Int J Primatol (2008) 29:509–530
DOI 10.1007/s10764-008-9245-x

Himalayan *Semnopithecus entellus* at Langtang National Park, Nepal: Diet, Activity Patterns, and Resources

Ken Sayers · Marilyn A. Norconk

Received: 8 January 2007 / Accepted: 15 September 2007 /

Abstract Though researchers have studied lowland gray langurs extensively, there is little information about the Himalayan populations. We provide foraging data from a field study of Himalayan langurs in Langtang National Park, Nepal at 3000–4000 m elevation. Phenological records show marked seasonality in resource abundance, with extremely low availability in winter, increasing abundance in spring and monsoon, and a reduction in fall. Activity budgets indicated greater time devoted to feeding as total vegetation abundance decreased. Diet included leaf buds, ripe fruit, and evergreen mature leaves in winter; deciduous young leaves in spring; and deciduous mature leaves in the monsoon and fall. Supplemental resources, such as underground storage organs, bark, and herbaceous vegetation, were also seasonally important. Among plant part classes included in the phenological sample, abundance and consumption correlate positively for all primary food resources except evergreen mature leaves and unripe fruit. Daily path lengths varied by season and, when controlled for overall vegetation abundance, positively relate to the consumption of soft underground storage organs, fruits, and deciduous mature leaves. The results contradict the common generalization of leaves as ubiquitous or nonpatchy resources.

Keywords colobines · diet · ranging · seasonality · *Semnopithecus entellus* · socioecology

Introduction

Gray langurs (*Semnopithecus entellus*) range from Sri Lanka to the Himalayas in habitats extending from semidesert and subtropical forest to subalpine scrub (Bishop

---

K. Sayers (✉) · M. A. Norconk
Department of Anthropology and School of Biomedical Sciences, Kent State University,
Kent, OH 44242, USA
e-mail: kasayers@kent.edu

1977, 1979; Brandon-Jones *et al.* 2004; Koenig and Borries 2001). Though researchers have studied lowland gray langurs extensively, there is little information about the Himalayan varieties, even their taxonomy. Bishop (1975, 1979) investigated langur social behavior at Melemchi, north-central Nepal (2442–3050 m), with special reference to auditory communication. Boggess (1976, 1980) studied social behavior and male membership changes at Junbesi (2442–3505 m), in the Everest region of Nepal, and Curtin (1975, 1982) concurrently collected data on ranging and preliminary information on langur foraging. The studies, along with several of shorter duration (Vogel 1971), have aided in the definition of a Himalayan pattern of langur ecology and behavior that is different in many respects from that of lowland populations. For example, Highland langurs form predominately multimale, multifemale troops, use expansive home ranges, employ vocalizations different from those of lowland langurs, and exhibit behavioral and morphological buffers to cold weather (Bishop 1979). Though Sugiyama (1976) collected seasonal data on Himalayan langur foraging in Himachal Pradesh, India (1500–3200 m), there has been no detailed long-term study that included systematic quantification of diet coupled with phenological sampling. There had also been no study on Himalayan langur food preference or the quantification of relationships among resource abundance, activity patterns, diet, and ranging.

In current models of primate socioecology, leaves are generally considered ubiquitous or nonpatchy resources that are unlikely targets of contest competition (Isbell 1991; Wrangham 1980). Researchers expect folivorous primates to exhibit shorter daily path lengths and smaller home ranges than those of frugivorous primates (Clutton-Brock and Harvey 1980), with rest-dominated, energy-minimizing, activity budgets (Oates 1987). Though comparative studies sometimes support the generalizations (Sterck *et al.* 1997), increasing evidence suggests that, under some circumstances, they are unlikely to be correct. When leaves occur on trees or shrubs that are separated from one another by areas with little food, one can consider them patchy (Astrom *et al.* 1990). The marginal value theorem (Charnov 1976) predicts that as overall food abundance decreases, patches will be further spaced out, and both travel times between patches (travel budget) and patch residence times (feeding budget) will increase (Stephens and Krebs 1986). Thus, at low enough levels of resource abundance, a folivorous primate would have daily path lengths and activity budgets similar to those of frugivorous primates at less marginal sites. For example, black snub-nosed monkeys (*Rhinopithecus bieti*) are conservatively estimated to travel an average of 1310 m each day even though they feed heavily on lichens, which, like leaves, are often labeled ubiquitous and non-patchy (Kirkpatrick 2007).

We present ecological and behavioral results from a Himalayan langur study designed: 1) to quantify gray langur diet, activity patterns, and resource availability at an extreme of their geographic range, 2) to identify food preference by comparing plant part consumption and abundance based on phenology scores, and 3) to relate feeding budgets and daily path lengths to the abundance and consumption of various plant parts. We compare and contrast the results with generalizations frequently made concerning the behavioral ecology of primate folivores.

Methods

Study Site

Langtang National Park is in north-central Nepal on the Tibetan border (Fig. 1). With altitudes varying from *ca*. 800 m to >7200 m, habitats range from subtropical forest to perpetual snow. A glacier-fed river, the Langtang Khola, cuts through the

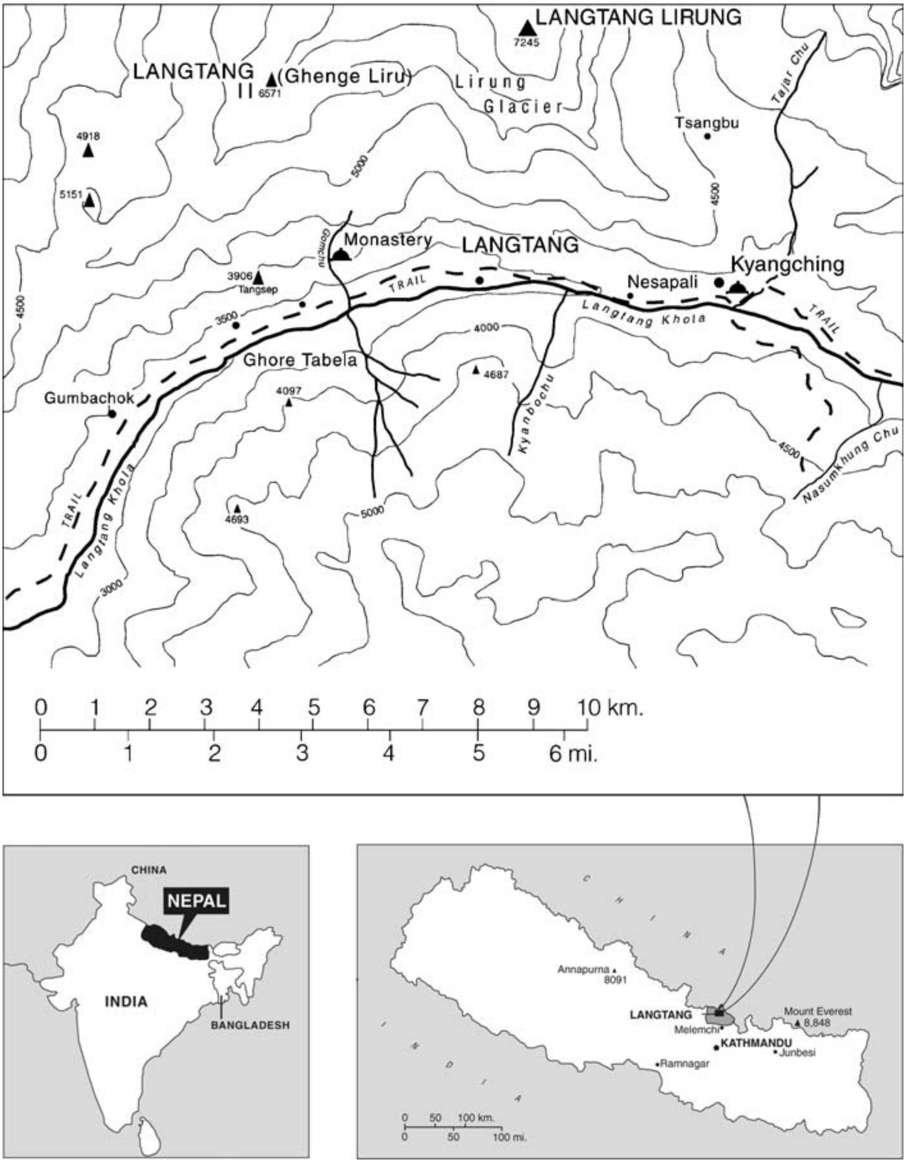

Fig. 1 Location of Langtang National Park, Nepal, and a topographical map of the main study area.

northern section, forming a steep-walled valley. The mammalian fauna includes red panda (*Ailurus fulgens*), Himalayan tahr (*Hemitragus jemlahicus*), and snow leopard (*Panthera uncial*; Green 1981).

The Langtang Valley between Ghore Tabela (3033 m) and Langtang village (3480 m) was our primary area of observation. Several vegetation types are present, with different woody species characterizing each (Fig. 2). On the north side of Langtang Khola, oak forest predominates to *ca.* 3100 m, above which oaks rarely occur, and smaller trees and shrubs make up much of the woody plant cover. The relative density of plant species within the zone varies markedly, and we refer to vegetation from 3100 m to 3200 m as scrub, and >3200 m as high scrub. While coniferous trees are comparatively rare on the north side of the river, the south side is largely coniferous forest. Other habitat types include fields (cultivated areas and yak pastures), rockslides, and cliffs. The village of Langtang is located at the northeastern extremity of the monkey range, but scattered human residences occur throughout the valley, mainly catering to foreign trekkers who travel through the area predominantly in spring and fall.

The climate at Ghore Tabela is highly seasonal (Fig. 3). Mean annual temperature for 2003, using monthly maximum-minimum midpoints, is 13.6°C. Winters (December–March) were characterized by cold nights, usually near freezing, and days that were generally clear and mild. During both spring (April–May) and fall (October–November), nights were cool and days were warm and sunny. Although snow occurred in varying amounts from November to May, 76% of the 1374 mm annual precipitation occurred as rain during the monsoon months from June to September. Because the monkeys moved over a considerable altitudinal range, temperature and precipitation often depended on the part of the habitat they were exploiting. During spring, e.g., rain at 3000 m elevation often turned to snow at 3200 m.

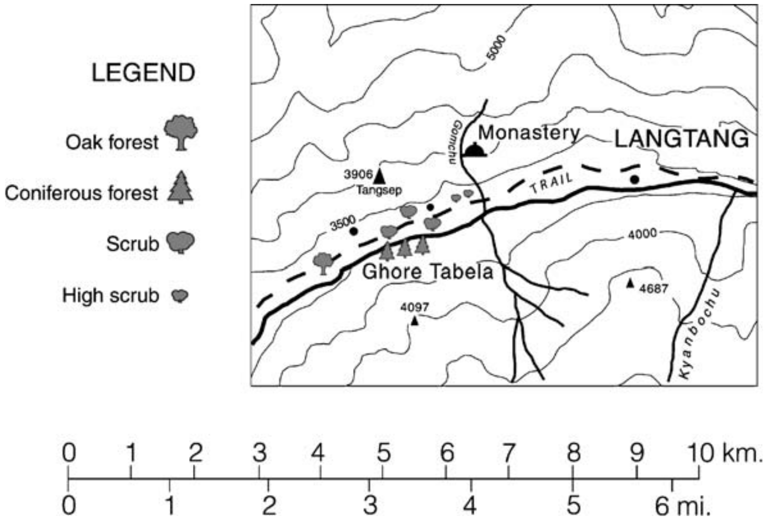

Fig. 2 Woody habitat types of the study area, with phenological plots indicated.

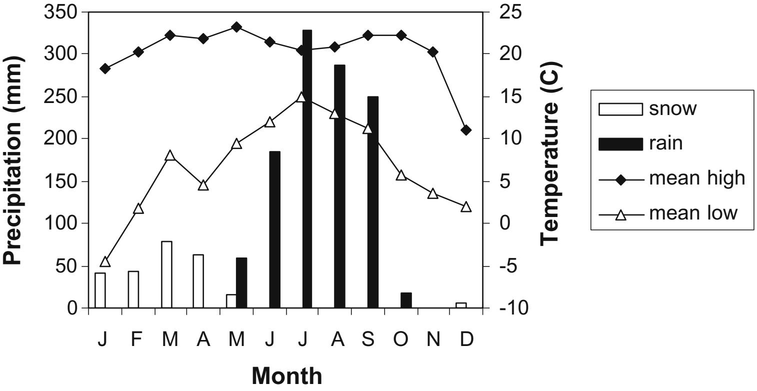

Fig. 3 Temperature and precipitation at Ghore Tabela (3033 m), Langtang National Park, Nepal, as recorded by max-min thermometer and standard rain gauge. Precipitation was snow/sleet or rain at the altitude the langurs were traveling; snow had melted before we recorded the amount. We did not record February max-min temperatures and assumed they represent midpoints between January and March.

Study Subjects

Age-sex classifications for the Langtang langurs are per Bishop (1975), as modified from Jay (1963; Dolhinow 1972). We chose the highest ranging troop in the main Langtang Valley, in terms of altitude, as the main study group (F troop). We never sighted F troop at <3000 m; they ranged from above Ghore Tabela (3033 m) to Langtang (3480 m), and moved on surrounding cliffs to altitudes estimated at ≥4000 m. After 3 mo of habituation, we could generally approach F troop to ≤10 m, but observations in all months were limited more by weather and habitat characteristics than by habituation. Group size for F troop ranged from 27 to 33 individuals, with a modal number of 3 adult males and 10 adult females. Five infants were born during the main observation period in F troop between December 2002 and early May 2003. Thus, timing of reproduction at Langtang corresponds to the birth peak for Himalayan langurs (Bishop 1979).

A secondary semihabituated troop, B troop, which traveled at 2500–3200 m, overlapped the range of F troop on the northern side of Langtang Khola. We did not know B troop as well as F troop, and followed it opportunistically in the monsoon of 2003 when we could not locate F troop. The highest count for B troop included 55 monkeys including 5 adult males.

Taxonomic Identification

Though Bishop (1979) suggested that only 1 Himalayan langur taxon be recognized, recent experts proposed 2 high-altitude subspecies (Brandon-Jones 2004; Brandon-Jones *et al.* 2004; Napier 1985) or species (Groves 2001): pale-armed (*Semnopithecus entellus schistaceus*) and dark-armed (*S. e. ajax*) Himalayan langurs. Pale-armed Himalayan langurs are apparently very widespread, ranging from Bhutan to possibly Afghanistan, and dark-armed Himalayan langurs are represented by specimens from Jammu and Kashmir, and Pakistan (Brandon-Jones 2004; Brandon-Jones, *pers. comm.*). The major feature delineating the subspecies is the darkness of the forelimbs.

In *Semnopithecus entellus schistaceus*, the forearms are similar in coloration to the upper arms and back or only slightly darker, while in *S. e. ajax* the forearms are dark brown or black (Napier 1985, p. 77).

Taxonomists generally place the langurs of Himalayan north-central Nepal, including Langtang, in *Semnopithecus* (or *Presbytis*) *entellus schistaceus* (Napier 1985) or *S. schistaceus* (Groves 2001). However, Brandon-Jones (2004) suggests that langurs in the region be classified as the dark-armed Himalayan langur (*Semnopithecus entellus ajax* or *S. ajax*) based on photographic evidence: dark forearms in photographs of Melemchi langurs (Bishop 1979). However, the only museum specimens from the Helambu Valley, where Melemchi is located, are referable to *Semnopithecus entellus schistaceus* (Brandon-Jones 2004).

To add to the confusion, Langtang langurs exhibit adult variation in forearm and back coloration, but none sported differences in forearm and back shading as striking as that of *Semnopithecus entellus ajax*. Accordingly, we retain them tentatively in *Semnopithecus entellus schistaceus*, though more data are needed on intra- and intertroop pelage variation (Oppenheimer 1977) from highland langurs across their range to test adequately the Brandon-Jones (2004) hypothesis. In addition, researchers often describe Himalayan langurs of both taxa as brown (Brandon-Jones 2004; Groves 2001; Hill 1939; Napier 1985; Pocock 1928). The Langtang langurs are not brown or brownish, but gray, like populations at Melemchi (Bishop and Bishop 1978) and Junbesi (Curtin 1975).

Activity and Feeding Data

Sayers or 2 Nepalese field assistants, or all 3, performed group follows on F troop during 10 mo between January 2003 and February 2004. We established contact with them during January 2003 and then monthly between March and May 2003, and from September 2003 to February 2004. Ideally, our group follows consisted of locating a troop in the morning near their sleeping site, generally cliffs, and following them until they entered another sleeping site that evening. However, there was never a certainty of contact with them. From June to August 2003 we did not contact F troop despite hundreds of hours of search by both the research team and hired local trackers. Thus, monsoon data from F troop is limited to observations from September 2003. We followed F troop for *ca.* 775 h between January 2003 and February 2004. The average number of individuals per scan via monthly means is 13.3±4.2 (40.3% of individuals, using modal group size).

We followed B troop for *ca.* 292 h during the monsoon of 2003, monthly from June to September. B troop generally used large trees as sleeping sites. B troop group follows were similar to the ones we performed on F troop, though more opportunistic owing largely to monsoon weather. On most days, thick fog rolled into the valley during the morning hours, and we often lost contact with the monkeys if they ascended cliffs outside of the range of visibility or human climbing. Owing to comparatively lush monsoon vegetation, the proportion of B troop individuals that we could see per scan (25.8%, or 14.2±1.1 individuals) was lower than that of F troop.

We generally conducted observations by naked eye or through binoculars, though a spotting scope facilitated observations when they used cliff habitats. We recorded general activity (feed, travel, rest, rest-huddle, rest-cling, groom, play, and miscellaneous social behavior) by scan sampling at 20-min intervals (Altmann 1974). We recorded activity for each visible individual at the moment we first observed it during scans. We also noted age and sex for each individual when possible. For each individual that was feeding during scans, we recorded the food species and plant part. The method unfortunately biases observations in favor of items that are more likely to be observable in the Himalayan environment (Curtin 1982). At Langtang, observations may have been biased toward arboreal feeding and terrestrial feeding in field habitats, and against terrestrial feeding in oak forest, scrub, and high scrub habitats, e.g., herbaceous plants, due to poor visibility.

We estimated daily path lengths via global positioning system (GPS) point-to-point sampling. For travel that we could not record with the unit, such as vertical movement on cliff faces, we estimated distance to the nearest 10 m. GPS checks on flat or slightly sloping ground suggests our distance estimations were accurate to ≤10 m for distances of ≤100 m.

Classification of Dietary Items

We often distinguished plant parts based on information in field guides on the flora of the region (Polunin and Stainton 1997; Stainton 1997). We categorized broad leaves as mature or young (based on size, color, and texture), bud (generally dormant winter buds), or petiole, and separated them *post hoc* into deciduous and evergreen. We categorized fruit as ripe or unripe based on color and size, or state of dehiscence, and noted the portion(s) of the fruit eaten. We considered unopened flowers as flower buds.

We classified underground storage organs as soft (mainly tubers) or hard (mainly woody roots). We used the miscellaneous category if we could not allocate underground resources to a more specific category. Herbaceous plant parts include herb leaves, herb fruits, herb flowers, young fern furled tops, and epiphytic fern rhizomes. We labeled coniferous vegetation as needle or cone only. Other plant parts and food items include bark, young bamboo shoots, mosses and lichens, grass blades, mushrooms, invertebrates, and earth (rock-licking).

Phenology

Sayers conducted phenological samples on 19 occasions in 9 plots (total area= 0.75 ha) during 2003. Sampling took place on the first or 15th of each month, or both, for 19 2-week sampling periods. We established 3 16.5×50 m plots in coniferous forest, 1 in forest of *Quercus semecarpofolia*, 3 in scrub (3100 m–3200 m), and 2 in high scrub (>3200 m; Fig. 2, Table I); we did not sample field and cliff habitats. We measured all trees, shrubs, and climbers with diameter-at-breast height of ≥10 cm. We collected voucher specimens from each species, and plant scientists at the Central Department of Botany, Tribhuvan University, Kathmandu, Nepal later identified them.

For broad-leaved species, we estimated abundance of mature leaves, young leaves, leaf buds, ripe fruit, unripe fruit, flower buds, and flowers, relative to maximum crown volume, for each species in each plot on a 0–5 scale in increments of 0.5 (modified from Dasilva 1994). A score of 5 indicates that the plant part occurs in all parts of the crown, and covers all visible portions of it. In practice this makes 5 the highest

Table I Phenological sample

Genus	Species	Type	Basal area	Part(s) eaten	% of diet (F troop)
Cotoneaster	*frigidus*	D	13.45	Bark, fruit, leaf, leaf bud	22.0
Berberis	*aristata*	D	11.64	Fruit, leaf, root	3.9
Elsholtzia	*fruticosa*	D	9.78	Flower, root	0.2
Caragana	*gerardiana*	D	8.83	Root, seed[a]	7.3
Tsuga	*dumosa*	C	6.49	Bark, cone, needle	0.3
Sorbus	*cuspidata*	D	5.91	Bark, fruit, leaf bud	6.9
Quercus	*semecarpifolia*	E	4.86	Leaf[b]	0.1
Rhododendron	*arboreum*	E	3.56		
Abies	*spectabilis*	C	3.13		
Zanthoxylum	*nepalense*	D	2.93	Bark, flower, leaf	13.8
Ribes	sp.	D	2.77	Leaf, leaf bud	0.2
Hippophae	*rhamnoides*	D	2.36	Fruit, leaf, leaf bud	6.3
Ilex	*dipyrena*	E	1.58	Leaf, petiole	0.4
Viburnum	*cotinifolium*	D	0.96	Leaf bud[c]	0.2
Acanthopanax	*cissifolius*	D	0.94		
Salix	*tetrasperma*	D	0.53	Flower, leaf, leaf bud	1.4
Cotoneaster	*acuminatus*	D	0.51	Fruit, leaf, leaf bud	0.3
Rhododendron	*barbatum*	E	0.50		
Jasminum	*humile*	D	0.33	Bark, fruit, leaf, leaf bud	6.7
Rosa	*macrophylla*	D	0.21	Fruit, leaf	1.3
Viburnum	*erubescens*	D	0.19	Leaf	0.2
Unidentified		D	0.18		
Unidentified		D	0.16	Fruit, leaf, leaf bud	1.7
Rosa	*sericea*	D	0.14	Fruit, leaf, leaf bud	1.6
Aster	*albescens*	D	0.12		
Betula	*utilis*	D	0.10		
Acer	*caudatum*	D	0.08		
Viburnum	*nervosum*	D	0.08		
Neillia	*thrysiflora*	D	0.05		
Rabdosia	sp.	D	0.05		
Pieris	*formosa*	E	0.04		
Larix	*himalaica*	C	0.02		
Rubus	sp.	D	0.01	Leaf	0.1
Clematis	*acuminata*	D	0.01		
Sum					74.9

Basal areas are given in m^2 per hectare across all plots. D = Broad-leaved deciduous, E = broad-leaved evergreen, C = coniferous

[a] Flower B troop consumed in monsoon.

[b] Seed B troop consumed in monsoon.

[c] Fruit B troop consumed in monsoon.

possible combined score for vegetative structures (mature leaves, young leaves, leaf buds) and reproductive structures (fruits and flowers). Because reproductive structures generally do not occur entirely throughout the crown, scores for the plant parts rarely approached the maximum value, which allows for estimation of absolute abundance of plant parts, and also allows for comparison between different plant part groups. We also divided broad-leaves *post hoc* into 2 groups: evergreen and deciduous. Thus, the plant parts for the species comprise evergreen mature leaves, evergreen young leaves, deciduous mature leaves, deciduous young leaves, leaf buds, ripe fruit, unripe fruit, flower buds, and flowers. Via the same sampling strategy, we measured the abundance of 2 plant parts on conifers, needles, and cones.

We calculated species-specific contribution to forest production via:

$$W_i = \left(\sum A_i \Big/ n_i\right) {}^{*} B_i$$

wherein W_i is the weighted abundance of a plant part, A_i is the phenological score, n_i is the number of individuals, and B_i is the basal area per hectare in square meters, all for species i (modified from Dasilva 1994). We summed totals for all species, and each plant part, for estimates of overall vegetation abundance.

Data Analysis

Our analyses are limited to data from F troop, though we provide the monsoon diet and path lengths of B troop for comparison. Unless stated otherwise, all behavioral data reflect observations of all visible F group members irrespective of age-sex class. A sampling period consisted of the day of phenological sampling and the 2-wk period thereafter, and 11 sampling periods corresponded with feeding data for F troop. We calculated Spearman rank correlation coefficients between the abundance score and the percentage contribution of a plant part to diet during a given sampling period. Correlations between the abundance and consumption of specific plant parts have been used to assess large-scale preferences in other primates (Dasilva 1994). Many such correlations are not meaningful in the sense of langur food preference, because Langtang subjects take some resources that are available year-round only in some seasons. Accordingly, we compare only the consumption of evergreen mature leaves and bark, 2 largely nonseasonal resources, with the abundance and consumption of other plant parts. We used Spearman correlations to identify the potential relationship between overall vegetation abundance and feeding budgets.

We used Kruskal-Wallis to test for seasonal differences in daily path lengths ($n=84$) for winter, spring, monsoon, and fall. To examine the relationship between travel distance and diet when controlling for vegetation abundance, we performed stepwise multiple regression with daily path length and summed phenological scores for individual days ($n=76$) as independent variables, and log transformed the percentages of food types ingested on the days as the dependent variable. We performed regressions separately for each food type. To avoid taking the natural log of zero for days when subjects did not eat a certain food type, we added a constant of 0.001 to each daily dietary percentage before log transformation. Sensitivity analysis with constants 0.01 and 0.0001 did not alter inclusion or exclusion of variables. Unless stated otherwise, analyses are 2-tailed and the level of significance is 0.05. We performed statistical analyses via SPSS 13.0 and Sigmaplot 8.0.

Results

Activity Patterns

The adult activity budget for F troop, based on 3379 records wherein we established age-sex identification, includes feeding (39.8%), travel (17.5%), resting (29.2%), huddling (3.2%), grooming (9.5%), and miscellaneous social behavior (0.9%). There is a significant negative correlation between estimates of total vegetation abundance and frequency of feeding records ($n=11$, Spearman, $r=0.96$, $p<0.001$).

Plant Production

The 34 woody plant species in the phenological sample accounted for 74.9% of langur diet (Table I). Conifers bore needles and cones throughout the year with little variation in abundance. Evergreen young leaves appeared only during a brief period of leaf turnover during the early monsoon (June–August). Broad-leaved species, particularly vegetative structures, had marked seasonality in plant production (Fig. 4). Considering all plots, broad-leaved deciduous plants were most abundant by basal area, and deciduous leaf portions were the most abundant plant parts for all seasons except winter. The availability of young deciduous leaves peaked in June, but by July most of them were mature. Leaf buds were available mainly in winter and spring.

Reproductive plant parts, with abundance scores consistently lower than vegetative parts, also varied seasonally in abundance (Fig. 5). Flowers had 2 peaks in abundance, the first in monsoon and the second in fall. Though spring flowering occurred in several species, monsoon flowering was characteristic of most plants in the sample. Unripe fruit was available mostly in monsoon and fall (June–November) with a peak in September. Ripe fruit, while available from August to April, was most abundant in late fall and winter (October–February).

Diet

Members of F troop fed on plant foods from ≥30 families, 39 genera, and 43 species. More than half (57.1%) of the 9-mo sample from F troop (March–May 2003, September 2003–February 2004: $n=9895$ feeding records) comprised leaf parts (Table II), including deciduous mature leaves, leaf buds, deciduous young leaves, evergreen mature leaves, herb leaves, unidentified leaves, coniferous needles, and evergreen mature leaf petioles. Ripe, unripe, and herbaceous fruit constituted 22.4%

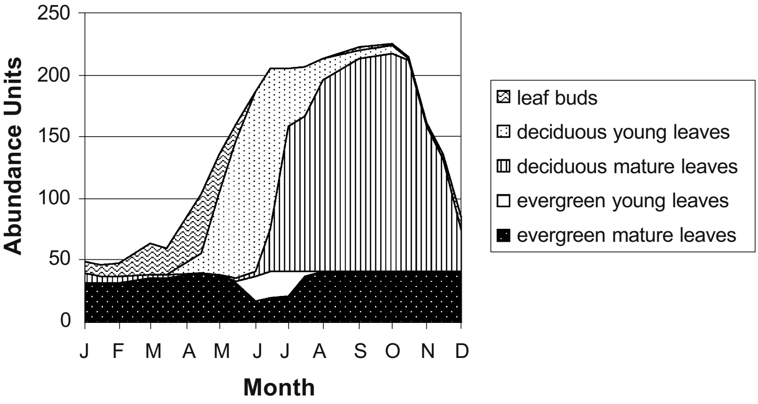

Fig. 4 Abundance of broad-leaved vegetative structures at Langtang as determined via phenological analysis.

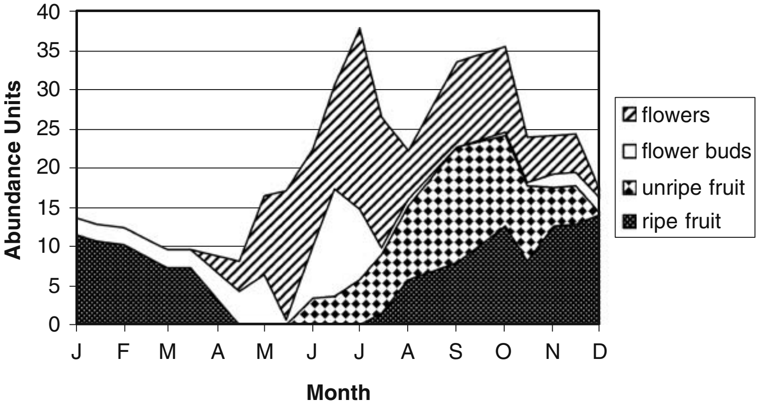

Fig. 5 Abundance of reproductive structures at Langtang as determined via phenological analysis.

of the total, with seeds representing an average of 7.3% of monthly records. Underground foods made up 7.7% of the diet, with 5.3% soft underground storage organs, and the rest miscellaneous underground resources and hard or woody underground storage organs. Flower parts, including flowers, herbaceous flowers, and flower buds, contributed 6.9% to the diet, and bark was 5.4%. Other items included mosses and lichens, coniferous cones, epiphytic fern rhizomes, grass, young bamboo shoots, suspected invertebrates, and earth (rock-licking). The top 10 items in the 9-mo sample constituted 58.5% of total feeding records (Table III).

Insectivory was limited to 1 case of suspected arthropod foraging (*sensu* Struhsaker 1978) during a winter scan and 1 case of a langur catching and consuming a grasshopper during fall nonscan sampling *ad libitum*.

Seasonal Diet

Winter (December–March) had the lowest scores for total vegetation abundance. The majority of the langur diet comprised leaf buds, particularly from *Cotoneaster frigidus* and *Sorbus cuspidata*, and ripe fruit, e.g., *Berberis aristata* and *Cotoneaster frigidus* (Table IV). Likely fallback foods include evergreen mature leaves (especially *Gaultheria* sp.). The resource is available all year, but the langurs regularly exploited it only in winter. Subjects took bark from ≥5 woody plant species.

Spring (April–May) showed the first leaf flush and deciduous young leaves made up much of the diet. The langurs foraged young-leaf clusters of *Zanthoxylum nepalense*, which was by far the most important spring food item, followed distantly by the young leaves of *Jasminum humile*. Bark continued to be a relatively important resource, making up approximately the same proportion of the diet in spring as it did in winter (Table IV). However, it was limited to 1 species: the green bark of *Jasminum humile* (136 of 140 bark feeding records).

Monsoon (June–September) marked the reduced availability of deciduous young leaves, a brief period of evergreen young leaf availability, and the flowering and fruiting of numerous plant species. F-troop data for the season are limited to September, when deciduous mature leaves were the majority of the diet, followed by

Table II Monthly percentages and 9-mo averages of feeding records for 12 food types

	Deciduous mature leaves	Leaf buds	Ripe fruit	Deciduous young leaves	Unripe fruit	Flowers	Bark	Soft USOs	Evergreen mature leaves	Herbaceous fruit	Herbaceous leaves	MURs	Other
March	0.0	45.3	3.5	0.0	0.0	0.0	14.0	0.5	19.9	0.0	0.0	14.5	2.3
April	0.0	18.5	0.0	36.7	0.0	27.5	8.4	0.0	0.0	0.0	4.4	3.1	1.2
May	0.0	0.6	0.0	55.2	0.0	31.8	7.5	0.0	0.0	0.0	4.9	0.0	0.0
September	64.4	0.0	9.3	0.0	4.7	0.0	1.1	0.0	0.0	4.2	3.9	0.0	12.9
October	48.4	0.0	5.5	0.0	13.8	1.0	0.1	14.3	0.0	12.3	3.9	0.0	0.7
November	40.7	0.0	20.6	0.0	18.7	0.8	0.6	12.5	0.5	2.3	2.7	< 0.1	0.4
December	33.3	5.1	19.8	0.0	28.8	0.0	0.9	9.0	0.0	1.2	0.0	1.2	0.6
January	0.0	41.7	34.5	0.0	0.0	0.0	7.5	8.6	3.9	0.9	0.0	0.0	2.9
February	0.0	62.6	9.8	0.0	0.0	0.0	7.9	2.4	15.1	0.2	0.0	0.0	2.1
9-mo average (F troop)	20.8	19.3	11.4	10.2	7.3	6.8	5.4	5.3	4.4	2.3	2.1	2.1	2.6

USO = Underground storage organ; MUR = miscellaneous underground resource.

Table III Top 10 food items in the Langtang Himalayan langur diet, listed by average monthly percentage of feeding records from the 9-mo sample

Family	Genus	Species	Part eaten	Season(s)	% of diet (F troop)
Rosaceae	*Cotoneaster*	*frigidus*	Deciduous mature leaf	W, M, F	12.6
Rutaceae	*Zanthoxylum*	*nepalense*	Deciduous young leaf and flower	S	10.8
Leguminosae	*Caragana*	*gerardiana*	Seed	M, F, W	7.3
Rosaceae	*Cotoneaster*	*frigidus*	Leaf bud	W	6.6
Oleaceae	*Jasminum*	*humile*	Bark	W, S	4.0
Rosaceae	*Sorbus*	*cuspidata*	Leaf bud	W	3.9
Ericaceae	*Gaultheria*	sp.	Evergreen mature leaf	W	3.8
Berberidaceae	*Berberis*	*aristata*	Ripe fruit	W, F	3.4
Elaeagnaceae	*Hippophae*	*rhamnoides*	Deciduous mature leaf	M, F	3.1
Elaeagnaceae	*Hippophae*	*rhamnoides*	Leaf bud	W	3.0
Total					58.5

The plant part was included in a season if it contributed >1.0% of records. W = Winter; S = spring; M = monsoon; F = fall; USO = underground storage organ.

Table IV Seasonal diets from March 2003 to February 2004: winter (December-March), spring (April–May), monsoon (June–September), and fall (October–November)

	Winter	Spring	Late monsoon	Monsoon (B troop)	Fall
Deciduous mature leaves	8.3	0.0	64.4	36.7	44.6
Deciduous young leaves	0.0	45.9	0.0	23.0	0.0
Evergreen mature leaves	9.8	0.0	0.0	0.1	0.3
Evergreen young leaves	0.0	0.0	0.0	5.1	0.0
Leaf buds	38.6	9.6	0.0	0.0	< 0.1
Ripe fruit	16.9	0.0	9.3	1.3	13.1
Unripe fruit	7.2	0.0	4.7	15.8	16.3
Flowers	0.0	29.7	0.0	9.5	0.9
Soft underground storage organs	5.1	0.0	0.0	0.0	13.4
Bark	7.6	8.0	1.1	0.0	0.4
Herbaceous leaves	0.0	4.7	3.4	4.5	3.3
Herbaceous fruit	0.6	0.0	4.2	0.9	7.3
Miscellaneous underground resources	3.9	1.6	0.0	0.0	0.0
Other	2.01[a]	0.62[b]	12.93[c]	3.14[d]	0.55[e]

All values reflect average monthly contribution to feeding records. All data are from F troop except unless noted otherwise.

[a] Hard and/or woody underground storage organs (0.8%), mosses or lichens (0.8%), unclassified leaves (0.1%), coniferous needles (0.1%), evergreen mature leaf petioles (0.1%), grass blades (0.1%), and suspected invertebrates (< 0.1%).

[b] Unclassified leaves (0.3%), epiphytic fern rhizomes (0.1%), flower buds (0.1%), and mosses or lichens (< 0.1%).

[c] Unidentified fruit (11.4%), coniferous needles (0.7%), and coniferous cones (0.7%).

[d] Young bamboo shoots (1.8%), unidentified fruit (0.7%), fern furled tops (0.3%), herb flowers (0.2%), and mushrooms (0.1%)

[e] Herb flowers (0.4%), young bamboo shoots (0.1%), hard and/or woody underground storage organs (0.1%), and rock licking (< 0.1%)

fruit. We collected observations from B troop in all months during the monsoon (Table IV).

Fall (October–November) showed a decrease in overall plant part availability as deciduous leaf drop began. Deciduous mature leaves were the main dietary component for F troop, with *Cotoneaster frigidus* and *Zanthoxylum nepalense* the primary species exploited. Subjects frequently consumed unripe fruit, particularly legume seeds (husks discarded) of *Caragana gerardiana*, and an assortment of fleshy ripe fruits. However, perhaps the most striking aspect of the fall diet was the inclusion of soft underground storage organs, herb fruits, and herb leaves. Subjects extensively used potatoes (*Solanum tuberosum*) from cultivated fields and radishes (*Raphanus sativus*).

Food Selection

Positive correlations between consumption and abundance are strongest ($p<0.001$) for deciduous mature leaves (Table V). There are also significant positive correlations ($p<0.05$) for leaf buds, flowers, deciduous young leaves, and ripe fruit. There is no significant positive correlation for coniferous needles, unripe fruit, or evergreen mature leaves. Subjects did not exploit coniferous cones and flower buds

Table V Spearman rank correlation coefficients comparing consumption (F troop) and abundance of plant part groups

	Consumption								
Abundance	Deciduous mature leaves	Deciduous young leaves	Evergreen mature leaves	Leaf buds	Ripe fruit	Unripe fruit	Flowers	Coniferous needles	Bark
Deciduous mature leaves	0.98**	–0.67*	–0.15	–0.74**	0.42	0.73*	–0.11	–0.2	–0.86**
Deciduous young leaves	–0.22	0.69*	–0.63*	–0.23	–0.78**	–0.2	0.9**	–0.05	0.12
Evergreen mature leaves	0.64*	–0.09	–0.74**	–0.80**	–0.12	0.86**	0.35	–0.26	–0.71*
Leaf buds	–0.95**	0.66*	0.01	0.72*	–0.49	–0.58	0.1	0.2	0.82**
Ripe fruit	0.77**	–0.67*	0.01	–0.51	0.63*	0.78**	–0.46	–0.25	–0.77**
Unripe fruit	0.86*	–0.35	–0.38	–0.83**	0.09	0.58	0.25	–0.23	–0.8**
Flowers	0.44	0.33	–0.79**	–0.84**	–0.32	0.42	0.70*	–0.36	–0.62*
Flower buds	–0.99**	0.68*	0.17	0.72*	–0.45	–0.74**	0.14	0.25	0.88**
Coniferous needles	0.03	0.69*	–0.87**	–0.59	–0.53	0.2	0.9**	–0.36	–0.3
Coniferous cones	–0.63*	0.08	0.67*	0.84**	–0.09	–0.91**	–0.33	0.37	0.74**
Overall vegetation	0.58	0.08	–0.73*	–0.85**	–0.27	0.58	0.59	–0.3	–0.65*

*$p<0.05$, **$p<0.01$. See text for details

during any phenological sampling period, and evergreen young leaves were not available during observations of F troop.

Evergreen mature leaf consumption correlates negatively with flower consumption and abundance, herb leaf consumption, deciduous young leaf abundance, and total vegetation abundance (Table VI). Bark-feeding correlates negatively with deciduous mature leaf consumption and abundance, unripe fruit consumption and abundance, ripe fruit abundance, soft underground storage organ consumption, herb fruit consumption, evergreen mature leaf abundance, flower abundance, and total vegetation abundance.

Daily Path Lengths

Using mean values for each month ($n=9$), the average daily path length for Himalayan langurs is 1.50±1.00 km. Daily paths lengths differed significantly among seasons (Kruskal-Wallis, $p<0.001$), with the longest in winter and the shortest in monsoon and spring (Fig. 6). Fall values were intermediate between them and winter.

Daily path length relates positively to consumption of soft underground storage organs, unripe fruit, ripe fruit, deciduous mature leaves, and herbaceous fruit in the stepwise regression model (Table VII). Conversely, daily path length relates negatively to the consumption of deciduous young leaves, flowers, and bark. Overall vegetation abundance contributed significantly to all of the models except ripe fruit, flowers, and deciduous young leaves. Abundance was the only independent variable included in the models for evergreen mature leaves, leaf buds, herb leaves, and miscellaneous underground resources.

Table VI Spearman rank correlation coefficients between evergreen mature leaf and bark consumption and the consumption of other plant part groups (F troop)

Consumption	Evergreen mature leaf consumption	Bark consumption
Deciduous mature leaves	–0.17	–0.90**
Deciduous young leaves	–0.47	0.36
Evergreen mature leaves	——	0.40
Leaf buds	0.52	0.84**
Ripe fruit	0.54	–0.41
Unripe fruit	–0.42	–0.74**
Flowers	–0.63*	–0.02
Coniferous needles	0.32	0.50
Bark	0.40	——
Soft underground storage organs	–0.28	–0.76**
Herbaceous fruit	–0.49	–0.87**
Herbaceous leaves	–0.66*	–0.14
Miscellaneous underground resources	0.63*	0.78**

*$p<0.05$; **$p<0.01$.

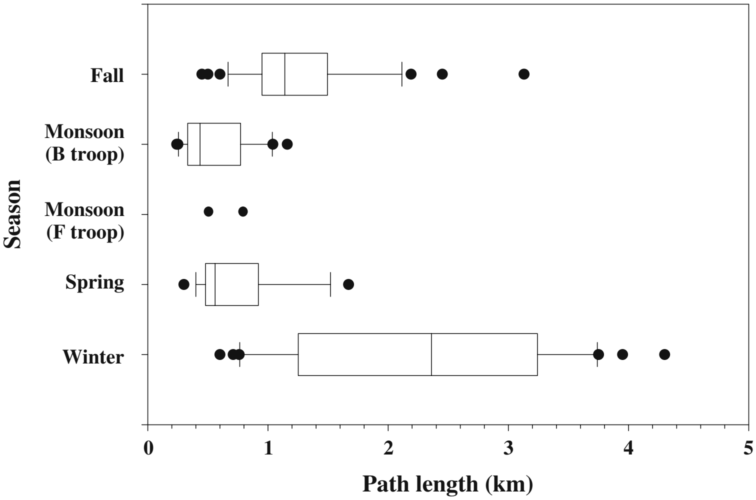

Fig. 6 Seasonal daily paths for Himalayan langurs at Langtang. Box: median with 25th and 75th percent confidence intervals. Whiskers: 10th and 90th percent confidence intervals. All data are from F troop unless noted otherwise. Solid circles represent outliers on box plots, data points for F troop monsoon.

Discussion

Researchers have examined the foraging behavior of *Semnopithecus entellus* (*sensu* Brandon-Jones *et al.* 2004) in ≥10 long-term studies from ≥8 sites (Table VIII). Data from the studies substantiate the reputation of the species as generalist feeders. Though the studies represent a wide range of habitats from Sri Lanka to the Himalayas, the overall contribution of primary food types differs surprisingly little; leaf parts range from 45 to 60% of the diet. Supplemental and fallback foods are more variable. Langurs include insects as a primary supplemental resource at lowland sites, but fallback foods in the Himalayas are underground storage organs and bark.

In a recent review, Koenig and Borries (2001, p. 125) noted the positive correlation between consumption and abundance for young leaves, flowers, and fruit in lowland gray langur populations, and suggested they “feed on everything that is available except mature leaves.” The current study fits the pattern if evergreen mature leaves specifically, and several other resources, are substituted as the fallback foods. Himalayan langurs broaden the feeding repertoire of gray langurs by inhabiting an environment so marginal that they ingest deciduous mature leaves whenever they are available. The ability to subsist at least seasonally on nonpreferred foods is likely one reason for the expansive geographical and ecological range of gray langurs, including decidedly marginal habitats such as the Himalayas. Ecological generalism and diversity in feeding techniques characterizes numerous wide-ranging primates, including howlers and macaques (Glander 1981; Nakayama *et al.* 1999). Given the observations, one should view critically recent statements that apes possess greater foraging flexibility than that of monkeys, or that the flexibility allows apes to inhabit environments where monkeys cannot live (Byrne 2001).

Most colobines, while having diverse diets, favor young leaves or seeds or whole fruits over mature leaves, often related to generalizations concerning the chemical

Table VII Stepwise multiple regressions: % daily records on each plant part (log transformed dependent variable) on overall vegetation abundance and daily path length for those days (F troop only, n=76)

Dependent variable	R^2	Predictors	Unstandardized coefficient	Standardized coefficient	Model significance
Deciduous mature leaves	0.536	Constant	–13.278	0.657	0.000
		abundance	0.052	0.259	
		path length	2.607		
Deciduous young leaves	0.120	Constant	–1.652	–0.346	0.002
		path length	–2.916		
Evergreen mature leaves	0.300	Constant	1.691	–0.548	0.000
		abundance	–0.036		
Leaf buds	0.547	Constant	6.703	–0.739	0.000
		abundance	–0.055		
Ripe fruit	0.118	Constant	–4.899	0.344	0.002
		path length	3.230		
Unripe fruit	0.575	Constant	–14.292	0.615	0.000
		abundance	0.045	0.380	
		path length	3.503		
Flowers	0.077	Constant	–1.719	–0.277	0.016
		Path length	–2.345		
Soft underground storage organs	0.315	Constant	–10.723	0.468	0.000
		path length	4.097	0.262	
		abundance	0.018		
Bark	0.259	Constant	3.807	–0.416	0.000
		abundance	–0.028	–0.249	
		path length	–2.104		
Herbaceous leaves	0.127	Constant	–8.028	0.357	0.002
		abundance	0.021		
Herbaceous fruit	0.627	Constant	–13.645	0.744	0.000
		abundance	0.047	0.200	
		path length	1.612		
Miscellaneous underground resources	0.337	Constant	1.775	–0.580	0.000
		abundance	–0.035		

Only significant predictors are given.

attributes of the plant parts in question (Kirkpatrick 1999; Waterman and Kool 1994). Himalayan langurs clearly prefer broad-leaved deciduous leaves, both mature and young, to evergreen mature leaves, because they take the former but not the latter in close relation to their abundance. In colobine dietary studies, the distinction between evergreen and deciduous broad-leaves is often not made, or is not singled out as a factor in diet selection. However, Oates (1977) noted high selection ratios for certain deciduous species that *Colobus guereza* fed upon and suggested it is related to greater amounts of young leaves, retained over a longer period, than in evergreen species. However, a more general rule may be at play, because colonizer plant species, e.g., deciduous woody plants in Langtang National Park, may devote less of their resources to the production of secondary compounds or other antifeedants than noncolonizers do (Cates and Orians 1975; Marsh 1981).

Some Colobinae select seeds more strongly than any other food type, including young leaves (*Colobus satanus*, McKey *et al*. 1981; *C. polykomos*, Dasilva 1994). However, making generalizations about plant part quality in the absence of nutritional data is problematic (Schülke *et al*. 2006). In Himalayan langurs, fruits

Table VIII Comparison of *Semnopithecus entellus* foraging behavior from long-term (≥6 mo) field sites

Site	Habitat	Feed (%)	Avg. path length (m)	L	ML	YL	LB	FR	FL	Primary supplemental resource(s)	Sources[a]
Polonnaruwa (Sri Lanka)	Semideciduous tropical forest			48	21	27		45	7	Earth, insects	1
Dharwar (Mysore, India)	Dry deciduous tropical forest	44[b]	60–1300[c]	>54				>6	13	Soft stalks, bark, insects	2
Kahna (Madhya Pradesh, India)	Moist deciduous forest, meadow	26	1083	49	35	4	11	24	10	Insects, gum	3
Singur (West Bengal, India)	Village, agricultural land	29		54				37	5	Provisioned foods	4
Jodhpur (Rajasthan, India)	Village, semidesert	24		67	39	28		23	7	Provisioned foods	5
Ramnagar (southern Nepal)	Semievergreen sal forest	34		58	47	14		20	8	Insects	6
Junbesi (northern Nepal)	Himalayan	39	1179[d]	>45	>31	>14		>1		crops, USOs, bark	7
Langtang (northern Nepal)	Himalayan	40	1497	57	25[e]	12[f]	19	22[g]	7[h]	USOs including crop species, bark	8

Feed = Percentage of diurnal activity devoted to feeding, L = all leaves, ML = mature leaves, YL = young leaves, LB = leaf buds, FR = fruit and seeds, FL = flowers.

[a] 1. Hladik 1977 (Fig. 4 and text pp. 337–338); 2. Yoshiba 1967 (Table 5 and text pp. 136 and 140); 3. Newton 1992 (Tables I, II and III); 4. Oppenheimer 1978 (text p. 337); 5. Srivastava 1989, cited in Newton 1992 (Table VI); feeding % from Winkler 1988; 6. Koenig and Borries 2001 (Table 1); here averaged from Podzuweit 1994, Chalise 1995, and Nikolei unpublished data; 7. Curtin 1975 (Table 21 and text p. 61), Curtin 1982 (Table III); 8. this study.

[b] Based on 10 d of focal sampling.

[c] Range. Mode listed as 300–700 m.

[d] Mean of 4 3-mo averages from January to December 1973. For reasons given in Curtin (1975, 1982), it is likely an underestimate of path length.

[e] Includes mature broadleaves, broadleaf petioles, coniferous needles, and unidentified leaves.

[f] Includes young broadleaves and herbaceous leaves.

[g] Includes fruit from woody species as well as herbaceous fruit.

[h] Includes flowers from woody species as well as herbaceous flowers.

and seeds are clearly important seasonal foods. However, given that deciduous leaves, ripe fruits, flowers, and leaf buds peaked in availability at different times of year, and subjects consumed them in relation to their abundance, it is difficult to argue for gross preferences of one type over another.

Himalayan langur daily path lengths varied considerably over the course of the study, and we found this to be related to season and the proportion of certain foods that subjects consumed. When controlling for overall vegetation abundance, the langurs traveled longer distances on days when they consumed soft underground storage organs, fruits, and deciduous mature leaves at higher rates.

Daily paths were shorter when langurs exploited deciduous young leaves, flowers, and bark. Deciduous young leaves are abundant in spring, and we often observed the langurs then spending the entire day feeding from trees and shrubs within a single gully. The negative relationship between flower consumption and daily path is likely related to the spring exploitation of *Zanthoxylum nepalense*, the flowers of which langurs consumed along with its young leaves. These findings accord with Curtin's (1975) observation that Himalayan langurs at Junbesi, Nepal traveled further in the winter when meadow feeding on fruits, particularly *Cotoneaster microphyllus*, was especially important. Kirkpatrick (2007) noted similar relationships between diet and ranging patterns for lowland gray langurs and several other Asian colobines. *Semnopithecus entellus* at Kahna Tiger Reserve, India, had smaller ranges and traveled less when banqueting on mature leaves (Newton 1992). Travel distances in capped langurs (*Trachypithecus pileatus*) in Madhupar National Park, Bangladesh relate positively to fruit consumption and negatively to mature leaf feeding (Stanford 1991). Similar trends occur in banded (*Presbytis melalophos*) and maroon leaf monkeys (*P. rubicunda*) (Bennett 1986; Davies 1984, cited in Kirkpatrick 2007).

However, as Newton (1992) noted, there is a danger in making broad generalizations about the consumption of leaves and its influence on primate socioecology. The common practice of labeling leaves as a ubiquitous or nonpatchy resource is an example. Though deciduous mature leaves are relatively abundant during monsoon and early fall at Langtang, they are increasingly less available in the months that follow. Indeed, it could be argued that in late fall and winter, deciduous mature leaves are a resource more patchily distributed than ripe fruits are at many subtropical or tropical primate field sites. This may account for why, when overall vegetation abundance is controlled for, deciduous mature leaf consumption actually relates positively to daily path length in Himalayan langurs. Thus, while using broadly defined plant categories as a correlate to ranging behavior or competitive regime is a necessary step in first-generation models of primate socioecology (Isbell 1991; Sterck *et al*. 1997; Wrangham 1980), future workers will need to incorporate the idea that under certain circumstances many foodstuffs, even leaf parts, can be a rare resource, e.g., mature leaves for *Colobus satanas* (McKey and Waterman 1982) and young leaves for *Procolobus badius* (Snaith and Chapman 2005). This can lead to activity budgets similar to those of nonfolivores. Indeed, in Himalayan and other gray langurs, the amount of time devoted to feeding and travel, and the distance traveled in a given day (Table VIII), overlap those of highly frugivorous spider monkeys (Suarez, 2006). One must view the stereotype of the lazy leaf-eater with caution.

Acknowledgments We thank L. S. B Leakey Foundation and Kent State University School of Biomedical Sciences for their financial support. Ram Rimal and Ranger Ming Mav Chhewang Tamang provided invaluable field assistance, and the Langtang National Park staff provided welcome aid and encouragement. Achyut Ahdikari waded through botanical minutiae, Nina Jablonski and Mukesh Chalise offered advice on Nepalese fieldwork, and Ryan Seltzer helped with data analysis. We also thank Daniel Taylor-Ide and Robert Fleming, Jr. for their assistance in the selection of Langtang as a Himalayan langur field site, Himalayan Glacier Trekking and Cemat Water Lab for handling logistics, and Dindu Lama and family for everything else. We conducted this research in conjunction with the Nepal Ministry of Forests and Soil Conservation and Department of National Parks and Wildlife Conservation.

References

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227–267.

Astrom, M., Lundberg, P., & Danell, K. (1990). Partial prey consumption by browsers: Trees as patches. *Journal of Animal Ecology*, *59*, 287–300.

Bennett, E. L. (1986). Environmental correlates of ranging behavior in the banded langur, *Presbytis melalophos*. *Folia Primatologica*, *47*, 26–38.

Bishop, N. H. (1975). *Social Behavior of Langur Monkeys* (*Presbytis entellus*) *in a High Altitude Environment*. Ph.D. Dissertation, University of California at Berkeley, Berkeley, CA.

Bishop, N. H. (1977). Langurs living at high altitudes. *Journal of the Bombay Natural History Society*, *74*, 518–520.

Bishop, N. H. (1979). Himalayan langurs: Temperate colobines. *Journal of Human Evolution*, *8*, 251–281.

Bishop, J. M., & Bishop, N. H. (1978). *An Ever-changing Place*. New York: Simon and Schuster.

Boggess, J. (1976). *Social Behavior of the Himalayan Langur* (*Presbytis entellus*) *in Eastern Nepal*. Ph.D. Dissertation, University of California at Berkeley, Berkeley, CA.

Boggess, J. (1980). Intermale relations and troop male membership changes in langurs (*Presbytis entellus*) in Nepal. *International Journal of Primatology*, *1*, 233–274.

Brandon-Jones, D. (2004). A taxonomic revision of the langurs and leaf monkeys (Primates: Colobinae) of South Asia. *Zoos' Print Journal*, *19*, 1552–1594.

Brandon-Jones, D., Eudey, A. A., Geissmann, T., Groves, C. P., Melnick, D. J., Morales, J. C., *et al.* (2004). Asian primate classification. *International Journal of Primatology*, *25*, 97–164.

Byrne, R. W. (2001). Social and technical forms of primate intelligence. In F. de Waal (Ed.), *Tree of Origin: What Primate Behavior Can Tell Us About Human Social Evolution* (pp. 145–172). Harvard Cambridge, MA: University Press.

Cates, R. G., & Orians, G. H. (1975). Sucessional status and the palatability of plants to generalized herbivores. *Ecology*, *56*, 410–418.

Chalise, M. K. (1995). *Comparative Study of Feeding Ecology and Behaviour of Male and Female Langurs* (Presbytis entellus). Ph.D. Thesis, Tribhuvan University, Kathmandu, Nepal.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*, 129–136.

Clutton-Brock, T. H., & Harvey, P. H. (1980). Primates, brains, and ecology. *Journal* of *Zoology*, *190*, 309–323.

Curtin, R. A. (1975). *The Socioecology of the Common Langur*, Presbytis entellus, *in the Nepal Himalaya*. Ph.D. Dissertation, University of California at Berkeley, Berkeley, CA.

Curtin, R. A. (1982). Range use of gray langurs in highland Nepal. *Folia Primatologica*, *38*, 1–18.

Dasilva, G. L. (1994). Diet of *Colobus polykomos* on Tiwai island: Selection of food in relation to its seasonal abundance and nutritional quality. *International Journal of Primatology*, *15*, 655–680.

Davies, A. G. (1984). *An Ecological Study of the Red Leaf Monkey* (Presbytis rubicunda) *in the Dipterocarp Forest of Northern Borneo*. Ph.D. Dissertation, Cambridge University, Cambridge, U.K.

Dolhinow, P. (1972). The north Indian langur. In P. Dolhinow (Ed.), *Primate Patterns* (pp. 181–239). New York: Holt, Rhinehart and Winston.

Glander, K. E. (1981). Feeding patterns in mantled howling monkeys. In A. C. Kamil, & T. D. Sargent (Eds.), *Foraging behavior: ecological, ethological, and psychological approaches* (pp. 231–257). New York: Garland STPM Press.

Green, M. J. B. (1981). A check-list and some notes concerning the mammals of the Langtang National Park, Nepal. *Journal of the Bombay Natural History Society*, *78*, 77–87.

Groves, C. P. (2001). *Primate Taxonomy.* Washington, D.C.: Smithsonian Institution Press.

Hill, W. C. O. (1939). An annotated systematic list of the leaf-monkeys. *Ceylon Journal of Science B*, *21*, 277–305.

Hladik, C. M. (1977). A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In T. H. Clutton-Brock (Ed.), *Primate Ecology* (pp. 333–353). London: Academic Press.

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*, 143–155.

Jay, P. (1963). *The Social Behavior of the Langur Monkey.* Ph.D. Dissertation, University of Chicago, Chicago.

Kirkpatrick, R. C. (1999). Colobine diet and social organization. In P. Dolhinow, & A. Fuentes (Eds.), *The Nonhuman Primates* (pp. 93–105). Mountain View, CA: Mayfield Publishing.

Kirkpatrick, R. C. (2007). The Asian colobines: Diversity among leaf-eating monkeys. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in Perspective* (pp. 186–200). Oxford: Oxford University Press.

Koenig, A., & Borries, C. (2001). Socioecology of hanuman langurs: The story of their success. *Evolutionary Anthropology*, *10*, 122–137.

Marsh, C. W. (1981). Diet choice among red colobus (*Colobus badius rufomitratus*) on the Tana River, Kenya. *Folia Primatologica*, *35*, 147–178.

McKey, D., Gartlan, J. S., Waterman, P. G., & Choo, G. M. (1981). Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biological Journal of the Linnean Society*, *16*, 115–146.

McKey, D., & Waterman, P. G. (1982). Ranging behaviour of a group of black colobus (*Colobus satanas*) in Douala-Edea Reserve, Cameroon. *Folia Primatologica*, *39*, 264–304.

Nakayama, Y. G. S., Matsuoka, S. G. S., & Watanuki, Y. G. S. (1999). Feeding rates and energy deficits of juvenile and adult Japanese monkeys in a cool temperate area with snow coverage. *Ecological Research*, *14*, 291–301.

Napier, P. H. (1985). *Catalogue of Primates in the British Museum (Natural History) and elsewhere in the British Isles Part III: Family Cercopithecidae, Subfamily Colobinae*. London: Britsh Museum (Natural History).

Newton, P. (1992). Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). *International Journal of Primatology*, *13*, 245–285.

Oates, J. F. (1977). The guereza and its food. In T. H. Clutton-Brock (Ed.), *Primate Ecology* (pp. 275–321). London: Academic Press.

Oates, J. F. (1987). Food distribution and foraging behavior. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 197–209). Chicago: The University of Chicago Press.

Oppenheimer, J. R. (1977). *Presbytis entellus*, the Hanuman langur. In H. S. H. Prince Rainier III, & G. H. Bourne (Eds.), *Primate Conservation* (pp. 469–512). New York: Academic Press.

Oppenheimer, J. R. (1978). Aspects of the diet of the Hanuman langur. In D. J. Chivers, & J. Herbert (Eds.), *Recent Advances in Primatology. Vol. I: Behaviour* (pp. 337–342). London: Academic Press.

Pocock, R. I. (1928). The langurs, or leaf monkeys, of British India. *Journal of the Bombay Natural History Society*, *32*, 472–504, 660–677.

Podzuweit, D. (1994). *Sozio-ökologie weiblicher Hanuman Languren* (Presbytis entellus) *in Ramnagar, Südnepal*. Ph.D. Dissertation, Göttingen, Cuvillier.

Polunin, O., & Stainton, A. (1997). *Flowers of the Himalaya*. Delhi: Oxford University Press.

Schülke, O., Chalise, M., & Koenig, A. (2006). The importance of ingestion rates for estimating food quality and energy intake. *American Journal of Primatology*, *68*, 951–965.

Snaith, T. V., & Chapman, C. A. (2005). Towards an ecological solution to the folivore paradox: Patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Piliocolobus tephrosceles*). *Behavioral Ecology and Sociobiology*, *59*, 185–190.

Srivastava, A. (1989). *Feeding Ecology and Behaviour of the Hanuman Langur*, Presbytis entellus, Ph.D. Dissertation, University of Jodhpur, Jodhpur.

Stainton, A. (1997). *Flowers of the Himalaya: A Supplement*. Delhi: Oxford University Press.

Stanford, C. B. (1991). *The Capped Langur in Bangladesh: Behavioral Ecology and Reproductive Tactics*. Basel: S. Karger.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory*. Princeton: Princeton University Press.

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*, 291–309.

Struhsaker, T. T. (1978). Interrelations of red colobus monkeys and rain-forest trees in the Kibale Forest, Uganda. In G.G. Montgomery (Ed.), *The Ecology of Arboreal Folivores* (pp. 397–422). Washington, D.C.: Smithsonian Institution Press.

Suarez, S. A. (2006). Diet and travel costs for spider monkeys in a nonseasonal, hyperdiverse environment. *International Journal of Primatology*, *27*, 411–436.

Sugiyama, Y. (1976). Characteristics of the ecology of the Himalayan langurs. *Journal of Human Evolution*, *5*, 249–277.

Vogel, C. (1971). Behavioral differences of *Presbytis entellus* in two different habitats. *Proceedings of the Third International Congress of Primatology*: 41–47.

Waterman, P. G., & Kool, K. M. (1994). Colobine food selection and plant chemistry. In A. G. Davies, & J. F. Oates (Eds.), *Colobine Monkeys: Their Ecology, Behaviour, and Evolution* (pp. 251–284). Cambridge, U.K.: Cambridge University Press.

Winkler, P. (1988). Feeding behavior of a food-enhanced troop of Hanuman langurs (*Presbytis entellus*) in Jodhpur, India. In J. E. Fa, & C. H. Southwick (Eds.), *Ecology and Behavior of Food-enhanced Primate Groups* (pp. 3–24). New York: Alan R. Liss.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*, 262–300.

Yoshiba, K. (1967). An ecological study of Hanuman langurs, *Presbytis entellus*. *Primates*, *8*, 127–154.