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Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India

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Abstract

We conducted a field study of diets of three sympatric large carnivores, the tiger *Panthera tigris*, the leopard *Panthera pardus* and the dhole *Cuon alpinus* in Bandipur Tiger Reserve, India, based on analyses of 381, 111 and 181 scats, respectively. The frequency of occurrence of prey items in scats was converted to relative biomass and number of prey consumed using regression equations based on earlier feeding trials. The results showed that although these predators kill ~11–15 species of vertebrate prey, relatively abundant ungulate species provide 88–97% of biomass consumed by them. Although the dietary niche overlap among the three species was high (Pianka's index of 0.75–0.93), some specialized predation was observed. The largest ungulates, gaur *Bos gaurus* and sambar *Cervus unicolor*, provided 73% of biomass consumed by tigers, whereas medium-sized chital *Axis axis* and wild pig *Sus scrofa* formed 65 and 83% of the biomass intake of leopards and dholes, respectively. In terms of the relative numbers of prey animals killed by the three predators, chital, which is the most abundant prey species, dominated their diets (tiger = 33%, leopard = 39% and dhole = 73%). The results of the study, in conjunction with earlier work, support the prediction that abundance of ungulate prey species, as well as their availability in different size classes, are both critical factors that facilitate sympatry among the three predators.

Introduction

The tiger *Panthera tigris* is the obligate terrestrial carnivore in all of the mammalian assemblages in which it occurs (Seidensticker, Christie & Jackson, 1999). Being an umbrella species, its effective conservation enhances survival prospects for other forms of biodiversity (Karanth, 2003*b*). Past studies of tigers (Schaller, 1967; Sunquist, 1981; Karanth & Sunquist, 1995, 2000; Karanth *et al*., 2004) and co-predators, such as the leopard *Panthera pardus* and dhole *Cuon alpinus*, indicate that they play a major role in shaping prey communities (Karanth *et al*., 2004). These three predators are specialized killers of large ungulate prey such as cervids, bovids and suids (Rabinowitz, 1989; Johnsingh, 1992; Venkataraman, Arumugam & Sukumar, 1995; Sunquist, Karanth & Sunquist, 1999). Therefore, scientific data on their food habits and resource partitioning are vital for scientific understanding as well as for setting conservation targets.

A widely used field technique for understanding predator diets is the identification of recognizable parts of prey that have passed through their digestive systems in comparison with reference collections of potential food items (Koppikar & Sabnis, 1976; Putman, 1984). Carnivore scats can provide a snapshot of the types of prey consumed and have an advantage over other techniques such as examination of gut content or direct observation of feeding because of the relative ease of obtaining samples and the non-invasive nature of the sampling procedure. Furthermore, advanced analytic methods (Floyd, Mech & Jordan, 1978; Ackerman, Lindzey & Hernker, 1984; Reynolds & Aebischer, 1991; Trites & Joy, 2005) can be applied to such scat data to obtain accurate prey profiles.

The overall goal of the present study is to understand the prey profiles of tigers, leopards and dholes with the following specific objectives:
(1) To determine the frequency of occurrence of different principal prey species in predator diets.
(2) To determine relative biomass and relative numbers of different species of principal prey in predator diets.
(3) To examine the implications of these diet profiles for understanding resource partitioning patterns and ecological sympatry among the three predators in Bandipur.

Study area and species

The study was conducted in the 880 km^2 Bandipur Tiger Reserve (76°12′–76°46′E and 11°37′–11°57′N), located in Karnataka State, India (Fig. 1). The altitude in the park ranges from 680 to 1454 m, the mean annual rainfall ranges between 625 and 1250 mm and the annual temperatures

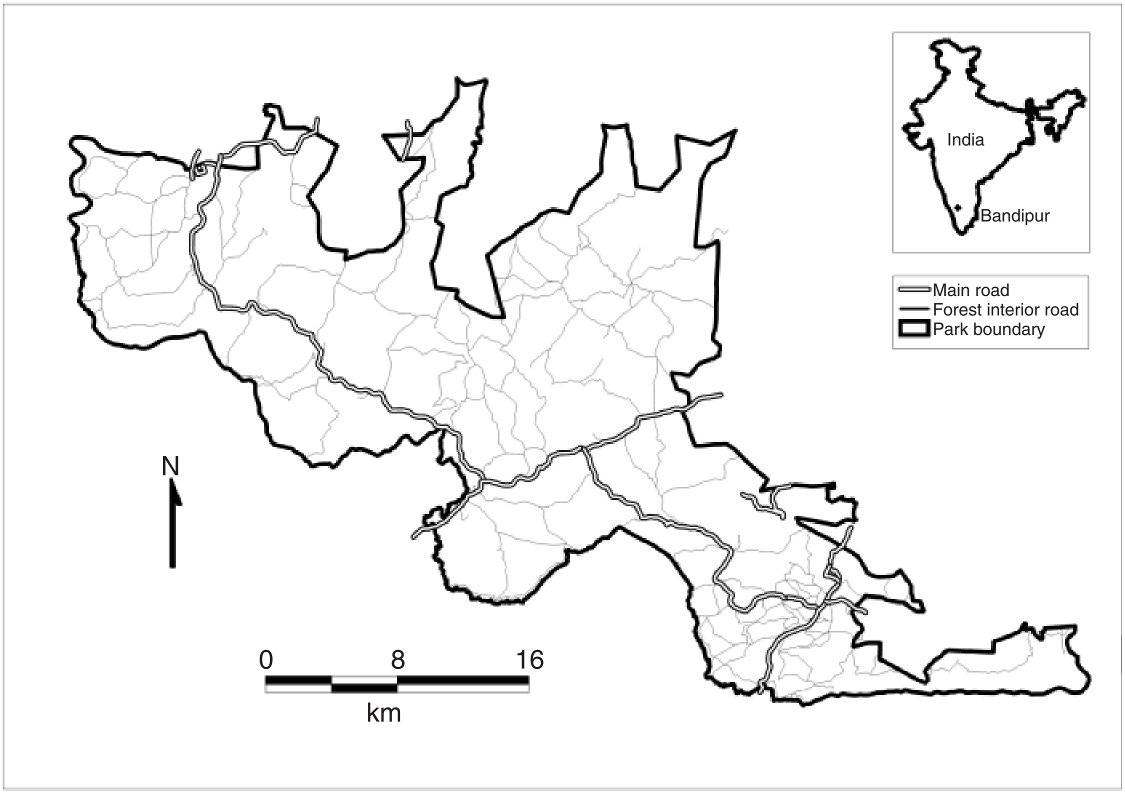

Figure 1 Map of Bandipur Tiger Reserve showing boundaries and forest interior roads.

range from 18 to 29 °C. The rivers Moyar, Nugu and Kabini and their tributaries are the major sources of perennial water.

The vegetation consists of dry deciduous forests that support a diverse assemblage of large herbivorous prey species, such as chital *Axis axis* (Erxleben), sambar *Cervus unicolor* (Kerr), gaur *Bos gaurus* (Smith), wild pig *Sus scrofa* (Linnaeus), muntjac *Muntiacus muntjak* (Zimmermann), chevrotain *Tragulus meminna* (Erxleben) and four-horned antelope *Tetracerus quadricornis* (Blainville). Additionally, several smaller prey species such as hanuman langur *Semnopithecus entellus* (Dufresne), bonnet macaque *Macaca radiata* (Geoffrey), blacknaped hare *Lepus nigricollis* (Cuvier), porcupine *Hystrix indica* (Kerr) and small carnivores (felids, viverrids and herpestids) also occur. Bandipur reserve has an extensive network of forest roads that facilitate collection of scats deposited by the three carnivore species.

Methods

Field sampling of predator scats

Tigers, leopards and dholes prefer to use forest roads as travel routes along which they deposit scats as a social communication mechanism (Smith, McDougal & Miquelle, 1989; Karanth & Sunquist, 2000). The first author and field assistants trained to identify scats of predator species, walked in teams of two persons each, to sample a network of forest roads (Total length = 2332.8 km) to collect predator scats according to the following sampling scheme.

Extensive sampling (42 days): 18 scat-routes amounting to a total length of 234.5 km were sampled six times by three teams of two field assistants each between 6 March and 15 April 2006. For logistic convenience, the routes were grouped into three sets of six each. Each of the three teams covered six routes on 6 successive days. A total of 1412.4 km of forest roads were sampled.

Intensive sampling (12 days): Six out of the above 18 routes were sampled by six teams of two field assistants each between 19 April and 30 April 2006. Each route was sampled 12 times on 12 successive days. A total of 920.4 km of road was sampled to meet an ancillary goal of estimating scat deposition rates (Andheria, 2006).

Identification of predator species from scats

Scats of tigers and leopards are much larger and deposited on the grassy strips at the center or edges of forest roads. On the other hand, the group-living dholes deposit their smaller scats in clusters on the bare soil along the wheel-track, making them easily distinguishable from felid scats (Johnsingh, 1983; Karanth & Sunquist, 1995). Tiger and leopard scats were distinguished from each other using supplementary evidences such as the differences in quantity, typical diameter ranges, the presence of ancillary signs like tracks and by avoiding collection of scats of indeterminate origin as described in earlier surveys (Johnsingh, 1992; Karanth & Sunquist, 1995). Subsequent faecal DNA tests (Mukherjee, 2006) confirmed the accuracy of these field classifications.

Collection and treatment of scats

After identification, a portion of the scat containing adequate amount of prey remains such as hair and other undigested body parts was stored in an airtight plastic bag. These scats were subsequently washed in flowing water through a fine (<1 mm) nylon sieve (Cunningham, Gustavson & Ballard, 1999). The sieved prey remains, grass and soil were sun dried in thin paper bags for 3 days to avoid fungal growth. The dried scat samples were then labelled and stored in airtight bags.

Identification of prey species from scats

The hair of prey species, which passes out undigested through the gut of predators, was the primary source of information for identifying the prey consumed (Sunquist, 1981; Mukherjee, Goyal & Chellam, 1994*a*,*b*; Karanth & Sunquist, 1995). Prey species were identified based on macroscopic and microscopic features of the hair in comparison with reference collections at the Centre for Wildlife Studies, Bangalore. The identification was based on the general appearance of the hair, colour, relative length, relative width, texture, basal configuration, cortex pigmentation, medullary width and patterns as described by earlier workers (Putman, 1984; Karanth & Sunquist, 1995; Sujai, 2004).

Estimation of frequency of occurrence, relative biomass and relative number of prey consumed

The frequency of occurrence (per cent of a particular species in the total number of prey items found) was calculated. The 95% confidence intervals for these per cent occurrences were generated from 1000 bootstrap simulations (Tibshirani, 1993). The frequency of occurrence (A, expressed as a per cent of scats in which a particular prey item is found) is a commonly used measure of prey intake and composition. However, if the body sizes of different prey items are highly variable, frequency of occurrence can be a misleading metric because of the surface to volume ratio problem initially highlighted by Floyd *et al.* (1978) and Ackerman *et al.* (1984). Because of their relatively greater surface area in relation to volume in smaller prey types, their consumption results in the production of relatively more predator scats compared with larger prey types. This leads to an overestimation of the proportion of small prey and underestimation of large prey in predator diet profiles when the frequency of occurrence is used as a measure.

To overcome this problem, earlier studies of wolves, *Canis lupus*, (Floyd *et al.*, 1978) and cougars, *Puma concolor*, (Ackerman *et al.*, 1984) developed regression equations based on feeding trials in captivity using known prey of different body sizes. Karanth & Sunquist (1995) successfully adopted these regressions in their dietary studies of tigers, leopard and dhole in Nagarahole. However, given the logistical difficulties in conducting species-specific trials, they adopted the regressions developed for cougars for tigers and leopards and those of wolves for dholes. This approach for correcting diet frequency data has since been successfully used by Biswas & Sankar (2002) for tigers and by Sujai (2004) for tigers, leopards and dholes.

The regression equations relate the average live weight of a prey animal consumed (X) to the weight of consumed prey represented by one field-collectible scat (Y):

$$Y = 1.980 + 0.035X \text{(for tiger and leopard)}$$
$$Y = 0.035 + 0.02X \text{(for dhole)}$$

The term Y is used as a correction factor and multiplied to the observed frequency of occurrence data, to correct the over-representation of smaller prey. The details of this approach have been fully described elsewhere (Floyd *et al.*, 1978; Ackerman *et al.*, 1984; Karanth & Sunquist, 1995). The live weights of different prey species (X) used in our analyses were based on Karanth & Sunquist (1995). Using the correction factor Y, the relative biomass (D, the proportion of meat of a specific prey item in the predator's overall diet) and the relative number of a prey species consumed (E, the proportion of numbers of that prey taken among all prey numbers consumed by the predator) were estimated as below (expressed as per cent):

$$D = (A \times Y)/\Sigma(A \times Y) \times 100$$
$$E = (D/X)/\Sigma(D/X) \times 100$$

The prey species were additionally categorized into three size classes, with gaur and sambar being classified as large prey (>175 kg), chital and pig as medium-sized prey (between 30 and 175 kg) and muntjac, four-horned antelope, langur and chevrotain being classified as small prey (between 5 and 30 kg). Prey species <5 kg body mass were excluded from our analyses.

Results

We collected 381 tiger scats, 111 leopard scats and 181 dhole scats that could be analysed. The major prey species were listed individually and the remaining minor prey were combined into groups as shown in Table 1. Although most scats contained a single prey type, sometimes >1 prey items were found, resulting in the average prey item per scat values of 1.17 for tigers, 1.18 for leopards and 1.22 for dholes. About 14.5% of tiger scats, 15.5% of leopard scats and 4.3% of dhole scats also contained varying amounts of grass with or without prey remains. About 7.9% of tiger scats, 24.4% of leopard scats and 3.2% of dhole scats contained varying amounts of soil.

Composition and overlap of predator diets

Table 1 shows that gaur, sambar, chital and wild pig constituted ~88% of prey consumed by tigers and ~69% of prey taken by leopards and ~68% of prey of dholes.

A variety of diet overlap indices are used in field measurements of ecological niche separation (Pianka, 1973;

Table 1 Number of prey items and proportion (%) of different prey species in predator diet (per cent occurrence) as derived from scat data from Bandipur

Predator	Prey	No.	%	95% confidence interval
Tiger *Panthera tigris* (n=444)	Sambar *Cervus unicolor*	99	22.30	18.24–26.35
	Chital *Axis axis*	145	32.66	28.38–36.71
	Muntjac *Muntiacus muntjak*	11	2.48	1.13–3.83
	Four-horned antelope *Tetracerus quadricornis*	5	1.13	0.23–2.03
	Chevrotain *Tragulus meminna*	6	1.35	0.23–2.48
	Wild pig *Sus scrofa*	40	9.01	6.17–11.71
	Gaur *Bos gaurus*	106	23.87	19.90–27.93
	Langur *Semnopithecus entellus*	10	2.25	0.90–3.60
	Hare *Lepus nigricollis*	8	1.80	0.63–2.93
	Sloth bear	3	0.68	0.00–1.35
	Cattle	2	0.45	0.00–1.13
	Other small prey	9	2.03	0.90–3.38
Leopard *Panthera pardus* (n=131)	Sambar	8	6.11	2.29–9.92
	Chital	60	45.80	36.64–53.44
	Muntjac	2	1.53	0.00–3.05
	Four-horned antelope	4	3.05	0.76–6.87
	Chevrotain	2	1.53	0.00–3.05
	Wild pig	11	8.40	3.82–12.98
	Gaur	12	9.16	3.82–13.74
	Langur	12	9.16	3.82–13.74
	Hare	5	3.82	0.76–7.63
	Cattle	3	2.29	0.00–4.58
	Other small prey	12	9.16	3.82–13.74
Dhole *Cuon alpinus* (n=220)	Sambar	16	7.30	4.09–10.91
	Chital	121	55.00	48.18–60.91
	Muntjac	4	1.82	0.46–3.64
	Four-horned antelope	9	4.09	1.82–6.82
	Chevrotain	1	0.45	0.00–1.36
	Wild pig	12	5.50	2.73–8.64
	Gaur	1	0.45	0.00–1.36
	Langur	1	0.45	0.00–1.36
	Hare	27	12.30	7.73–15.91
	Wild dog	2	0.91	0.00–2.27
	Other small prey	26	11.80	7.73–15.91

These figures are based on the analysis of 381 tiger scats, 111 leopard scats and 181 dhole scats, which contained 444, 131 and 220 prey items, respectively. Ninety-five per cent confidence limits for the percentage of each food item were generated using 1000 bootstrap simulations. Other small prey species include small cat, civet and rodent.

Feinsinger, Spears & Poole, 1981). We used Pianka's index for measuring diet overlap between predators. This index ranges in value from 0 (indicating no overlap between two predator species) to 1.0 (complete overlap). The overlap indices for the three predators in Bandipur were 0.84 between tiger and leopard, 0.75 between tiger and dhole and 0.93 between leopard and dhole.

Relative frequency of occurrence, biomass and numbers of individual prey consumed

The frequency of occurrence, relative biomass and estimates of relative number of individuals of prey consumed by the three sympatric carnivores based on our analyses are presented in Table 2. These data show that the relative importance of different prey types varied substantially when the three measures of prey intake (simple frequency of occurrence, corrected relative biomass consumption and relative numbers of different prey species killed by each predators) were used for comparisons. These prey consumption patterns are discussed in the following section.

Discussion

Over most of their range, tigers co-exist with other predatory carnivores such as leopards and dholes. The densities of different predator species within such guilds appear to be greatly influenced by the relative abundance of different size classes of prey species in the assemblage (Karanth & Sunquist, 1995; Sunquist *et al*., 1999; Karanth & Sunquist, 2000; Karanth *et al*., 2004). We examine our results in the light of findings from earlier studies in an attempt to understand the role of tigers and other co-predators in shaping these prey–predator communities in Bandipur.

Table 2 Frequency of occurrence (*A*), relative biomass consumed (*D*) and relative number of prey individuals consumed (*E*) by tiger, leopard and dhole, based on 381, 111 and 181 scats, respectively

Predator	Prey	*X* (kg)	*A* (%)	*Y* (kg/scat)	*D* (%)	*E* (%)
Tiger *Panthera tigris*	Gaur *Bos gaurus*	287	27.82	12.03	42.31	14.44
	Sambar *Cervus unicolor*	212	25.98	9.40	30.89	14.27
	Chital *Axis axis*	55	38.06	3.91	18.79	33.47
	Wild pig *Sus scrofa*	38	10.50	3.31	4.39	11.33
	Muntjac *Muntiacus muntjak*	20	2.89	2.68	0.98	4.79
	Four-horned antelope *Tetracerus quadricornis*	19	1.31	2.65	0.44	2.26
	Langur *Semnopithecus entellus*	8	2.62	2.26	0.75	9.18
	Chevrotain *Tragulus meminna*	5	1.57	2.16	0.43	8.41
Leopard *Panthera pardus*	Gaur	85	10.81	4.96	15.03	5.90
	Sambar	62	7.21	4.15	8.39	4.51
	Chital	48	54.05	3.66	55.50	38.57
	Wild pig	37	9.91	3.28	9.11	8.21
	Muntjac	20	1.80	2.68	1.35	2.26
	Four-horned antelope	19	3.60	2.65	2.67	4.69
	Langur	8	10.81	2.26	6.85	28.58
	Chevrotain	5	1.80	2.16	1.09	7.27
Dhole *Cuon alpinus*	Gaur	75	0.55	1.54	0.87	0.60
	Sambar	70	8.84	1.44	13.08	9.55
	Chital	55	66.85	1.14	78.26	72.71
	Wild pig	31	6.63	0.66	4.48	7.38
	Muntjac	20	2.21	0.44	0.99	2.53
	Four-horned antelope	19	4.97	0.42	2.13	5.72
	Langur	8	0.55	0.20	0.11	0.71
	Chevrotain	5	0.55	0.14	0.08	0.79

In this context, we would like to point out that many earlier studies of large carnivore diet in the region (Schaller, 1967; Sunquist, 1981; Rabinowitz, 1989; Johnsingh, 1992; Venkataraman *et al*., 1995) have used raw frequency of occurrence data to estimate prey composition in predator diets. Given the large variations in body size classes among prey species in this region, the use of approaches that correct for the relative prey size that we used (see 'Methods') is a superior approach for accurate estimation of predator diets. Secondly, our results sampled a relatively large area of $>500\,km^2$, and thus may provide a more reliable measure of dietary patterns in these wide-ranging predators. However, comparison of our results with some of the earlier studies needs to consider that our data pertain primarily to the dry season.

Dietary comparisons among predators

Our results (Table 2) show that large-sized prey (sambar and gaur) comprised of 73.2% of prey biomass of tigers, with medium-sized prey (chital, wild pig) comprising of 23.2% and small prey (muntjac, four-horned antelope, langur, chevrotain) providing only 2.6% of biomass consumed. On the other hand, medium-sized prey dominated leopard diet, contributing to 64.6% of the prey biomass, with a single species, chital, constituting ~55% of biomass taken. Large prey was less important for leopards (~23% of biomass), and smaller prey providing about 12%. Dholes depend even more predominantly on medium-sized prey (~83% biomass), with chital being the overwhelmingly dominant species (~78%).

The proportion of large ungulates (gaur and sambar) was considerably lower in diets of leopards and dholes in comparison with the tiger. The presence of large ungulate species in the prey assemblage is thus more important for tigers than for leopards and dholes. The tiger's larger size (120–270 kg) enables safe capture of large and potentially dangerous prey such as adult gaur and sambar and possibly explains this pattern.

In terms of biomass consumed, chital were most important prey of dhole (~78%), followed by leopard (~55%) and tiger (~19%). In terms of the relative numbers of individuals taken, chital was the dominant prey among all three predators. However, the relative importance of chital varied among the three predators (tigers = ~33%, leopard = ~39% and dhole = ~73%). This result seems to confirm findings of an earlier study in the region (Karanth & Sunquist, 1995).

When combined, the four numerically dominant ungulates (chital, sambar, gaur and wild pig) provided 96% of the biomass consumed by tigers, 88% by leopards, 97% by dholes, clearly establishing the importance of role of large and medium ungulates for maintaining high densities and viable populations of tigers and other large carnivores as shown by earlier workers (Karanth & Stith, 1999; Karanth *et al*., 2004). Even in terms of the relative number of prey animals taken, these four ungulate species constitute a high proportion of predator diets. Very large prey such as elephants (only calves are killed by tigers), or low-density ungulates such as muntjac and four-horned antelope, do not appear to be important in predator diets. Among non-ungulate prey, only langur monkeys appear to be of some importance to leopards.

Other studies (Biswas & Sankar, 2002; Reddy, Srinivasulu & Rao, 2004) have speculated that tigers and other large predators may not take livestock if wild ungulate prey is abundant. A large number of livestock from villages adjacent to our study area sometimes grazed illegally in it (Madhusudan, 2000). Because such clandestine grazing was confined to the edges of the park and occurred mostly in the wet season, as well as because livestock were guarded and corralled outside the forest at night, the contribution of domestic stock to predator diets was negligible (0.5–2.3%) in this study. In the absence of such constraints on predators, we expect that livestock will be killed by predators as reported from the Bhadra tiger reserve (Karanth, 2003*a*; Madhusudan, 2003) and the Nagarjunasagar reserve (Reddy *et al*., 2004).

Overall, although we could not measure prey selectivity, our results appear to converge with studies (Karanth & Sunquist, 1995; Karanth & Nichols, 1998) that showed that niche separation and co-existence of these three predator species are facilitated by prey selectivity patterns that are enabled because of the availability of abundant prey in different size classes. However, we stress that, additionally, other behavioral factors that render particular prey species vulnerable to particular predator species, such as vulnerability of chital to diurnal dholes (Cohen *et al*., 1975; Venkataraman *et al*., 1995) or of primates to the leopards, as well as temporal separation of hunting activities among predators, may also contribute to the predatory patterns we observed as shown by another study in Nagarahole reserve (Karanth & Sunquist, 2000).

The results in Table 2 show that chital dominated the diet of dholes and leopards, whereas tigers took relatively greater proportions of gaur and sambar. This could be a manifestation of the temporal separation between the three carnivores. Dholes are almost totally diurnal hunters (Venkataraman *et al*., 1995), while tigers and leopards are relatively more crepuscular or nocturnal (Karanth & Sunquist, 2000) in habit. Among felids, leopards show higher activity levels, both during the day and night, compared with tigers. Our study clearly shows a relatively greater proportion of diurnal prey species such as langur and chital in leopard diet. Moreover, leopard diets also show a high proportion of smaller nocturnal prey. Similar observations are reported in earlier studies in the adjacent Nagarahole reserve (Karanth & Sunquist, 1995; Karanth & Sunquist, 2000).

Our results differ from those of an earlier study in Bandipur (Johnsingh, 1992) that showed a preponderance of smaller prey in the diets of predators. This difference is likely to be because the earlier study covered only a 32 km^2 of the driest part of our study area, and, its analyses did not correct for the over-representation of smaller prey that result with the use of raw frequency of occurrence data. Several studies have also been carried out on the diet of these predators in the Indian subcontinent over the years (Schaller, 1967; Johnsingh, 1992; Chundawat, Gogate & Johnsingh, 1999; Reddy *et al*., 2004). However, most of these earlier studies report only the frequency of occurrence of different prey types in predator scats. Our study shows that current methods of diet analyses can yield information on prey biomass and relative numbers taken by predators (Karanth & Sunquist, 1995; Biswas & Sankar, 2002; Bagchi, Goyal & Sankar, 2003; Sujai, 2004) and can be applied with profit for understanding predator dietary patterns.

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