minor pastures were not sampled) was characterized by visual estimation using a double sampling technique (Hilmon, 1959) in 18 randomly located  $0.125\text{-m}^2$  plots.

Vegetation type selection was determined by recording the location of a single predetermined herd of female yak, and a herd of small ruminants (goats and sheep) within vegetation types in 8 daylight observations (around 0900, 1000, 1100, 1200, 1500, 1600, 1700, 1800 local time). Observations were obtained on 6 d in each grazing area. Selection frequencies were compared using contingency

table  $\chi^2$  to test differences between small ruminant and yak herds in the same area, among small ruminant herds in different areas, and among yak herds in different areas. Observations of vegetation type selection were compared to an expected null model distribution using goodness-of-fit  $\chi^2$  ( $DF = 6$ ). The null model, an expectation of random selection, was generated from the surface areas ( $A$ ) of each vegetation type ( $i = 1, 2, \dots, n; n = 7$ ) as proportions of the total area of major pasture in the grazing area,

$$E_i = (A_i / \sum_n A_n) \sum_n O_n$$

where  $E$  is the null model expected frequency and  $O$  is the observed frequency.

Herd movement was characterized by estimating daily horizontal distances traveled and daily maximum vertical displacement. Horizontal distances traveled were calculated on a map by summing the straight line distances from encampment, through the 8 daily observed locations, and returning home ( $n = 6$ ). Although this method underestimates animal movement, we assumed that it provided an adequate comparative estimate. Maximum vertical displacement of a herd was assumed to be equal to the absolute value of the difference between the herd's highest or lowest observed altitude, and the altitude of the family camp. Estimates were compared using a 2-way ANOVA to determine the effects of area ( $DF = 2$ ), herd type ( $DF = 1$ ), and herd  $\times$  area interactions ( $DF = 2$ ).

#### BOTANICAL COMPOSITION OF DIET

The bite-count technique (Walmo and Neft, 1970; Hobbs et al., 1979; Coppock et al., 1986a), a visual estimation method, was used to record the particular plant



species, plant part (leaf, stem, inflorescence, seeds, whole plant), and condition (green, dry) of the diet items of a livestock species (Cincotta, 1989). Frequencies of items (as percentages of total bites) was calculated from three daily half-hour bouts ( $n=5$ ) using a pocket computer algorithm (Cincotta, 1989). Dietary items were then grouped into five broad forage classes that included both life form and taxonomical (according to Porter, 1967) considerations: (1) sedges (species from the family Cyperaceae); (2) grasses (species from the family Poaceae); (3) forbs (all herbaceous dicots, excepting species from the family Fabaceae); (4) legumes (species from the family Fabaceae); (5) shrubs (woody stemmed species). The modified Morisita index (Horn, 1966) was used to calculate dietary overlap of pairs of livestock species on the basis of the forage classes.  $C_x$ , the coefficient of overlap, can range from 0.0 for completely dissimilar pairs, to 1.0 for complete overlap.

#### FORAGE QUALITY

Hand-picked replicates of livestock diets (Cincotta, 1989) were analyzed using detergent methods of fiber fractionation described by Van Soest (1967) and Van Soest and Wine (1967, 1968). Opalite silica content of forages

and sand contamination were determined by detergent fractionation methods (Van Soest and Wine, 1968). Percentage crude protein (CP) was determined from oven-dried samples (48 h at 60°C) using Kjeldahl N procedures (Pierce and Haenisch, 1947;  $CP = 6.25 \times N$ ). True *in vitro* digestibility of dry matter (IVDDM) for ruminants was determined by methods outlined by Tilley and Terry (1963) and modified by Van Soest et al. (1966). IVDDM was corrected for loss of biogenic silica in the neutral detergent reflux (Van Soest, 1982). The inoculant donor for the anaerobic fermentation step of the *in vitro* procedure was a Jersey cow fed on a 50%-50% mixture of timothy hay and alfalfa (CP: 13.1%; IVDDM: 51.2%).

Dietary forage quality parameters were statistically compared using a 2-way ANOVA to test the effects of livestock species (DF = 2), grazing area (DF = 2), and livestock  $\times$  grazing area interactions (DF = 4). Percentage data were transformed for analyses using the arcsine transformation (Zar, 1984).

In all correlations, the null hypothesis that the product-moment correlation coefficient,  $r$ , equalled zero was tested using the  $F$ -statistic (Cacoullos, 1965; Zar, 1984). For all test statistics, we assumed that  $H_0$  was rejected when  $P \leq 0.05$  for acceptance was calculated.

## RESULTS

#### DISTRIBUTION OF VEGETATION TYPES

Only about 28% (22.3 km<sup>2</sup>) of the combined summer grazing areas surrounding the three encampments supported major pastures, while minor pastures covered the remainder (72%). Glacier-fed riparian types covered 4.5 km<sup>2</sup>, roughly 6% of the total surface area. Two vegetation types occurred in riparian areas: hilly wet meadows (3.1 km<sup>2</sup>) dominated by *Kobresia* spp.; and shrublands dominated by *Potentilla parvifolia* (1.4 km<sup>2</sup>). Available forage biomass was more abundant in glacier-fed riparian vegetation than in nonriparian types (Table 2).

Nonriparian vegetation (in semiarid valleys and on vegetated slopes) accounted for 17.8 km<sup>2</sup> of major pastures, roughly 22% of the total grazing land. Semiarid valley types covered 9.9 km<sup>2</sup>, an area within which resided three vegetation types: *Calamagrostis-Stipa*, 0.9 km<sup>2</sup>; *Stipa* and associates, 7.6 km<sup>2</sup>; and *Artemisia* types, 1.4 km<sup>2</sup>. Vegetated slopes covered 8.0 km<sup>2</sup>, within which there were two types: forb mixes, 2.2 km<sup>2</sup>; and montane sedges, 5.8 km<sup>2</sup>.

Grazing areas were dissimilar in respect to the surface area occupied by each vegetation type within major pastures (Figure 5). In Shagar, major pastures were restricted largely to nonriparian vegetation (6.9 km<sup>2</sup>) that covered a sandy, flat valley. Small patches of wet meadows (0.3 km<sup>2</sup>) surrounded springs that emerged near the lake shore. In contrast, the Chamar population had access to a large wet meadow (3.3 km<sup>2</sup>) of relatively abundant, early-growth forage. In addition, Chamar livestock grazed pastures on the surrounding vegetated slopes (3.1 km<sup>2</sup>) of the valley. Unlike the other areas, the Berak population depended

heavily on vegetated slopes (3.8 km<sup>2</sup>), though some wet meadow pasture (0.9 km<sup>2</sup>) was available as well.

#### VEGETATION TYPE SELECTION AND HERD MOVEMENT

The frequency at which vegetation types were selected by lactating herds of goats and sheep (mixed small ruminants) compared with herds of lactating yak was non-homogeneous in Shagar ( $P=0.01$ ), Chamar ( $P<0.01$ ), and Berak ( $P=0.02$ ). Differences in selection among livestock herd types (Figure 6) may have been affected by the degree to which herders controlled each herd type. Herds of mixed goats and sheep were closely tended. In

TABLE 2  
Estimates of available AGNPP in vegetation types present in three grazing areas in Phala, 1987<sup>a</sup>

Vegetation type	Shagar July 4-8 ( $n=18$ )	Chamar July 11-18 ( $n=18$ )	Berak July 25-29 ( $n=18$ )
<i>Kobresia</i> hillocks	94 (14) <sup>b</sup>	139 (25)	51 (10)
Montane sedges	7 (2)	7 (2)	12 (3)
<i>Stipa</i> and associates	7 (3)	7 (2)	16 (3)
<i>Calamagrostis-Stipa</i>	31 (4)	<sup>d</sup>	<sup>d</sup>
Mixed forbs	<sup>d</sup>	13 (3)	15 (2)
Shrublands	<sup>c</sup>	77 (15)	90 (14)
<i>Artemisia</i>	<sup>d</sup>	15 (3)	<sup>c</sup>

<sup>a</sup>Data are in grams per square meter.

<sup>b</sup>Mean ( $\pm 1$  SD).

<sup>c</sup>Absent from area.

<sup>d</sup>Present but not sampled.





contrast, yak were rarely tended for the full day during the summer season; after morning milking, a family member usually directed the yak toward a pasture, and then abandoned the herd to forage independently until they were retrieved in the evening. An exception to this practice was observed in Chamar, where young herders were often assigned to move yak to predetermined pastures for the full day.

Comparisons of vegetation type selection between areas were also nonhomogeneous; i.e.,  $P$  for homogeneity in the set of observations of small ruminants in Shagar and Chamar, Shagar and Berak, and Chamar and Berak, was (in each case)  $<0.01$ . For the same comparisons between yak herds,  $P < 0.01$ . In all grazing areas, the observed frequencies of vegetation type selection for mixed small ruminants and for yak herds were different ( $P < 0.01$ ) than null model expectations based upon the type's surface area. Thus, the nonrandom patterns of vegetation type selection may be attributable to other associated factors, or combinations of factors (i.e., indicators of herder preference, such as species composition, productivity, spatial distribution) rather than herd type alone.

Differences in daily traveling distances for herds were attributed to the effects of grazing area ( $P < 0.01$ ) and herd type ( $P < 0.01$ ). Average distances for small ruminant herds were  $11.3 \pm 1.7$  (mean  $\pm$  SD),  $7.9 \pm 1.7$ , and  $7.6 \pm 1.2$  km for Shagar, Chamar, and Berak, respectively. Yaks traveled  $8.5 \pm 2.2$ ,  $5.9 \pm 1.3$ , and  $6.3 \pm 1.3$  km in these same areas.

Differences in daily maximum vertical deviation of herds were attributed only to grazing area effects ( $P < 0.01$ ). For small ruminant herds, the vertical deviation from their home encampment was  $110 \pm 27$  m (mean  $\pm$  SD) for Shagar, where the majority of grazing occurred on the valleyfloor;  $113 \pm 67$  m in Chamar, where

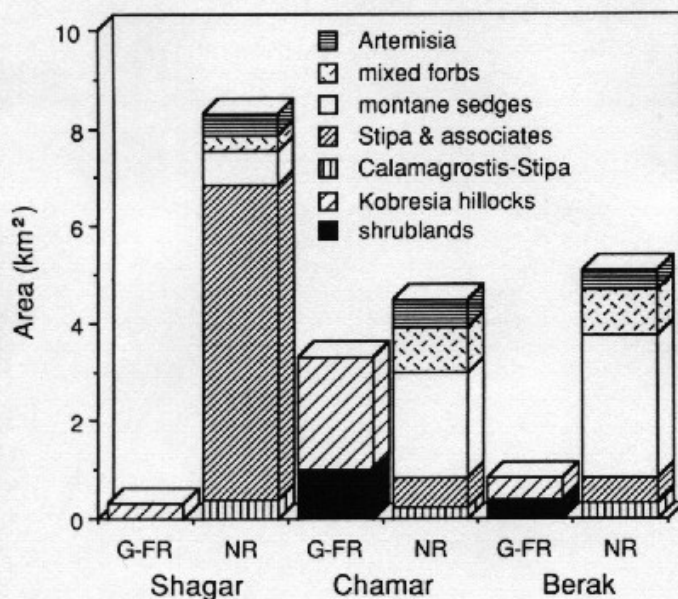


FIGURE 5. Surface area covered by vegetation types, showing glacier-fed riparian vegetation (G-FR) and nonriparian vegetation (NR) in each of the three grazing areas studied. Graph shows major pastures (AGNPP  $> 10$  g m $^{-2}$ ) only.

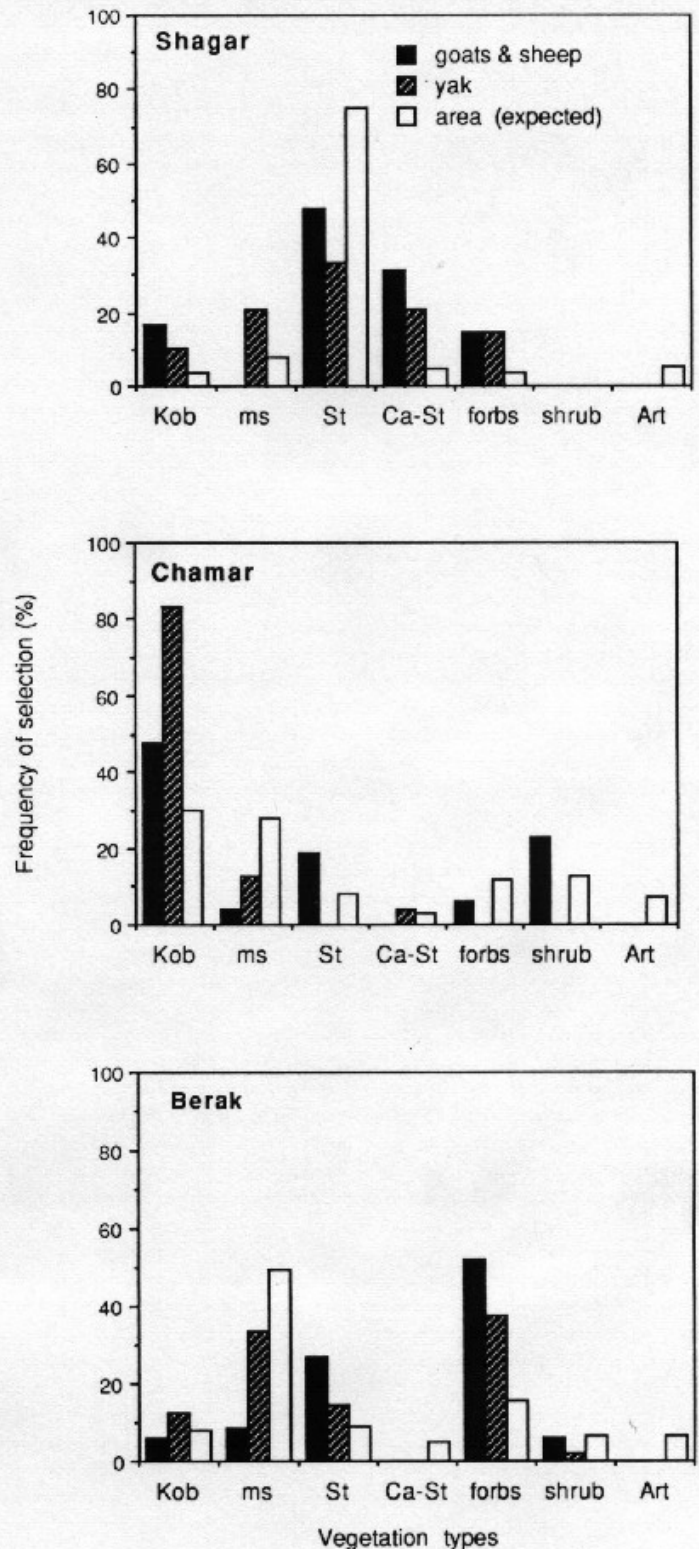


FIGURE 6. Frequency of vegetation type selection by the two livestock herd types in three adjacent summer grazing areas in Phala (Kob = *Kobresia* hillocks, ms = montane sedges, Stipa = *Stipa* and associates, Ca-St = *Calamagrostis-Stipa* mixes, forbs = mixed forbs, shrub = shrub-dominated types, Art = *Artemisia*). The null model expectations, i.e., the expected frequency of selection based upon the surface area occupied by each type as a proportion of the total area covered by major pastures (AGNPP  $> 10$  g m $^{-2}$ ), is also shown.

much of the grazing occurred in a large wet meadow, with occasional traverses along vegetated slopes; and  $167 \pm 59$  m in Berak, where  $>70\%$  of the area of major pastures was situated on vegetated slopes. Yak herds climbed  $103 \pm 54$ ,  $83 \pm 45$ , and  $201 \pm 48$  m in the respective areas.

#### FORAGE SELECTION

Average livestock diets (Table 3) differed principally in the selection of sedges and shrub forage. Both sheep and goats avoided selecting two coarse sedge forages ( $<1\%$  of diets); (1) the rigid flowering stalks of large (up to 30 cm) wet meadow sedges, *Kobresia schoenoides* (C.A. Mey.) Steud. and *K. royleana* (Nees) Boeck; and (2) the coarse leaves of a dryland species, *Carex capillaceae* Boott. These forages were selected more readily by yak, which consumed them as 3.4 and 7.5% of their total diet, respectively. In addition, the only shrub species of significant abundance to be important in livestock diets, *Potentilla parvifolia*, was browsed more heavily by goats (31.2% of diet) and sheep (17.9%) than by yak (4.1%).

Although monsoonal rains quickly brought on the initiation of plant growth and the appearance of green foliage, small quantities of lower quality residual dried (brown) leaf material were ingested by yak (3%), goats (1%), and sheep ( $<1\%$ ) when selecting bunches of needlegrasses, such as *Ptiligrostis concinna* (Hook f.) Roshev, *Stipa bungeana* Trin., and *S. aliena* Keng. Other grasses of importance to livestock included *Calamagrostis emodensis* Griseb., *Littledalea tibetica* Hemsl., and *Poa alpigena* (Blytt.) Lindm.

Yak consumed significant amounts of forages that we expected to be consumed only by the small-mouthed, selective feeders (goats and sheep). These forages included sharp, spiny plants, and relatively small herbaceous material. Leaf, stem, and flower parts of a heavily spined forb, *Cryptothladia kokonorica* (Hao) M. Cannon (family: Morinaceae), were readily selected regardless of phenological stage by yak (2.0%). Yak foraged heavily on species of sedges between 2 and 3 cm tall by "licking" the soil surface and wedging the leaf parts between their tongue and dental pad. This method of feeding was noted principally on a montane sedge species, *K. pygmaea* (7.8% of diet) and on minute species of wet meadow pastures (22.3%), including *K. angusta* C.B. Clarke and *Carex sagaensis* Y.C. Yang.

TABLE 3  
Average summer diets for lactating livestock  
in Phala, 1987<sup>a</sup>

Forage class	Goats (n = 15)	Sheep (n = 15)	Yak (n = 15)
Sedges	35.3	38.4	64.1
Grasses	11.1	23.6	23.9
Forbs	21.5	16.2	7.6
Legumes	0.6	3.3	0.3
Shrubs	31.5	18.5	4.1

<sup>a</sup>Data are percent of diet.

*Cryptothladia kokonorica* was also consumed by sheep (1.7%) and goats (2.0%), as were small herbaceous dicots, including several minute dryland and wetland cinquefoils (genus *Potentilla*). Foliage of large wetland sedges, mainly *K. schoenoides* and *K. royleana*, comprised 12.8% of goat diets and 6.2% of sheep diets. Goats selected 4.3% and 0.8% of the small ( $<4$  cm high) sedge

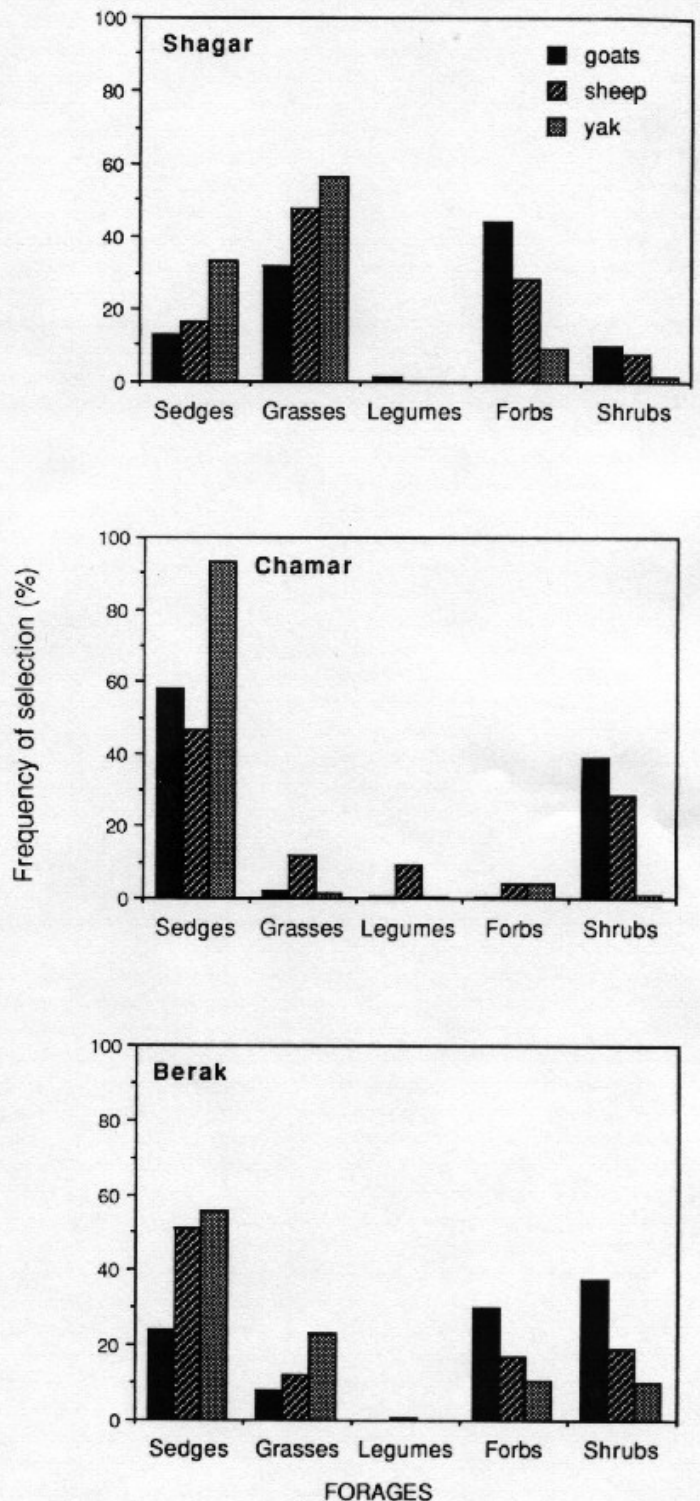


FIGURE 7. Summer diets of livestock species by forage class in three grazing areas in Phala, western Tibet.



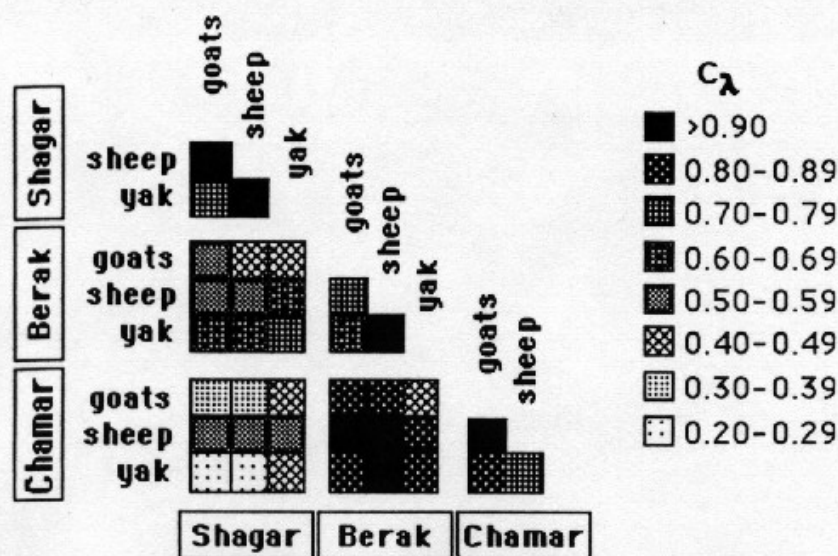


FIGURE 8. Overlaps of summer livestock diets in three grazing areas in Phala. Overlap is expressed by the Morisita index ( $C_{\lambda}$ ).

species *K. pygmaea* and *K. angusta* (intermixed with *Carex capillaceae*), respectively; whereas sheep diets contained 5.6 and 0.7% of these species. *Artemisia welbyi* was rarely selected by livestock (<0.1% of any diet).

Forage type availability probably accounted for the observed differences in the selection of forage classes among grazing areas (Figure 7). The heavy selection of grasses and forbs in Shagar diets reflected the abundance of nonriparian vegetation and the paucity of browse in that area. Chamar selections clearly reflected a reliance on wet meadow sedge forages and the use of abundant browse by small ruminants. Patterns of forage selection in Berak showed it to be intermediate between its two geographical neighbors.

Paired livestock diets within grazing areas were strongly similar in respect to diet component overlap. Overlap of goat and sheep diets within grazing areas was  $0.89 \pm 0.09$  (mean  $\pm$  SD); goats and yak,  $0.75 \pm 0.08$ ; and sheep and yak,  $0.88 \pm 0.13$ . However, differential forage availability substantially reduced diet overlaps between areas (Figure 8); intraspecies diet overlaps were lowest in comparisons of Shagar and Chamar diets (goats-goats, 0.38; sheep-sheep, 0.56; yak-yak, 0.25). Chamar and Berak diets were highly overlapped, both in intra- and interspecies computations. Overlaps in Shagar and Berak generally ranged between those of Shagar-Chamar and Chamar-Berak.

#### DIETARY FORAGE QUALITY

The means of fiber fractions were similar to values for early growth grass and sedge forages in temperate climates (National Research Council, 1982). Dietary cell wall fractions, such as hemicellulose, cellulose, and lignin, were moderate and occasionally low (Table 4). There was no effect from livestock species on any of the fiber nutritional parameters tested in summer diets ( $P < 0.05$ ). However, there was significant variance attributable to the effect of grazing area in dietary NDF, CP, IVDDM (Figure 9), and cellulose. Dietary NDF accounted for a greater

TABLE 4  
Estimates of nutritional parameters of dietary forage for lactating livestock in Phala, 1987<sup>a</sup>

Parameter	Goats (n = 15)	Sheep (n = 15)	Yak (n = 15)
Neutral detergent fiber	44.7 (10.8) <sup>b</sup>	45.1 (10.7)	50.0 (9.4)
Hemicellulose	13.8 ( 8.0)	16.2 ( 9.4)	20.3 (7.1)
Cellulose	23.7 ( 5.1)	22.8 ( 4.2)	24.4 (3.8)
Lignin	5.1 ( 2.0)	4.2 ( 1.9)	3.6 (1.0)
Crude protein	16.6 ( 3.4)	16.9 ( 2.9)	16.4 (4.7)
In vitro digestibility	66.6 ( 7.9)	71.1 ( 7.0)	68.4 (5.4)

<sup>a</sup>Data are percent dry matter.

<sup>b</sup>Mean ( $\pm$  1 SD).

proportion of dry matter in Chamar ( $55.0 \pm 11.1\%$ ) than in either Shagar ( $42.8 \pm 9.2\%$ ) or Berak ( $41.9 \pm 4.9\%$ ), reflecting the abundance of relatively fibrous forage in phenologically advanced, wet meadow pastures in Chamar. Differences between means of NDF in grazing areas were clearly attributable to corresponding differences in dietary cellulose contents of  $27.9 \pm 3.5\%$ ,  $21.9 \pm 3.2\%$ , and  $21.0 \pm 3.0\%$  for Chamar, Shagar, and Berak, respectively. Means of dietary hemicellulose (overall mean:  $16.8 \pm 8.7\%$ ), a fraction that is generally more digestible than cellulose, were similarly ranked by area, though not significantly different. Mean IVDDM for all livestock species was high ( $68.7 \pm 4.3\%$ ). Dietary IVDDM was greater in Shagar ( $71.7 \pm 4.9\%$ ) and Berak ( $70.2 \pm 7.8\%$ ) than in the more fibrous and lignified diets collected in Chamar ( $64.2 \pm 5.9\%$ ). Dietary CP (overall mean:  $16.6 \pm 8.0\%$ ) was greater in Berak ( $19.9 \pm 4.2\%$ ) than in Shagar ( $14.9 \pm 3.3\%$ ), while the mean CP in Chamar ( $16.0 \pm 2.3\%$ ) was intermediate. There were no significant livestock species  $\times$  area interactions. Dietary biogenic silica accounted for only 1.1% of dry matter, and did not vary between livestock species or area.

## DISCUSSION

### RESOURCE DISTRIBUTION

The availabilities of glacier-fed riparian and non-riparian biomass represent an important constraint in Phala summer grazing strategies, and may have a critical impact on animal production. Fed by glacial spring water, wet meadow vegetation represents a "low risk" forage resource. When riparian pastures are widespread in a locality, they provide herds with a high density forage that emerges in spring, before the arrival of the monsoon, at a time when livestock are in a weakened state. This vegetation then matures independently of the amount and timing of contemporary monsoonal precipitation.

Where wet meadows are small or absent, livestock must depend on nonriparian forage. For herds in this situation, delayed monsoons extend foraging on dried vegetation into the summer months, thus lowering milk productivity, and probably impeding growth and reproduction. This may have occurred during our study in 1987. In Chamar, where livestock had ready access to 3.3 km<sup>2</sup> of glacier-fed meadow, daily milk output per lactating female was twice that of either Shagar or Berak (Beall, unpublished data). When monsoonal moisture allows nonriparian vegetation to initiate growth, total forage biomass on the broad plain of Shagar is far greater than present herds can possibly consume before resident grasses and sedges disperse seed and foliage desiccates. Therefore, among nonriparian vegetation in Phala, it is doubtful that livestock have a significant impact on plant populations. This may not be the case in glacier-fed riparian vegetation, although presently there is insufficient evidence to assess the impact on these types.

Although wet meadow forage is greatly valued, herders point out that the late growth of *K. pygmaea*, a constituent of vegetated slopes, is a critical fall and winter forage. This short, bunched sedge was the last major forage species to emerge during 1987. Its delayed phenology may indicate a retention of high forage quality after the quality of wet meadow sedges and *P. parvifolia* has declined.

Topography also represents a major constraint in Phala summer grazing strategies. Distances traveled and the altitudinal changes associated with daily herd movements reflect the dissimilarity in topographic environments among the three summer grazing areas. The relatively short daily circuits observed in Chamar were due to frequent (though not exclusive) use of high density wet meadow forage situated at the valley bottom. In contrast, Shagar herds were moved long distances, grazing several discrete, scattered pockets of green vegetation daily, generally 2.5 to 4.5 km from the encampment, and often 2 km from each other. In Berak, a hillside encampment, herders regularly drove livestock to sedge-dominated pastures hundreds of meters above the elevation of the central tent site.

A third constraint to Phala summer grazing strategies is the necessity for planned deferment and the avoidance of certain vegetation types. In addition to the wet season deferment of fall pasturage (Goldstein et al., 1990), small

pastures (< 30 ha) are reserved for spring grazing of herds of female small ruminants shortly after parturition. Also, herders report that *A. welbyi* is of low palatability to livestock and sites dominated by this species are rarely grazed.

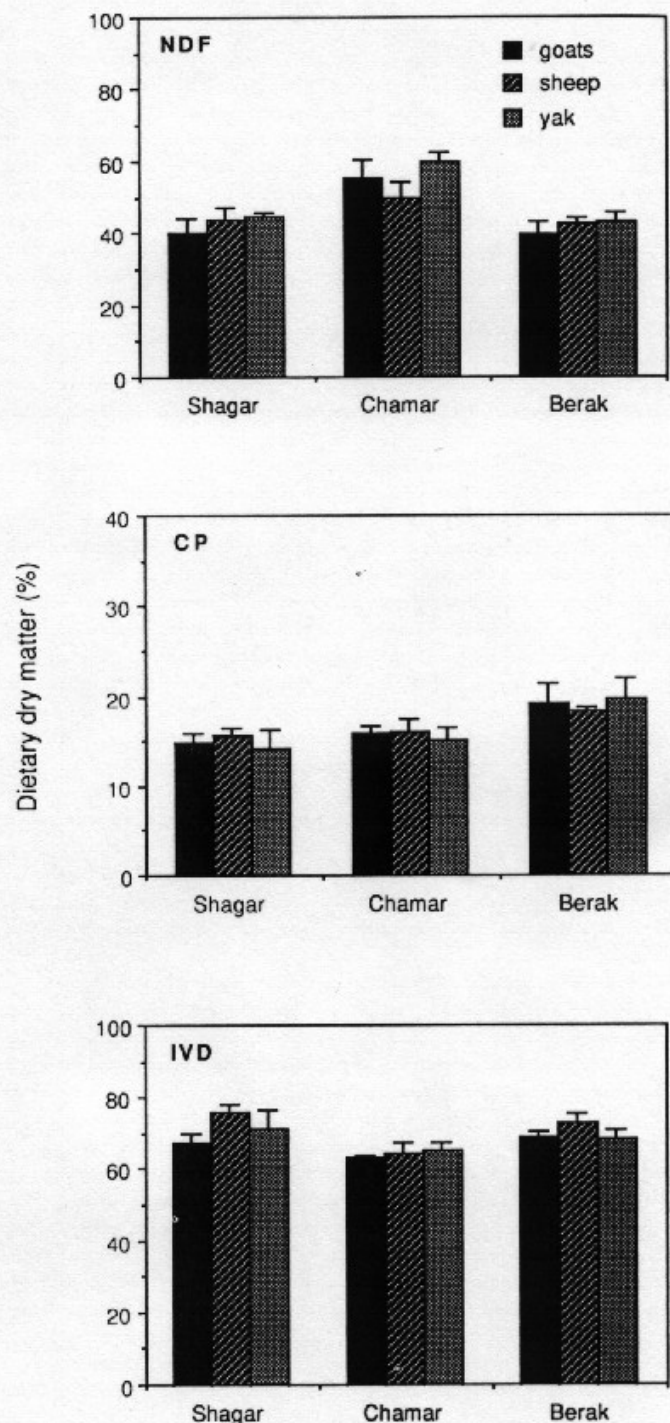


FIGURE 9. Neutral detergent fiber (NDF), crude protein (CP), and *in vitro* digestibility (IVD) as proportions of dry matter in diets of lactating livestock in three adjacent summer grazing areas in Phala.



## RESOURCE PARTITIONING

Many forage selection studies have demonstrated differences in selection of plant species and plant parts among livestock species (Vavra and Sneva, 1978; cf. Squires, 1982; cf. Hanley and Hanley, 1982). The ability of large ruminants to digest highly fibrous forages can be explained by the metabolic energy requirements and fiber processing constraints related to ruminant body size (Hanley, 1982; Demment and Van Soest, 1985). Resource partitioning among herbivores may, as well, be partly explained by physical (height, small mouths, and prehensile lips) and behavioral differences among livestock species (e.g., the ability of goats to climb and to support themselves on their hind legs while browsing; Pfister et al., 1988), which are modulated by geographical and vertical stratification of forage. In addition, the adaptive processes of dietary sampling and social learning (between mother and offspring and among conspecifics; cf. Provenza and Balph, 1990) have recently been shown to be important mediators of dietary preference. Thus, although there is clearly a potential for partitioning of dietary botanical composition and forage quality among domestic ruminant species, it is not always realized, especially when forage quality is not highly stratified or selection is constrained. Forage availability, herding, fencing, and learning experiences no doubt affect selection, but their impacts are complex and cannot be generalized. In our study, the impact (if any) on the realization of resource partitioning, either from herding small ruminants or from permitting yak to forage freely, is unknown.

The lack of demonstrable partitioning in forage quality parameters of Phala summer season was probably due to ubiquitous high quality forage and absence of vertical stratification in the vegetation. In semiarid pastoral systems in tropical Africa, small trees and shrubs provide domestic selective feeders (goats, sheep, camels) with forage that is high in cell solubles (nonstructural carbohydrates, proteins). In Phala, palatable browse is represented primarily by a single species, *P. parvifolia*, which is generally short (below 0.6 m) and within reach of all livestock species. As expected, we found that when shrubs were encountered, small ruminants utilized browse more readily than yak. However, this shrub is encountered much less frequently in Shagar than in Chamar or Berak. In addition, in the early summer, grasses and sedges tend to be low in fiber and highly digestible, thus presenting a narrow spectrum of forage qualities. The yak's adaptations for survival on high desert forage and in mountainous topography (Epstein, 1974; Bonnemaire, 1976; Dor, 1976) make partitioning even more difficult to discern on the gross level of forage classes. Consequently, summer livestock diet overlaps on the basis of forage classes were high within grazing areas (>0.80).

## OTHER LIVESTOCK-RELATED FACTORS

For ruminants, the high proportion of cell solubles in browse is offset by (1) depressed cell wall digestibility associated with lignin-cellulose complexing (Hartley, 1972; cf. Van Soest, 1982) and (2) the presence of diges-

tive inhibitors that are frequently sequestered by woody plants (Rhoades, 1979). In a Turkana pastoral ecosystem in Kenya, Coppock et al. (1986a) noted that IVDDM in all diets during the mid and late dry seasons was positively related to the proportion of dietary herbaceous forage (i.e., negatively related to dietary browse). In the same diets, dietary N (CP/6.25) could be predicted as a negatively sloped linear function of dietary herbaceous forage.

Although Phala summer (wet season) diets were not expected to depict the same dry season "trade-off" between browse and herbaceous forage, differences were observed (Figure 10). Whereas there was no correlation between dietary N in Phala summer diets and dietary browse for any of the livestock species, IVDDM for diets of small ruminants was negatively related to dietary browse. For goats and sheep, IVDDM dropped from

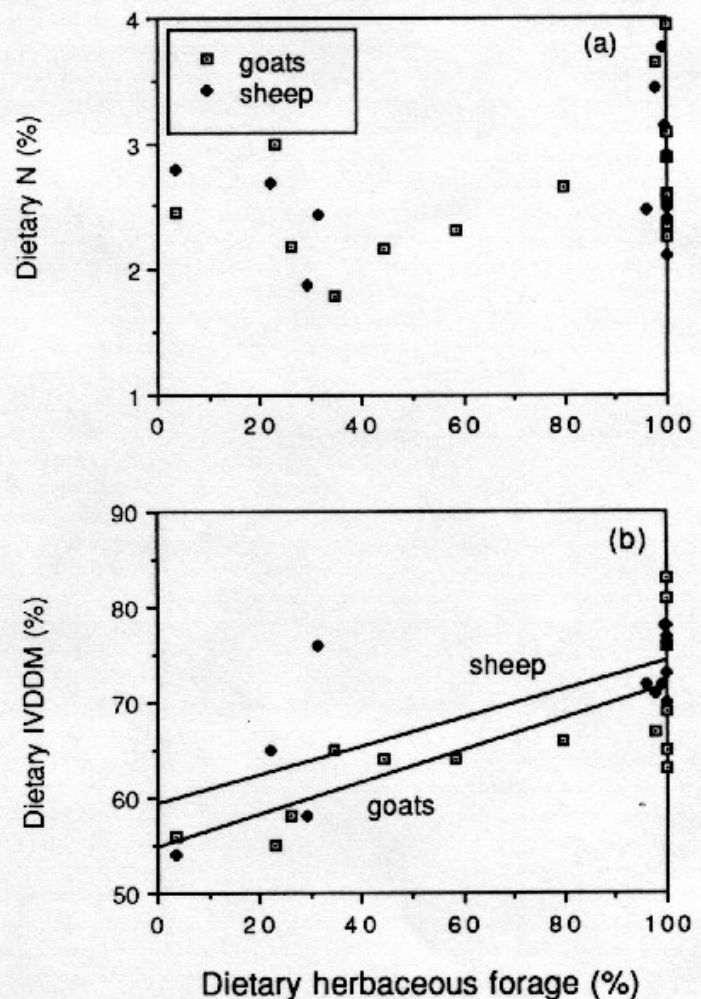


FIGURE 10. (a) Dietary N versus herbaceous forage in sheep and goat summer diets in Phala. (b) The apparent increase in IVDDM with increased herbaceous material (i.e., decreased dietary browse) by goats and sheep. For sheep, % IVDDM is related to % herbaceous forage (HF) by:  $IVDDM = 0.168(HF) + 54.8$ ,  $r^2 = 0.54$ ; for goats:  $IVDDM = 0.149(HF) + 59.4$ ,  $r^2 = 0.56$ . There is no statistical difference between regression lines of the two species. Similar statistical models do not fit data for dietary N.



71.6% and 74.3% in pure herbaceous diets to 54.8% and 59.4%, respectively, in pure browse diets. Although the proportion of dietary browse for yaks was also negatively correlated with IVDDM, bouts dominated by browsing were not observed in this species; thus data covered too narrow a range for extrapolation.

As expected, all dietary values of CP ranged well above maintenance requirements for sheep (8.5% CP; NRC, 1975) and goats (9.2%; NRC, 1981). The high digestibility of some early-growth herbaceous forage, most markedly in livestock diets (of all species) on mountain slopes in which *K. pygmaea* was a major constituent, is notable (range of dietary IVDDM: 74–83%). Estimates of seasonal weight gains (not measured in this study) are needed to assess the rapidity with which these livestock are capable of taking advantage of high quality forage resources.

In our study, lignin content was negatively correlated with IVDDM ( $r=0.78$ ,  $P<0.01$ ,  $n=30$ ) in pooled sheep and goat diets. Thus, as a major constituent in the bud scales and growing shoots of browse, the presence of dietary lignin may explain depression of digestibility in high browse diets. Presently, we have no evidence for the activity of other plant-defensive compounds in the high-altitude browse of *P. parvifolia*.

Although good forage quality in these high-altitude rangelands should promote livestock survival when forage is senescent, catastrophic herd losses in long winters and

during severe snow storms are common (Goldstein et al., 1990; for accounts of similar density-independent losses in other high-altitude ecosystems, see Shahrani, 1979; and Ekvall, 1968; for a perspective on the significance of density-independent herd losses, see Ellis and Swift, 1988). Thus, the uncertainty intrinsic to animal husbandry in this and similar high-altitude ecosystems prevents any broad generalization of the potential for livestock productivity in Phala.

#### ACKNOWLEDGMENTS

Field work was supported in part by grants from the National Geographic Foundation and the Committee for Scholarly Communication with the People's Republic of China, National Academy of Sciences. Further logistic and research support was provided by the Tibetan Academy of Social Sciences. Development of a Tibetan forage reference collection was made possible by a U.S. State Department grant (1753-900561) to the U.S. Man and the Biosphere Program. Laboratory materials and labor was supported fully by the Cornell Fiber Analysis Laboratory, Department of Animal Sciences, Cornell University. We wish to thank field workers Tringley Dorje, A. Goldstein, Kunrig, and Tringley Namgye; and Dr. N. Conklin and T. Hernandez for laboratory instruction. Valuable assistance was rendered by P. Edwards of Kew Botanical Gardens, who supervised plant identification.

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Ms submitted June 1990