SEASONAL AND HABITAT-RELATED DIETS OF SLOTH BEARS IN NEPAL

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Most bears are opportunistic omnivores; their diets consist of fruits, other vegetative material, and in lesser amounts, mammals, fishes, and insects. Sloth bears (*Melursus ursinus*) are the only species of ursid specifically adapted to feed on insects, especially termites and ants, although they also feed on fruits when available. We studied diets of sloth bears in Royal Chitwan National Park, Nepal, where fruits are available for ca. 4 months (May–August) and access to colonies of termites is reduced in lowlands that are flooded during the fruiting season. We analyzed feces and observed sloth bears foraging to investigate their responses to changes in availability of food. Diets of sloth bears were dominated by insects (>90%), especially termites (≥50%), from September through April, but they relied heavily on fruits from May through August. Seasonal movements between lowland and upland habitats seemed to be prompted mainly by availability of termites. Termites were more dominant in the diets of sloth bears in our study than in a study conducted 20 years ago in Royal Chitwan National Park and in studies in India. The dietary shift of sloth bears in Royal Chitwan National Park may have been related to changes in habitat conditions associated with relocation of people out of the Park. It appears that sloth bears, like other bears but unlike other myrmecophagous mammals, can adapt their diet to changing food conditions.

Key words: *Melursus ursinus,* sloth bear, diet, foraging observations, myrmecophagous, Nepal, point sampling fecal analysis

All species of bears, except polar bears (*Ursus maritimus*), feed on insects, especially ants. Although insects may comprise >40% of the diet of bears in some areas during some seasons (Mattson et al., 1991*b*; Raine and Kansas, 1990), they are usually a small portion of the annual diet: ≤11% in American black bears (*U. americanus*—Eagle and Pelton, 1983; Graber and White, 1983; Grenfell and Brody, 1983; Holcroft and Herrero, 1991; MacHutchon, 1989), ≤10% in brown bears (*U. arctos*—Clevenger et al., 1992; Elgmork and Kaasa, 1992; Mattson et al., 1991*a*; Mertzanis, 1994; Ohdachi and Aoi, 1987), ≤3% in spectacled bears (*Tremarctos ornatus*—Mondolfi, 1989; Peyton, 1980), and ≤1% in Asiatic black bears (*U. thibetanus*—Nozaki et al., 1983; Reid et al., 1991; Schaller, 1970; Schaller et al., 1989). Little is known of the diet of sun bears (*Helarctos malayanus*), which may consume more insects (especially bees and termites) than Asiatic black bears, but they are still predominantly frugivorous (Kunkun, 1985; Lekagul and McNeely, 1977). In contrast, insects are a staple of sloth bears (*Melursus ursinus*—Laurie and Seidensticker, 1977; Schaller, 1967). Among the ursids, only sloth bears have morphological adaptations for feeding on insects, including absence of the first maxillary incisors, a raised elongated palate, mobile lips, a nearly naked snout, long curved front claws, and a long shaggy coat.

Despite their adaptations for myrmecophagy, results of past studies indicate that diets of sloth bears may vary seasonally and geographically across their range from Nepal south through India and Sri Lanka, depending on availability of fruit and hardness of mounds that harbor colonies of termites (Baskaran, 1990; Davidar, 1983; Eisenberg and Lockhart, 1972; Gokula et al., 1995; Gopal, 1991; Johnsingh, 1981; Laurie and Seidensticker, 1977; Norris, 1969; Schaller, 1967). We found that sloth bears in Royal Chitwan National Park, Nepal, moved seasonally between lowland and upland habitats (Joshi et al., 1995) and hypothesized that changing availability of food prompted these shifts in home range. Our purpose was to test this hypothesis by investigating dietary variation by season and habitat. A second objective was to ascertain if diets of sloth bears in Nepal differed from those in areas further south and also if sloth bears in Royal Chitwan National Park had changed their diet since Laurie and Seidensticker's (1977) study there in 1973–1975, as a consequence of changes in use of land and resulting alterations in habitat that occurred during the past 15–20 years.

MATERIALS AND METHODS

Study area.—Our study was conducted in the 932-km^2 Royal Chitwan National Park in south-central Nepal on the border with India (84°20′E, 27°30′N). Climate was monsoonal; mean monthly rainfall exceeded 10 cm from May to September. However, we defined the wet season as extending from May through November because soils remained saturated and most sloth bears that left flooded lowlands at the start of the monsoon did not return until mid-November (Joshi et al., 1995).

About 30% of the Park was alluvial floodplain with either tall (5–8 m) grass (*Saccharum, Themeda, Narenga,* and *Phragmites*) or riverine forest (*Bombax ceiba, Trewia nudiflora, Litsea monopetala, Acacia catechu,* and *Mallotus philippinensis*). The remainder of the Park was uplands dominated by sal (*Shorea robusta*) forest. Principal fruiting species included *Zizyphus mauritiana, Grewia sclerophylla,* and *Miliusa velutina* in grasslands, and *Murraya koenigii, Coffea bengalensis,* and *Bridellia stipularis* in riverine forests. *Ficus* occurred along riverbeds in the lowlands, and *Cassia fistula, Syzygium cumini,* and *S. jambolana* were in uplands. Although some fruits were available throughout the year, most were ripe May–August (fruiting season). We defined September–April as the nonfruiting season. Termite mounds, which often were 1–2 m tall and nearly as wide at the base, were common in uplands (ca. 17/ha), less common in grasslands (ca. 5/ha), and virtually absent in riverine forest. Conversely, based on the extent of holes dug by sloth bears, underground colonies of termites (without mounds) appeared to be most common in grasslands.

Foraging observations.—We captured and radiocollared sloth bears and monitored them from the back of an elephant (Joshi et al., 1995). We radiotracked each sloth bear about twice a week from February 1990 through November 1993, except during the monsoon, when we located them less frequently but conducted longer (≤12-h) monitoring sessions.

Sloth bears were approached until they were seen, unless the vegetation was too dense. We conducted observations with the aid of binoculars from a distance of 30–50 m and recorded activity, location, and surrounding habitat of the bear. Our presence did not seem to affect their activities. If a sloth bear was seen foraging, we attempted to discern the type of food that it was eating (termites, ants, other insects, fruits, or honey) and recorded if it was taking food from a tree, bush, surface of the ground, digging a hole in the ground, or digging in a termite mound. After a sloth bear left a feeding site, we looked for uneaten food items, collected samples, and recorded other pertinent data (e.g., amount and type of food remaining, reactions of termites and ants). A sample unit was considered a feeding episode, which we defined as a sloth bear feeding on predominantly one type of food at one place (e.g., a single colony of termites, column of ants, bush with fruit).

Analysis of feces.—We systematically searched for and collected feces along three transects, each ca. 8-km long, ca. twice a week (when possible) from April 1991 through March 1993. These routes bisected home ranges of nearly all of our radiocollared sloth bears. One route was in tall grass and riverine forest, the second ran along the ecotone between tall grass and sal forest, and the third was in sal forest. We also collected feces opportunistically at trap sites, feeding or resting sites, and along trails. Feces were soaked in water for 4–6 h, washed through 0.7- and 0.4-mm-mesh sieves, and dried in the sun.

To assess composition of feces, we found it necessary to develop a procedure that would not require separation of innumerable fragments of termites and ants. Most previous studies of food habits of bears separated particles in feces into different types and then quantified composition by dry weights (Baskaran, 1990; Gokula et al, 1995; Ohdachi and Aoi, 1987) or volumes that were assessed either visually (Clevenger et al., 1992; Elgmork and Kaasa, 1992; Graber and White, 1983; Grenfell and Brody, 1983; Mattson et al., 1991*a*; Reid et al., 1991) or by displacement of water (Cicnjak et al., 1987; Holcroft and Herrero, 1991; Landers et al., 1979; Peyton, 1980).

At least two previous studies of food habits of bears used a sampling procedure to analyze feces (Eagle and Pelton, 1983; Hellgren, 1993). They estimated relative density of foods by their frequency of occurrence in random samples drawn from a fecal sample or a composite of feces. Fracker and Brischle (1944) and Johnson (1982) described the mathematical rationale for converting frequency of occurrence to density of particles, and Sparks and Malecheck (1968) found that this conversion corresponded well with actual counts of particles in simulated feces of herbivores. Holechek and Gross (1982) found that if particles from simulated feces were ground to a uniform size and spread uniformly across the observation field, errors associated with food-specific differences in identifiability and fragmentation of the particles had less effect on estimated composition derived from frequency of occurrence than counts of particles. These sources of error were not concerns in our study because we did not grind particles and >99% were identifiable. Moreover, because the particles were different sizes (e.g., heads of insects versus various-sized seeds) and because we sought to estimate relative numbers of different items of food that were consumed, rather than relative weights or volumes of undigested remains, we chose to count particles. However, to increase efficiency, we developed a point-sampling procedure. To our knowledge, this procedure has not been used previously to analyze feces of bears, although an analogous point-sampling technique was used to quantify rumen contents of white-tailed deer (*Odocoileus virginianus*—Chamrad and Box, 1964).

We sprinkled ca. 1 ml of dried material from a fecal sample in a thin layer of nonoverlapping particles on a petri dish that was marked with nine sample points. We used a binocular dissecting scope (45×) to identify the fragment on or closest to each of the nine marked sample points and categorized each sample fragment as head of a termite (which we subdivided into soldier and worker castes), head of an ant, head of an insect other than a termite or ant, part of an insect other than a head (although these generally were small enough to pass through our sieves), seed of a fruit, part of a plant other than a seed, unidentified item, or debris. We saved seeds for later identification. We then discarded the material on the petri dish, extracted more from the same scat, identified nine more fragments, and continued in this manner until 100 fragments of food (i.e., fragments other than debris) were identified or the fecal sample was entirely gone (in which case the smaller number of identified fragments was standardized to 100). For statistical analyses, each fecal sample was considered an independent sample unit.

We used loglinear models (Agresti, 1990) to investigate associations between composition of feces, months, and habitat. Because the two habitats were not intermixed and sloth bears did not routinely move between them, samples found in a given habitat were likely to have been from a sloth bear that had fed there.

When the loglinear model indicated association (significant lack of independence) among variables, we used correspondence analysis to examine these interactions (Dixon et al., 1988). Correspondence analysis reduces a contingency table of interrelated rows and columns to a low-dimensional plot (often two-axis) in which the position of points and distance between them depicts their degree of relatedness in terms of the variables considered (Greenacre, 1984). This procedure is like principal-components analysis, except that data are discrete rather than continuous. Specifically, in our situation, composition of samples was described in terms of the number of times each type of food landed on a point in the petri dish, so each fecal sample was characterized by a frequency distribution among discrete types of food. A distinct advantage of correspondence analysis is that it displays an overlay of two sets of relationships plotted on the same axes (Carroll et al., 1986; Hoffman and Franke, 1986). In our case, we examined dietary relatedness by month and habitat, overlaid with a graphical depiction of the relatedness (degree of co-occurrence) of the different types of food in feces. Thus, distance between two points, each representing a specific month and habitat, indicated dietary similarity, and the proximity of these points to the overlaid set of points representing types of food indicated the relative representations of these foods in the diet for the indicated month and habitat.

Our results could not be compared statistically with those of other studies due to differences in methods, but general comparisons were possible. We computed seasonal and yearly estimates of composition of the diet in our study by combining habitats and averaging monthly values for composition of feces. Schaller (1967) and Johnsingh (1981) analyzed fecal samples of sloth bears, but they reported frequency of occurrence rather than composition. They combined termites and ants into a single group and seeds into another group and observed that feces contained either insects or fruits, but not both. Thus, their data on frequency of occurrence could be equated directly to dietary composition simply by dividing by the number of feces. Laurie and Seidensticker (1977) also presented frequency of occurrence of various types of insects and fruits, but they did not present data for insects and fruits as groups. However, they indicated that 85% of fecal samples contained only one type of food, and the frequency of occurrence for all individual types of food summed to 100%. Thus, we simply collapsed foods into broader categories by summing percentage frequency of occurrence for six types of insects and eight types of fruit that occurred in more than trace amounts. Baskaran (1990) and Gokula et al. (1995) presented both frequency of occurrence and relative dry weights for several types of insects and fruits, but the total frequency of occurrence for all types exceeded 100%, which indicated that scats contained a mixture of different items. Therefore, it was not possible to estimate composition from frequency of occurrence; instead, we used relative dry weights.

TABLE 1.—*Types of food consumed by sloth bears (*Melursus ursinus*) in Royal Chitwan National Park, Nepal, determined from periodic observations (2 times/week) of radiocollared bears foraging during nonfruiting (September–April) and fruiting (May-August) seasons and continuous observations ($\leq$12-h periods) during the fruiting season, 1990–1993.*

Food type	Periodic observation				Continuous observation	
	Nonfruiting season		Fruiting season		Fruiting season	
	n^a	Percent	n^a	Percent	n^a	Percent
Termites	36	59.0	42	40.0	321	45.6
Ants	8	13.1	19	18.1	164	23.3
Other insects	4	6.5	0	0	0	0
Fruits	10	16.4	40	38.1	219	31.1
Honey	3	4.9	4	3.8	0	0
Unidentified	36		60		6	
Total	97		165		710	

[a] Number of episodes in which sloth bears were seen feeding on the indicated food item; episode corresponded to a single feeding site (e.g., termite mound, column of ants, fruit-laden bush).

RESULTS

Foraging observations.—We captured and radiocollared 18 sloth bears. During biweekly monitoring, we observed them feeding at 97 of 1,573 locations during the nonfruiting season and identified the type of food at 61 of these sites. We observed feeding at 165 of 886 locations during the fruiting season and identified the food at 105 sites. We also conducted 78 continuous monitoring sessions on six sloth bears during the fruiting season, during which we made 710 feeding observations and identified the food consumed in all but six of these. Fruits comprised a higher proportion of the food items identified during feeding observations in the fruiting season (biweekly and continuous observations combined due to similarity of results) than the nonfruiting season ($\chi^2 = 6.5$, $d.f. = 1$, $P = 0.01$; Table 1). Sloth bears generally obtained fruit from the ground litter, except *Zizyphus*, which typically was taken off the bush.

Termites (*Macrotermes, Odontotermes, Microcerotermes, Hypotermes*, and *Reticulitermes*) were the most frequently obtained food in both the fruiting and nonfruiting seasons (Table 1). While foraging for termites, sloth bears sniffed along the ground to locate nests, either in mounds or underground colonies, and dug them out with their front claws, periodically sucking in termites and blowing away debris. Sloth bears typically spent 10–15 min foraging on a colony of termites. We observed sloth bears digging termites out of 53 (46%) mounds and 61 underground colonies during the wet season and 8 (18%) mounds and 37 underground colonies during the dry season. The ratio of mounds to underground colonies that were dug by sloth bears was higher during the wet season than the dry season ($\chi^2 = 11.25$, $d.f. = 1$, $P \leq 0.001$).

Ants were the next most commonly identified insect that we observed sloth bears foraging on (Table 1). We observed sloth bears slowly walking and sucking up columns of traveling ants or ants foraging in groups on the surface. Bears also may have obtained ants that invaded and inhabited colonies of termites, but we could not discern this from our observations. Larvae of beetles were the only other insect identified during foraging observations. From September through December, sloth bears uprooted clumps of grass in the alluvium to find these larvae. We also observed sloth bears sucking up items on the surface that we presumed were insects, possibly small groups of ants, but we could not be certain, so we categorized these foods as unidentified (Table 1).

From March through May, we observed seven instances of sloth bears feeding on honeycombs in trees ca. 20 m above the ground. They sucked out the honey for 8–10 min and then, with their snouts covered with red sting marks, apparently were forced to retreat by the swarm of bees.

Analysis of feces.—During the fruiting season, we collected 110 feces from grasslands and riverine forests and 139 from sal forest. During the nonfruiting season, we collected 203 feces from grasslands and riverine forests and 175 from sal forest.

Termites were the most common food in feces during both seasons in both habitats. Overall, 81% of the samples contained termites, 10% contained only termites, and 40% contained ants and termites (Table 2). Ants occurred in 69% of the feces. Other insects in feces included larvae of the beetle *Phyleophaga rugosa*, other beetles, crickets, dragonflies, and centipedes. Insects occurred in >98% of feces from the nonfruiting season and 80% of feces from the fruiting season.

Seeds of fruits occurred in 69% of fecal samples from the fruiting season but only 9% from the nonfruiting season; 30% of feces from the fruiting season contained only seeds and other parts of plants. The most commonly occurring seeds were *Syzygium jambolana*, *Ficus cunia*, *Phoenix acaulis*, and *Grewia sclerophylla*, all of which occurred in ≥10% of feces from the fruiting season (Table 2). *Zizyphus mauritiana*, which fruited December-February, was the only fruit common in feces during the nonfruiting season. Parts of plants other than seeds (leaf or woody particles) occurred in 30% of feces collected during the fruiting-season and 26% of feces collected in the nonfruiting season. These items generally comprised <5% of the particles identified in feces; only nine feces were comprised largely or entirely of leafy or woody fragments, suggesting that this material was typically obtained incidental to the consumption of other foods.

During the nonfruiting season, fecal samples from both habitats were comprised of predominantly termites and secondly ants (Table 3). Although soldier and worker-caste termites occurred in a similar percentage of feces (Table 2), soldiers outnumbered workers ca. 3:1 during both the nonfruiting and fruiting season. During the fruiting season, termites still dominated composition of fecal samples from sal forest, but seeds exceeded ants. In contrast, feces from grasslands and riverine forest during this season contained more seeds than termites or ants (Table 3). In both habitats, the ratio of termites to ants was about twice as high during the fruiting season

TABLE 2.—*Frequency of occurrence of food items in feces of sloth bears from nonfruiting (*n *= 378) and fruiting (*n *= 249) seasons in Royal Chitwan National Park, Nepal, 1990–1993.*

Food item	Nonfruiting season		Fruiting season		Annual	
	n	Percent	*n*	Percent	*n*	Percent
Insects						
Soldier termites	307	81.2	134	53.8	441	70.3
Worker termites	287	75.9	118	47.4	405	64.6
Black ants	245	64.8	89	35.7	334	53.3
Red ants	192	50.8	79	31.7	271	43.2
Other ants	91	24.1	46	18.5	137	21.9
Larvae of beetles	64	16.9	1	0.4	65	10.4
Other insects	92	24.3	34	13.7	126	20.1
Plants						
Bombax ceiba	6	1.6	5	2.0	11	1.8
Cassia fistula	1	0.3	11	4.4	12	1.9
Ficus cuni	1	0.3	35	14.1	36	5.7
Ficus glomerata	1	0.3	7	2.8	8	1.3
Grewia schlerophylla	0	0	25	10.0	25	4.0
Magnifera indica	0	0	4	1.6	4	0.6
Milius velutina	0	0	15	6.0	15	2.4
Murraya koenigii	0	0	3	1.2	3	0.5
Phoenix acaulis	0	0	28	11.2	28	4.5
Syzigium cumini	0	0	10	4.0	10	1.6
Syzigium jambolana	0	0	36	14.5	36	5.7
Zizyphus mauritiana	8	2.1	0	0.0	8	1.3
Fragments of plants	97	25.7	75	30.1	172	27.4
Unidentified	5	1.3	4	1.6	9	1.4
Summary						
Insects	372	98.4	199	79.9	571	91.1
Fruits	34	9.0	172	69.1	206	32.9
Ants and termites	219	57.9	34	13.7	253	40.4
Only ants	8	2.1	0	0	8	1.3
Only termites	52	13.8	9	3.6	61	9.7
Only larvae of beetles	30	7.9	0	0	30	4.8
Only fruits	8	2.1	75	30.1	83	13.2

TABLE 3.—*Mean percentage composition of feces of sloth bears collected in Royal Chitwan National Park, Nepal, at different times of year and in different habitats, 1990–1993.*

Type of food	Nonfruiting season		Fruiting season	
	Grassland	Sal forest	Grassland	Sal forest
	(n^a = 203)	(n = 175)	(n = 110)	(n = 139)
Termites	50.0	68.5	35.5	52.7
Ants	24.4	27.7	8.0	12.0
Other insects	19.6	0.9	7.4	3.9
Fragments of plants	2.6	1.5	2.4	5.8
Seeds	3.3	1.3	46.6	25.6
Unidentified	0.1	0.1	0.1	0.2

[a] Total number of scats examined within season and habitat; however, percentage composition was calculated from the mean among months, not the mean among individual scats.

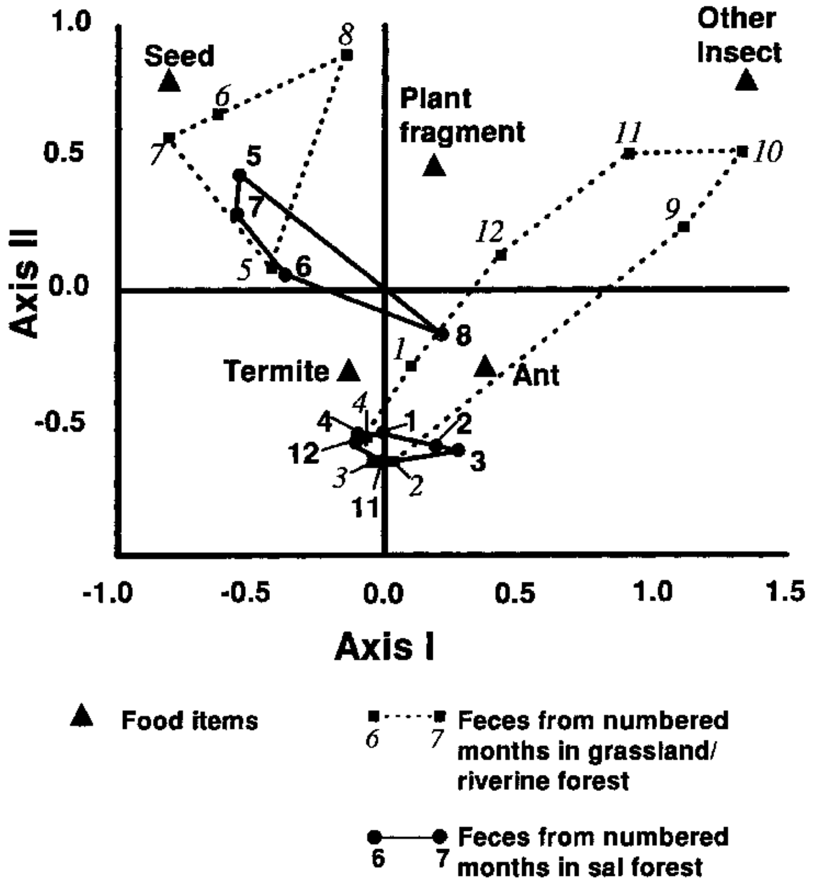

FIG. 1.—Seasonal (fruiting or nonfruiting) and habitat-related (grassland-riverine forest or sal forest) groupings of mean monthly composition of feces of sloth bears from Royal Chitwan National Park, Nepal. Correspondence analysis was used to generate a two-axis plot of chi-square distances (Carroll et al., 1986; Hoffman and Franke, 1986) among five common types of food found in the diet of sloth bears; the distance between these points reflects their degree of co-occurrence in the diet. Monthly composition of feces (indicated by numbered points) were plotted with respect to the same axes. Proximity of monthly points to each of the five types of food indicates the relative representation of these foods in feces from the indicated month and habitat (i.e., points in the upper-left corner represented a diet composed largely of seeds, points in the upper right represented a diet with a high percentage of insects other than termites or ants, etc.).

(4.4:1) as during the nonfruiting season (2–2.5:1; Table 3).

Some of the variation in composition of fecal samples became more apparent when considered on a monthly rather than seasonal basis. Loglinear models ($F = 4.93$, $d.f. = 4,36$, $P < 0.001$) and correspondence analysis (Fig. 1) indicated significant associations among types of food, month, and habitat. In the correspondence analysis, 85% of these associations were explained by the first two principal axes (49% for first axis, 36% for second axis). The summary plot indicated a close association in time (month) and space (habitat) between consumption of termites and ants, and a negative association between these and consumption of fruits or other insects (Fig. 1). Likewise, fruits and other insects were separated widely in the plot, which indicated that sloth bears consumed these food types at different times or in different places.

TABLE 4.—*Comparison of diets of sloth bears based on composition of feces from national parks and wildlife sanctuaries in Nepal and India.*

Location	Time of year	*n* feces	Percentage composition			Reference
			Insects	Fruits	Other	
Nepal						
Royal Chitwan National Park, 1990–1993	Year-round	627	83	14	3	This study
	Fruiting season	249	58	38	4	This study
	Nonfruiting season	378	95	2	3	This study
Royal Chitwan National Park 1973–1975	Year-round	139	52	42	7	Laurie and Seidensticker, 1977
India						
Kanha National Park (central India)	Year-round	92	39	61	0	Schaller, 1967
Bandipur National Park (South India)	Year-round	95	53	37	10	Johnsingh, 1981
Mudumalai Wildlife Sanctuary (South India)	Fruiting season	350	8	90	2	Baskaran, 1990
Mundanthurai Wildlife Sanctuary (South India)	Nonfruiting season	111	75	25	1	Gokula et al., 1995

Fruits were a large component of the diet during May–August in grassland and riverine forest and during May–July in sal forest. Termites and ants became more common in diets of sloth bears in sal forest in August and dominated the diet in this habitat throughout the nonfruiting season (Fig. 1). In grasslands, however, other insects, especially larvae of beetles, constituted a large portion of the diet (37%) during the early part of the nonfruiting season (September–December). No feces were collected from sal forest in September and October, but feces from November and December showed no indication that beetles (<1%) were an important dietary component of sloth bears in that habitat.

Overall, feces of sloth bears in our study appeared to be dominated by insects more than in previous studies with comparable data (Table 4). Results of other studies were similar to ours from just the fruiting season.

DISCUSSION

Other ursids, like black bears and brown bears, exhibit appreciable variation in diet across their geographic ranges. Our objective was to assess variation in diets of sloth bears between seasons and habitats, between Royal Chitwan National Park and other areas, and within Royal Chitwan National Park between the present and past. Seasonal and habitat-related variation in diets was apparent. When fruits ripened, sloth bears included fruits in their diet. When beetle larvae were available in the grasslands, sloth bears consumed large numbers of them. However, our direct observations of foraging by sloth bears (Table 1) and analysis of their feces (Tables 2 and 3) indicated that termites remained their staple throughout the year.

It appears that this reliance on termites was more pronounced in our study than in other studies (Table 4), although our comparisons were obfuscated by differences in methods, presentation of data, and timing of collections of samples. Baskaran (1990) collected feces of sloth bears in a wildlife sanctuary in southern India during March–August, which spanned the main fruiting period. His results showed a relatively high percentage of fruits and correspondingly low percentage of insects compared to our results from the fruiting season (Table 4). Gokula et al. (1995) collected feces in another wildlife sanctuary in southern India during December–March, when most plants were not in fruit, but their results showed substantially more fruits than our results from the nonfruiting season. Johnsingh (1981) in southern India and Schaller (1967) in central India collected feces year-round, although they did not indicate what proportion were found during fruiting versus nonfruiting seasons. Both reported proportions of fruits in feces similar to what we observed during the fruiting season (Table 4). V. Iswariah (in litt.) did not present quantitative data, but she indicated that from June to December sloth bears at a site in southern India depended heavily on fruits, especially cultivated crops; termites were taken only after mounds were softened by monsoon rains. Gopal (1991) also could not quantify diets based on sightings of sloth bears that were foraging, but he concluded that fruits were eaten year-round in central India and were the mainstay of the diet from February to June; termites, ants, and honey were the predominate foods in other months (although he made few observations in these months). Overall, fruits appeared to be more plentiful in the parts of India where sloth bears have been studied than in our study area in Royal Chitwan National Park, Nepal.

Laurie and Seidensticker's (1977) results suggest that fruits may have been more plentiful and thus more prevalent in the diet of sloth bears in Royal Chitwan National Park 20 years before our study. Laurie and Seidensticker's (1977) study was initiated just after Chitwan was designated a national park in 1973. Prior to this, much of the alluvial floodplain was inhabited by people, who cultivated the land and grazed >20,000 head of livestock. In establishing the Park, most of the people were relocated and livestock grazing was prohibited, enabling regrowth of the tall grass, which was maintained by annual burning and cutting (Mishra, 1982; Mishra and Jeffries, 1991). This change in habitat may have prompted an increase in the density of termites or a decrease in fruits, and a concomitant change in the diet of sloth bears. Only one fruit, *Zizyphus mauritiana*, was abundant during winter in Royal Chitwan National Park, when most sloth bears resided in the grasslands and riverine forest (Joshi et al., 1995), and it appears, comparing Laurie and Seidensticker's (1977) data to ours, that sloth bears were more reliant on this fruit in the early 1970s (12% of their diet; referred to then as *Z. jujuba*) than in the early 1990s (1% frequency of occurrence = <1% dietary composition; Table 2). Another alluvial fruit, *Grewia asiatica*, which was ripe during summer and accounted for 13% of the diet of sloth bears in the early 1970s, was not found in feces during our study, nor did we observe it in the wild. *Zizyphus* is a thorny shrub commonly found in habitats degraded by grazing livestock (Champion and Seth, 1968; Puri, 1960), and *G. asiatica* is a tree often associated with cultivated areas (Gupta, 1969), so we suspect that both were more prevalent during the years of Laurie and Seidensticker's (1977) study than during ours.

Because of differences in methods between Laurie and Seidensticker's (1977) study and ours, we cannot definitively attribute apparent dietary shifts to changes in availability of food. Laurie and Seidensticker (1977:194) examined scats of sloth bears "on the spot" during the course of their studies of greater one-horned Indian rhinoceroses (*Rhinoceros unicornis*), tigers (*Panthera tigris*), and leopards (*P. pardus*). It thus seems probable that their fecal analysis was less thorough than ours, possibly explaining why they found more than one type of food in only 15% of the fecal samples that they examined. In contrast, we found multiple foods in 71% of the fecal samples. If they tended to characterize feces by the dominant food and focus on seeds more than exoskeletons of termites or ants, their results could have been skewed toward a higher proportion of fruits. Indeed, their incidental observations of sloth bears that were foraging ($n = 13$ on ants or termites, 9 most likely on insects, and only 6 [ca. 21%] on fruit—Laurie and Seidensticker, 1977) were consistent with our observations of foraging (Table 1) and indicative of a higher reliance on insects than implied by their data from feces.

In contrast to Laurie and Seidensticker (1977), we observed a higher proportion of fruits in foraging observations than in feces. Fecal samples collected during the nonfruiting season contained only 2% seeds (Table 3), but sloth bears consumed fruits during 16% of the foraging episodes that we observed during this season (Table 1). Conversely, fecal analysis and observational results were equivalent (ca. 35% fruits) during the fruiting season.

Feeding observations were an imperfect measure of diet in several respects. 1) These observations reflected only the frequency that sloth bears fed on certain types of food, not the quantity of food consumed. 2) The number of feeding episodes that we recorded was affected by the size of the patch of food, which varied by type of food (e.g., termite mound, group of ants, clump of fruit). 3) Feeding episodes were likely autocorrelated in that during an observation period, sloth bears tended to feed at different clumps of one type of food. 4) Small, dispersed foods, like ants, were more difficult for us to see than large fruits or termite mounds.

Analysis of feces also had shortcomings. In particular, varying numbers of seeds in different kinds of fruit (and possibly varying digestibility) affected representation of fruits in samples. For example, *Zizyphus*, the primary winter fruit, contained only one large seed, so it may have been underrepresented in feces compared to fruits eaten during the fruiting season. If we had obtained data on the number of seeds per fruit, average mass of the fleshy part of each kind of fruit, and mass of termites and ants, we could have estimated relative consumption of fruits and insects in terms of biomass. Although we did not do this, the potential to estimate relative numbers and biomass of consumed foods is an advantage of our method of fecal analysis. Other methods of assessing composition of feces of bears not only entail more effort, but also yield results that have less intuitive meaning because they estimate relative weight or volume of undigested particles. Seeds, the undigested remains of fruits, tend to be heavier than the hollow exoskeletons of digested insects, so dietary composition assessed from dry weights (e.g., Baskaran, 1990; Gokula et al., 1995; Table 4) may be biased toward fruits, especially those with large, heavy seeds.

Our method of fecal analysis probably yielded a reliable estimate of the relative consumption of termites:ants (excluding eggs and larvae without exoskeletons) because we counted numbers of heads. We found that termites outnumbered ants >2:1. Gokula et al. (1995) also found (comparing dry weights) that termites were 2:1 more common than ants in feces of sloth bears from southern India. However, Baskaran (1990) reported that in another nearby area of India, but in a different season, feces of sloth bears contained 2:1 more ants than termites (also based on dry weight). Area and seasonal-related variation in the relative representation of ants and termites in the diet has been recognized for many other species of myrmecophagous mammals (Redford, 1987).

We also were able to quantify relative consumption of soldier and worker termites. Although workers typically far outnumber soldiers in colonies of termites, including those of the genera preyed upon by sloth bears in our study (>10 workers:1 soldier—Haverty, 1977), soldiers predominated in feces of sloth bears, suggesting that they defended the colony when sloth bears invaded. Usually, when we inspected a termite colony just after it had been preyed on by a sloth bear, termites or eggs were not visible. However, on occasions when a sloth bear was disturbed and left an excavated colony prematurely, we observed remaining eggs and soldiers. We surmised that sloth bears consumed mainly the densest group of prey, consisting of eggs and defending soldiers; workers were consumed less frequently because they were more dispersed.

Although soldier termites use physical and chemical defenses against intruders (Delign et al., 1981; Redord, 1987), we saw no indication that these defenses were effective in deterring sloth bears. Myrmecophagous mammals may be somewhat tolerant of defensive secretions of termites (Richardson and Levitan, 1994), but persistent attacks by termite soldiers apparently cause feeding bouts of most termite-eating mammals to be short (often <1 min—Abensperg-Traun et al., 1991; Kruuk and Sands, 1972; Montgomery and Lubin, 1977; Nel, 1978; Redford, 1985; Richardson, 1987; Shaw et al., 1985). Sloth bears fed longer than other myrmecophagous mammals at colonies of termites, possibly because they sucked up termites with a vacuuming action, rather than using their tongue, as in other myrmecophagous mammals. The ability to feed on a colony of termites for a relatively long period may enable sloth bears to extract a large proportion of the 4,000–90,000 termites that occupy colonies that are typical of this area (Roonwal, 1970).

Our data and those from other studies (Davidar, 1983; Gopal, 1991) suggest that sloth bears may be deterred from feeding on termites by the hardness of their mounds. Bears preyed on termites both in mounds and underground colonies, but they favored mounds more during the wet season than the dry season. One explanation is that mounds were softened by monsoon rains. The monsoon also flooded the ground, which made excavation of underground colonies difficult in lowland areas. Many sloth bears moved from lowland grasslands and riverine forest to upland sal forest at the start of the wet season (Joshi et al., 1995), possibly due to restricted access to underground colonies of termites. The greater prevalence of termites in the diet of sloth bears that moved to sal forest compared to those that remained in grassland and riverine forest (Fig. 1) suggested that availability of fruit was not the principal factor prompting sloth bears to move. Bears returned to lowlands during the dry season, possibly because termite mounds in sal forest became hard, underground colonies of termites were more accessible in the soft, alluvial soil, and biomass of termites in the lowlands may have been higher than in sal forest. This last point is supported by the high density of sloth bears that we observed on the alluvial floodplain during the dry season (Joshi, 1996). Sloth bears also found larvae of beetles in the grasslands for several months (Fig. 1), which indicated the presence of another important source of food that was absent in the sal forest. The abundance of beetles and correspondingly lower relative percentage of termites in the diet of sloth bears in the grasslands compared to those in sal forest should not be construed as indicative of a low density of termites in the grasslands. We suggest that availability of alluvial grasslands may be the main reason that sloth bears in Royal Chitwan National Park were more myrmecophagous than sloth bears in other parts of their range.

It is apparent that despite morphological specializations for myrmecophagy, sloth bears are adaptable to seasonal and geographic variation in availability of food. Their diet is considerably broader than that of other myrmecophagous mammals (Redford, 1987), including the bat-eared fox (*Otocyon megalotis*—Kok and Nel, 1992; Nel, 1978; Nel and Mackie, 1990), which like the sloth bear, evolved from a lineage of omnivores. Bears often are characterized as generalist, opportunist feeders, and although sloth bears diverged toward a diet composed largely of insects, they appear to have retained the ability to use a variety of foods. However, their relatively restricted geographic range and the small extent of overlap between their range and that of the more omnivorous Asiatic black bear implies a dependence on some minimum availability of ants and termites.

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