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Prey abundance and food habit of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India

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Abstract

Food habits of tigers *Panthera tigris* and population attributes of prey species (population structure, density and biomass) were studied in the tropical dry deciduous forest of Pench National Park, Central India, from November 1998 to April 1999. Scat analysis and line transect method were used to estimate tiger food habits and density of major prey species, respectively. The 61.1 km^2 intensive study area was found to have very high ungulate density (90.3 animals km^{-2}) with chital *Axis axis* being the most common species (80.7 animals km^{-2}), followed by sambar *Cervus unicolor* (6.1 animals km^{-2}). Common langur *Presbytis entellus* was the most abundant (77.2 animals km^{-2}) primate species. When the density figures were multiplied by the average weight of each prey species, a high biomass density of 6013.25 kg km^{-2} was obtained for the intensive study area. Chital (47.3%) along with sambar (14.5%) and wild pig *Sus scrofa* (10.9%) constituted the major part of the tiger's diet. If there is food choice, tigers seem to kill medium- and large-sized species more often. Wild pig and sambar were consumed more than their availability, whereas chital were taken in proportion to their availability. Gaur *Bos gaurus* and nilgai *Bosephalus tragocamelus* were not represented in the tiger's diet. Common langur was consumed in lesser proportion by tigers than expected by estimates of its density. The average weight of animals consumed by tigers in the intensive study area was 82.1 kg. The analyses revealed that Pench harbours very high prey density and tigers are mostly dependent on the wild ungulates rather than on domestic livestock as is the case in many other areas in the Indian subcontinent. These two factors thus make Pench National Park a potential area for long-term conservation of tigers.

Key words: food habits, *Panthera tigris*, line transect, scat analysis, ungulates

INTRODUCTION

Tiger *Panthera tigris* L. distribution has been reduced drastically over the last century, including extinction of three of its subspecies (Bali tiger *P. t. balica;* Caspian tiger *P. t. virgata* and Javan tiger *P. t. sondaica*) and massive reduction in numbers of the rest (Sunquist, Karanth & Sunquist, 1999). Continued depletion of prey population and fragmentation of natural habitats, apart from poaching, were among two major factors that led to the present plight of tigers in the wild and will determine its survival in the future (Karanth & Stith, 1999; Sunquist *et al.,* 1999). With these factors constantly taking their toll, small fragmented tiger populations are always under the threat of extinction. Though this trend is alarming, recent studies indicate that this cat is resilient enough to recuperate from the problems associated with a small population (Gilpin & Soule, 1986) provided its habitat and prey species are well protected (Sunquist *et al.,* 1999).

Tigers are obligate carnivores preying upon the largest ungulates in all the ecosystems in which they occur (Seidensticker, 1997). Although they can potentially hunt prey varying from small mammals to the largest of the bovids, the mean weight of species hunted is around 60 kg. This is obtained predominantly from deer species, which contribute up to 75% of the prey biomass requirement of the tiger in most parts of its range (Sunquist *et al.,* 1999). Food habits comprise one of the major determinants of various life-history strategies in carnivores including spacing pattern, movement, habitat selection, social structure, success of reproduction and geographical distribution (Krebs, 1978; Bekoff, Daniels & Gittleman*,* 1984; Sunquist & Sunquist, 1989). Factors influencing large felid prey choice are a result of a complex interplay of various ecological parameters

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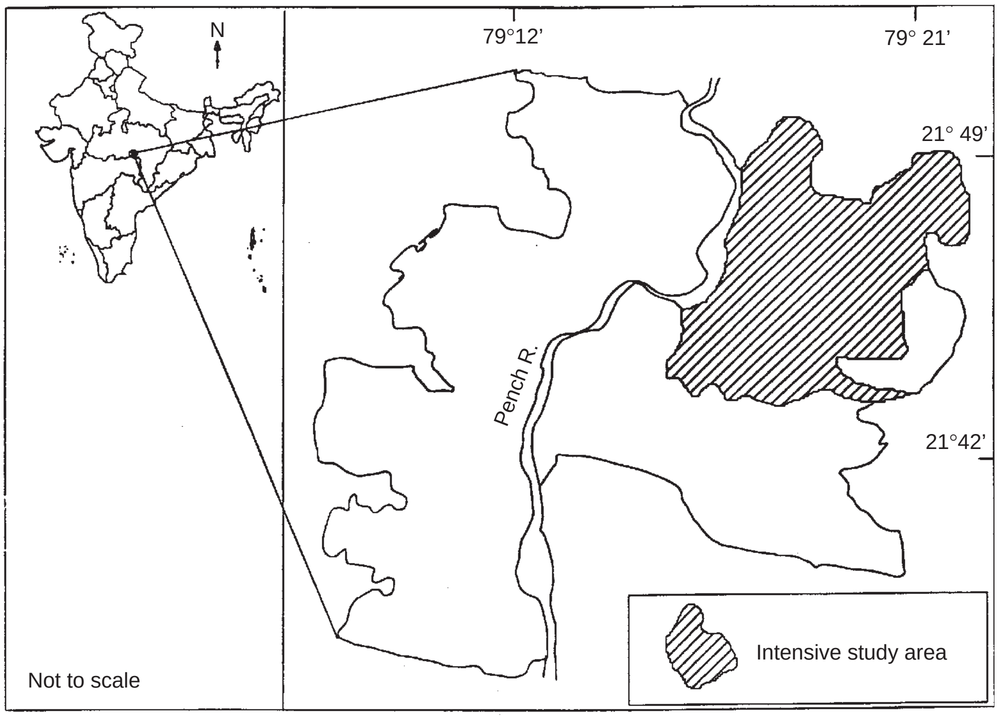

Fig. 1. Study area in Pench National Park, India.

that often varies at the extremes of distribution of the same species (Sunquist & Sunquist, 1989). Our understanding of this phenomenon is far from complete (Sunquist & Sunquist, 1989) and is urgently required for a highly endangered species like the tiger, which inhabits diverse ecosystems. Thus increasing knowledge of tiger food habits in both unfragmented and disturbed habitats will enable us to recognize the plasticity in the predator's ability to use the available resources in various human-modified ecological systems. Such a body of information would be extremely important for conceiving better management strategies as well as contributing to our understanding of large cat ecology.

Pench Tiger Reserve, which includes Pench National Park and Pench Sanctuary, along with Kanha Tiger Reserve constitutes one of the 11 level-I Tiger Conservation Units (TCU) in India classified by Wickramanayake *et al.* (1999) where tiger has the highest possibility of survival. Pench is predominantly a dry deciduous system and fewer studies on tiger ecology have been conducted in these habitats compared to those in tropical and subtropical moist deciduous forests and alluvial tall grasslands (Chundawat, Gogate & Johnsingh, 1999). With the intention of collecting base line information on tiger and its prey species, the present study was designed to: (1) estimate the density, biomass, population structure and grouping pattern of major prey species of tiger in the study area; (2) study the food habits of tigers with reference to its prey availability and utilization pattern.

STUDY AREA

The study was conducted in Pench National Park (PNP), which lies in the state of Madhya Pradesh (21°38′N–21°50′N, 79°08′E–79°47′E) and covers an area of 290 km^2 (Fig. 1). The intensive study area was 61.1 km^2 of the 145.24 km^2 eastern block of PNP. The tenure of the study was 6 months, from mid-November 1998 to April 1999. Pench experiences markedly seasonal climate with a distinct summer (March–June), monsoon (July–September) and winter (October–February) and receives a mean annual rainfall of *c.* 1400 mm. The temperature ranged from $-2\,°C$ in winter to $49.5\,°C$ in summer during the study. Vegetation in the area is broadly classified as having both tropical dry deciduous and tropical moist deciduous forests (Champion & Seth, 1968). Teak *Tectona grandis* L. and its associated species in the area represents a transition from tropical dry deciduous to tropical moist deciduous forests. The terrain is undulating in most areas of the Park. The Pench River, which is the major source of perennial water, is dammed downstream of the study area, leading to innundation of 54 km^2 of the PNP area. During winter, this area remains submerged, but as summer approaches the water recedes facilitating abundant growth of fresh forage for ungulates. In addition to Pench River, there are numerous seasonal streams in the Park. The eastern part of the PNP is largely undisturbed with occasional livestock grazing in the periphery, whereas the western block has high levels of anthropogenic disturbance (pers. obs). Potential prey species for tiger in the area includes gaur *Bos gaurus* Smith, sambar *Cervus unicolor* Kerr, chital *Axis axis* Erxleben, nilgai *Bosephalus tragocamelus* Pallas, wild pig *Sus scrofa* L., muntjac *Muntiacus muntjac* Zimmerman, chowsingha *Tetraceros quadricornis* Blainville, chinkara *Gazella gazella benneti* Sykes, common langur *Presbytis entellus*

Dufresne, rhesus macaque *Macaca mulatta* Zimmerman, Indian porcupine *Hystrix indica* Kerr and blacknaped hare *Lepus nigricollis ruficaudatus* Geoffrey. Domestic livestock (cattle, buffalo and goat) occur in areas outside the national park. Apart from tiger, leopard *Panthera pardus* L. and wild dog *Cuon alpinus* Pallas are the two other large carnivores in the area. The sloth bear *Melarsus ursinus* Shaw occurs infrequently in the area.

METHODS

Estimation of density, biomass, population structure and group size distribution of prey species

The line transect method (Eberhardt, 1968; Burnham, Anderson & Laake, 1980; Buckland *et al*., 1993) was used to estimate densities of prey species in the study area. This method has been effectively used to determine animal densities under similar tropical conditions (Karanth & Sunquist, 1992, 1995; Varman & Sukumar, 1995; Khan *et al.,* 1996). Fourteen transects varying in length between 1.2 and 2.7 km were randomly laid in the study area. The total transect length of 28.6 km was monitored 8 times during the beginning of the day and late afternoon, resulting in 457.7 km of transect walk. For each sighting on the transect, the following parameters were recorded: (1) sighting angle (with a compass); (2) sighting distance (visually estimated); (3) group size; (4) sex and age class of the individuals (whenever it was possible to classify them). Density of all the species was calculated using Distance program version 3.5 (Laake *et al*., 1998). The farthest sightings of the prey species on the transects (10% of all observations) were truncated to achieve a reliable density estimate (Buckland *et al.*, 1993). Since the sighting distances on transects were estimated visually, there was a chance of bias in density estimation due to heaping (Buckland *et al.*, 1993). To overcome this difficulty, the distance data were analysed again after grouping into different distance class intervals and were compared with the results from ungrouped data to arrive at the best estimates of prey density. We also checked for the size bias in the transect data using the Distance program version 3.5 (Laake *et al.*, 1998).

Density estimates obtained from transects were used to calculate the biomass of prey species in the study area. Observations on ungulates and primates from transects and opportunistic encounters were pooled to arrive at the population structure and grouping patterns of these species. Age and sex of individuals were estimated as suggested by Schaller (1967). Proportion of small (5–30 kg), medium (31–175 kg) and large (176–1000 kg) ungulate prey in the intensive study area was derived from the population structure data as classified by Karanth & Sunquist (1995).

Reconstruction of tiger diet

Scat analysis was used to estimate the proportion of different prey species consumed by tiger, since this method is non-destructive, and cost and time effective (Schaller, 1967; Sunquist, 1981; Johnsingh, 1983; Karanth & Sunquist, 1995). Tiger scats were collected whenever encountered. These scats were identified from those of other predators, particularly those of leopard, based on associated signs and tracks, size and appearance. Scats of tigers have a lower degree of coiling and relatively larger distance between two successive constrictions within a single piece of scat. Scats which could not be identified were excluded from the analysis. Collected scats were washed and the remains such as hair, bones, hooves, quills and teeth of the prey consumed were separated for species identification (Sunquist, 1981; Mukherjee, Goyal & Chellam, 1994*a*,*b*; Karanth & Sunquist, 1995).

The hairs of the prey species were sampled following Mukerjee *et al.*, (1994*a*) and compared with reference slides in the laboratory collection of the Wildlife Institute of India, Dehradun, India. Identification was based on the general appearance of the hair, colour, length, width, medullary structure, medullary width/hair width ratio and cuticle pattern (Moore, Spence & Dugnolle, 1974; Mukerjee *et al.*, 1994*b*). Quantification of the diet was based on both frequency of occurrence (proportion of total scats in which an item was found) and per cent occurrence (number of times a specific item was found as a percentage of all items found) (*sensu* Ackerman, Lindzey & Hernker, 1984).

To evaluate the effect of sample size on the results of scat analysis (Mukherjee *et al.,* 1994*a*,*b*) 10 tiger scats were chosen at random and their contents analysed. This was continued until all the 75 scats in the sample had been analysed once. The cumulating frequency of occurrence of different prey species in the tiger scats over successive random draws were then assessed to infer effect of the sample size on the final results.

Estimation of relative biomass and number of prey consumed by tiger from scat analysis, using correction factor

Frequencies of identifiable prey remains in scats do not give a representative picture of the consumed proportion of different prey species when the prey types vary in size to a considerable extent. Smaller prey species, having more hair per unit body weight produce more scats per unit prey weight consumed, leading to an overestimation of smaller prey species in the carnivore diet (Floyd, Mech & Jordan, 1978; Ackerman *et al.*, 1984). The correction factor developed by Ackerman *et al.* (1984) from feeding trials on cougar *Felis concolor concolor* L. was used to estimate the relative proportion of biomass of different prey species consumed by tigers in the study area. The equation used is as follows:

$$Y = 1.980 + 0.035X,$$

where Y = kg of prey consumed per field collectible scat; X = average weight of an individual of a particular prey

Table 1. Numerical and biomass density estimates[a] of principal ungulate and primate species in Pench National Park, Madhya Pradesh between November 1998 and April 1999

Species	*n*	D_G (km^{-2})	C_VD_G(%)	GS	D_I(km^{-2})	C_VD_I(%)	C_ID_I(km^{-2})	Biomass density (kg/km^{-2})
Sambar	140	3.5	8.42	1.7	6.09	9.57	4.9– 7.4	1291.08
Chital	975	27.35	8.04	3.44	80.75	8.61	66.8–97.6	4441.25
Common langur	454	12.25	6.83	6.12	77.16	8.42	63.9–93.0	617.28
Nilgai	11	0.23	37.1	1.75	0.43	44.0	0.18–1.03	79.12
Wild Pig	24	0.7	17.73	4.23	2.59	25.92	1.5– 4.3	98.42
Gaur	4	0.07	46.7	4.75	0.34	38.12	0.10–1.08	97.58
Chowsingha	12	0.24	18.0	1.17	0.29	21.0	0.19–0.44	5.8

[a] *n* = total number of groups detected; D_G = density of groups; D_I = density of individuals; GS = mean group size; C_VD_G = coefficient of variation of density of groups; C_VD_I = coefficient of variation of density of individuals; C_ID_I = 95 % confidence intervals of density estimates of groups and individuals.

type (Ackerman *et al.*, 1984). The average weight (X) of individuals of wild prey species was taken from Karanth & Sunquist (1995) and Khan *et al.* (1996) and that of domestic livestock from Schaller (1967). Solving the equation for Y gave an estimate of biomass consumed per collectible scat for each prey type. Multiplying each Y by the number of scats found to contain a particular prey species gave the relative weight of each prey type consumed. These values were used to estimate per cent biomass contribution of different prey species to the tiger diet.

Estimation of prey selectivity

The observed proportion of prey species in scats was compared with the expected proportions derived from their density estimates to conclude whether tigers in the intensive study area were showing selective predation. The expected proportion of scats containing a prey species was calculated as per the prediction of a hypothesis of non-selective predation (Manly, Miller & Cook, 1972). The multinomial likelihood estimator (see Link & Karanth, 1994 for detailed discussion) used to compute the expected proportion of scats from a kill of a particular prey species is:

$$\pi_i = \frac{d_i\ \lambda_i}{\sum_i d_i\ \lambda_i};$$

where prey species i has population density d_i, and λ_i($\lambda_i = X_i/Y_i$ derived from Ackerman's equation) is the number of scats produced from a single kill of species i. The program Scatman (developed by J. E. Hines and W. A. Link; Link & Karanth, 1994) was used to arrive at the expected proportions of prey species in scats. Density estimates of both individuals and groups of prey species was used to calculate 2 sets of expected scat frequencies based on the assumption of non-selective predation. Observed and expected proportions of prey species in the scats were then compared using the G test (Zar, 1984). Scats containing < 1 prey item were given equal weight as suggested by Karanth & Sunquist (1995). If there was a pattern of overall prey selection, use of each prey species as calculated by the program was inspected. Link & Karanth (1994) suggested that variability in the density estimates of each prey species and number of scats produced from a particular kill of any prey species is the potential source of inflation of type I error. Thus, the program also incorporates the effect of such variability (Link & Karanth, 1994) and reduces the inflation of type I error to produce an unbiased probability value. We also implemented the parametric bootstrap procedure of the program for 1000 times to elevate the above problem as suggested by Link & Karanth (1994).

Karanth & Sunquist (1995) used the results of a selectivity test obtained using the density of groups to make conclusons about a tiger predation pattern. They reasoned that predation on a prey species is likely to be determined by the density of groups rather than individuals, which influences the encounter rates between the predator and its prey in a forested ecosystem (Karanth & Sunquist, 1995). We are in agreement, but also add that, although density of groups affects encounter rates, group size would also be an important factor influencing the probability of sighting of prey by the predator. Using only density of groups for selectivity analysis does not take this into consideration. So, for the present study both results from density of groups and individuals were used for understanding the predation pattern of tigers in the study area.

RESULTS

Density and biomass of prey species

Estimate of densities of individuals and groups (along with mean group size, sample size, coefficient of variation and associated confidence intervals) of seven potential prey species present in the study area are summarized in Table 1. The study area was found to harbour a high ungulate density of 90.3 animals km^{-2} with chital and sambar constituting 96%. Density estimates of chital, sambar, wild pig, chowsingha and

Table 2. Proportions of different age and sex classes[a] among different ungulate species in Pench National Park, Madhya Pradesh between November 1998 and April 1999

Species	n	% in each age-size class AM	AF	YM	YF	YG
Chital	766	23.1	43	3.3	7.5	23.1
Sambar	216	25.1	47.1	1.3	4.7	21.7
Nilgai	38	39.1	30.4	2.9	8.7	18.8
Gaur	24	40	31	0	11	18
Wild pig[b]	28	71.6		28.4		
Chowsingha[b]	8	70.0		30.0		

[a] n, total number of groups classified; see the text for details of age–sex classes; %, proportion of individuals in each age–size class; AM, adult male; AF, adult female; YM, yearling male; YF, yearling female; YG, young.
[b] For wild pig and chowsingha, only adult and immature individuals are presented.

common langur did not differ markedly between estimates obtained from ungrouped and grouped data. Thus, for subsequent analyses, the ungrouped data were used. For nilgai, the ungrouped data produced higher density estimates, while the trend was the reverse for gaur. For both these species, the higher density estimates were retained for further analyses as these species often used certain human modified habitats and were rarely encountered on transects, which might have led to an underestimation of their densities. When transect data for different prey species were checked for presence of size bias, none gave positive results. Muntjac were sighted three times during the study period and only once on transects, while rhesus macaques were also seen three times during the study period but never on transects. Chinkara were not sighted during the study. The density figures of ungulates when multiplied with the average weight of the respective species gave a biomass density of 6013.25 kg km^{-2} for the intensive study area.

Population structure and grouping tendency

The age and sex class distribution of six ungulate species in the study area are given in Table 2. The sex ratio was found to be biased towards females of chital and sambar but towards males of nilgai and gaur. For all these species, the ratio of the adult female to fawns was *c.* 1: 0.5. The absence of yearling male gaur sightings was probably a sampling error. Age and sex composition data on common langur could not be collected because of the inexperience of the first author in identifying the different age–sex categories of this species in the field. The proportion of small, medium and large ungulates in the population were found to be 17.8%, 63.2% and 19%, respectively. Group size distributions of the ungulate species in the study area are presented in Table 3. For all species, except wild pig, solitary individuals and family associations (two to three individuals) comprised > 50% of all recorded individuals. Sighting of solitary individuals for species like chital, sambar, nilgai and gaur were mostly of adult males and they were twice as common compared to lone females. Adult males constituted up to the 81% of all solitary gaur sightings.

Composition of the tiger diet

The result of tiger scat analysis is summarized in Table 4. The analysis of 75 scats revealed the presence of nine prey species with a high preponderance of medium- to large-sized ungulates in the tiger's diet. Chital, sambar and wild pig together accounted for 72.7% of all prey consumed, while domestic livestock contributed 8.2%. No remains of gaur and nilgai were found in tiger scats, 4.5% of hair remains could not be identified, while 60%, 34.7%, 4% and 1.3% of the scats contained one, two, three and four types of hair, respectively. Estimation of the relative biomass contribution of different prey species to tiger diet using the equation developed by Ackerman *et al.,* (1984) gave a better assessment of the prey use than results obtained in terms of frequency of occurrence. Although in terms of number of scats, chital contributed three times (47.3%) more than sambar (14.5%), its biomass contribution was only one and a half times more than sambar. The combined biomass contribution of chital, sambar and wild pig to the tiger diet was 76.6%. Domestic livestock made up 12.3% of the biomass of the predator's diet. The average weight of the prey species consumed by tiger was 82.1 kg.

Table 3. Group size distribution[a] of the ungulates and common langur in Pench National Park, Madhya Pradesh between November 1998 and April 1999

Species	n	Range of group size	% in each group size class 1	2–3	4–10	11–30	30+
Chital	1331	1–36	28.9	35.1	30.4	5.7	0.2
Sambar	239	1–6	52.7	38.8	8.5	–	–
Nilgai	43	1–6	69.7	14.0	16.3	–	–
Gaur	43	1–11	39.6	20.9	37.2	2.3	–
Wild pig	75	1–16	25.3	20.0	48.0	6.6	–
Chowsingha	13	1–3	92.3	7.7	–	–	–
Common langur	438	1–38	12.7	25.3	47.6	14.0	0.2

[a] n, total number of groups recorded; %, proportion of groups in each class.

Table 4. Composition of tiger *Panthera tigris tigris* scats ($n = 75$) and relative biomass contribution of different prey species to tiger diet in Pench National Park, Madhya Pradesh between November 1998 and April 1999

Species	No. of scats	Frequency of occurrence[a]	Percentage occurrence[a]	Average body weight (kg)	(%) Biomass contribution
Chital	52	53.01	47.27	55	39.60
Sambar	16	13.78	14.55	212	29.33
Wild pig	12	8.88	10.91	38	7.75
Muntjac	5	5.34	4.55	20	2.61
Cow	6	4.34	5.45	180	9.68
Buffalo	3	2.00	2.73	273	2.64
Chowsingha	2	2.67	1.82	20	1.05
Common lungur	7	3.65	6.36	8	3.08
Sloth bear	2	1.33	1.82	90	2.00
Unknown	5	5.00	4.55	10	2.27

[a] Definitions of frequency of occurrence and percentage occurrence are according to Ackerman *et al.* (1984)

Table 5. Effect of sample size on the frequency of occurrence (*sensu* Ackerman *et al.,* 1984) of prey species in tiger *Panthera tigris tigris* scats as seen through seven increments of random sampling in Pench National Park, Madhya Pradesh between November 1998 and April 1999

No. of	Species									
scats	Chital	Sambar	Wild pig	Common langur	Muntjac	Chow-singha	Cow	Buffalo	Sloth bear	Unknown
10	78.3	8.3	0	8.3	0	0	5	0	0	0
20	60.8	16.6	4.15	5.3	0	5	2.5	2.5	2.5	0
30	57.2	16.1	4.4	3.9	5	3.3	3.3	1.7	1.7	3.3
40	57.9	14.6	4.6	2.9	6.25	5	3.7	1.25	1.25	2.5
50	57.3	13.7	3.7	2.3	8	4	6	1	1	3
60	54.0	13.05	8.9	3.2	6.7	3.3	5.4	1.7	0.8	2.9
70	55.6	13.3	9.04	3.4	5.7	2.9	4.6	1.4	1.4	2.7
75	53	13.8	8.88	3.6	5.3	2.7	4.3	2	1.3	3.7

Successive draws of 10 tiger scats randomly from the sample size of 75 scats gave the cumulative frequency of occurrence of different prey species as shown in Table 5. The proportion of different species in scats were similar once a sample of 50 tiger scats was analysed. Thus, we suggest that a minimum of 60 tiger scats should be analysed to understand the pattern of prey use by tigers in the intensive study area in PNP.

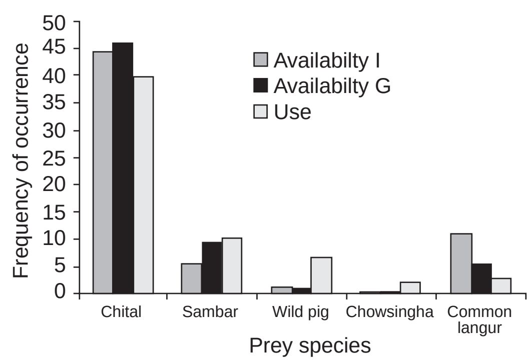

Fig. 2. Comparison of observed and expected proportions of prey use in scats based on group and individual densities of prey species of tiger *Panthera tigris tigris* in Pench National Park, Madhya Pradesh during November 1998 to April 1999. Availability I, Availability G, expected proportions of prey species in tiger scats calculated from density of individuals and groups of prey species, respectively.

Estimation of prey selectivity

Comparison of observed and expected proportions of prey species in tiger scats based on their group and individual densities, rejected the hypothesis of non-selective predation (group density, $G = 22.28$; $P < 0.001$, d.f. = 4; individual density, $G = 34.4$; $P < 0.001$, d.f. = 4). Since there was evidence of selective predation in the overall pattern of prey use by tigers, the results of the analysis were examined to infer the selectivity for each species. Wild pig ($P < 0.001$) and chowsingha ($P < 0.001$) were found to be preyed upon more than their availability, when group density was used to calculate expected proportion of scats (Fig 2). When individual densities were used to arrive at the figures for scat proportions, sambar ($P < 0.05$), wild pig ($P < 0.001$) and chowsingha ($P < 0.001$) were found to be consumed more than availability while common langur ($P < 0.01$) was taken less than availability (Fig. 2). Chital was found to be consumed in proportion to its availability using both group and individual densities.

Table 6. Densities of ungulate species from different areas[a] in south Asia

	ISA	PNCH	KNH	GIR	NGH	BDP	MML	RBNP	CTW
Chital	80.75	51.3	49.7	57.3	38.1	43–45	25.03	29.7–33.9	17.3
Sambar	6.09	9.6	1.5	3.5	4.2	8–9	6.61	–	2.9
Wild pig	2.59	0.8	2.5	–	3.3	2.5	–	4.2	5.8
Gaur	0.34	0.7	–	NP	4.5	0.5	14.38	–	–
Nilgai	0.43	0.7	NP	0.58	NP	NP	NP	5.0	–
Chowsingha	0.29	0.7	–	0.42	–	NP	NP	NP	NP
Wild Buffalo	NP	NP	NP	NP	NP	NP	NP	NP	NP
Muntjac	–	–	0.6	–	6.0	1	–	1.7	6.7

[a] ISA, present study; Pench (PNCH), Kanha (KNH), Nagarhole (NGH), Karanth & Nichols (1998); Bandipur (BDP), Johnsingh (1983); Mudumalai (MML), Varman & Sukumar (1995); Bardia (RBNP), Dinerstein (1980); Chitwan (CTW), Seidensticker (1976). NP, not present; –, very low density or information not available.

Table 7. Biomass of ungulate species from different tropical areas in South Asia

Locality	Forest type	Biomass density kg km^{-2}
Pench (present study)	Tropical dry deciduous	6013.25
Kanha (Schaller, 1967)	Tropical moist deciduous	3902.3–4805.7
Gir (Khan *et al.*, 1996)	Tropical dry deciduous and thorn	3292
Bandipur (Johnsingh, 1983)	Tropical dry deciduous	3382–3619
Nagarhole (Karanth & Sunquist, 1992)	Tropical dry and moist deciduous	7638
Bardia (Dinerstein, 1980)	Tropical moist with alluvial grasslands	2842–3120
Chitwan (Eisenberg & Seidensticker, 1976)	Tropical moist with alluvial grasslands	2933
Kaziranga (Karanth & Nichols, 1998)[a]	Tropical moist with alluvial grasslands	4252

[a] For Kaziranga, available density estimate was converted to biomass density by taking average weight of species from Eisenberg & Seidensticker (1976).

DISCUSSION

Density and biomass of prey species

Ungulate densities estimated in the present study, when compared with those from other areas in south Asia (Table 6), revealed that Pench harbours a high density of chital and sambar. The study area is dominated by fairly open canopy, mixed forest with considerable shrub cover interspersed with small open grassy patches. This condition of high habitat heterogeneity probably favoured the observed high density of browser and grazer (Eisenberg & Seidensticker, 1976) such as sambar and chital, respectively. Another factor, which might have influenced the high abundance of grazers such as chital in the area, was the availability of the grass *Cynodon dactylon* L., a nutritious forage during late winter and early summer months along the banks of Pench river when water from the submergence area recedes. Nilgai and gaur, because of the habitats they used, were poorly represented on transects and their density figures are probably underestimates. Nilgai mostly used open areas and relocated village sites while gaur herds were sighted more frequently close to roads during the early morning and the late afternoon. The density of common langur was also very high in the study area. The only other available estimate of prey density from Pench is that of Karanth & Nichols (1998). Their results also indicate the presence of a high prey density in the area, though the individual density figures for the ungulate species were different (Table 6). While comparing the prey biomass density between Pench and other areas (e.g. Nagarhole, Bandipur, Chitwan and Bardia) the estimates of elephant and rhino were excluded since they rarely contribute to the diet of tigers (Sunquist, 1981; Karanth & Sunquist, 1995). Comparisons revealed that Pench has the second highest prey biomass density after Nagahole (Table 7). Prey biomass densities in these areas varied between 2933 kg km^{-2} (Chitwan, Nepal) (Eisenberg & Seidensticker, 1976) to 7638 kg km^{-2} (Nagarhole in South India) (Karanth & Sunquist, 1992). As these sites represent few of the last remaining suitable habitats for tigers, tigers in the subcontinent have the highest chance of survival in areas that have high biomass densities comparable to these sites (Table 7). The prey biomass should be distributed across different age and sex classes of medium- to large-bodied prey species, because they make the biggest contribution to the tiger diet, as seen in this study and also in other areas (Table 8) (Karanth & Stith, 1999; Sunquist *et al.,* 1999).

Food habits of tigers

Results from scat analysis showed that selective predation by tigers was directed towards prey species with a medium and large body mass. Though Karanth & Sunquist (1995) found selective predation of tigers towards large-bodied prey in South India, they did not notice the same for medium-sized prey as seen in the present study. Deer species accounted for 72.13% of the

Table 8. Frequency of occurrence of major prey species in tiger *Panthera tigris tigris* scats from different areas of the Indian subcontinent

Species	Pench	Kanha	Bandipur	Nagarhole	Chitwan 1	Chitwan 2	Bardia
Chital	53.01	52.2	39	31.2	33.3	61.8[a]	77.7
Sambar	13.78	10.4	30.5	24.9	29.3	20.0	–
Muntjac	5.34	–	–	6.1	4.1	–	–
Barasingha	N.P.	8.6	N.P.	N.P.	N.P.	N.P.	1.4
Hog deer	N.P.	N.P.	N.P.	N.P.	15.4	–	7.7
Wild pig	8.88	0.8[b]	5.5	9.4	10.6	3.6	8.8
Gaur	–	8.3	5.5	17.4	N.P.	–	N.P.
Nilgai	–	–	N.P.	N.P.	–	–	1.9
Chowsingha	2.67	–	–	–	N.P.	N.P.	N.P.
Common langur	3.65	6.2	–	3.9	5.7	3.6	2.3
Cow	4.34	5.9	5.5[c]	–	–	1.8[c]	–
Buffalo	2.00	1.7		–	–		–
Others	6.33	6.1	14	7.1	1.6	9.0	5.2

[a] Includes percent occurrence of chital, hog deer and muntjac.
[b] Both domestic and wild pigs.
[c] Domestic livestock as a whole.
Pench, present study; Kanha, Schaller (1967); Bandipur, Johnsingh (1983); Nagarhole, Karanth & Sunquist (1995); Chitwan 1, McDougal (1977); Chitwan 2, Sunquist (1981); Bardia, Stoen & Wegge (1996).

prey species consumed by tigers in Pench. This pattern is corroborated by findings from other studies on the food habits of tigers (Table 8) (McDougal, 1977; Sunquist, 1981; Johnsingh, 1983; Karanth & Sunquist, 1995; Stoen & Wegge, 1996) where cervids contributed on average up to 75% of the total prey intake of tigers (Sunquist *et al.*, 1999). Chital in the study area contributed maximally to the diet of tiger and was consumed in proportion to its availability. Earlier studies (Johnsingh, 1983; Karanth & Sunquist, 1995; Stoen & Wegge, 1996) have reported an under use of this prey species by tigers when compared to its availability. In Pench, chital occurred in higher densities than in other areas, which might have increased their encounter rate with the predator, eventually increasing the chance of predation. The gregarious nature of chital is also supposed to be one of the factors that reduces the chance of tiger predation (Karanth & Sunquist, 1995). So we compared grouping tendency and mean group size of chital from Pench with those of Nagarhole and Chitwan (Seidensticker 1976; Karanth & Sunquist, 1992, 1995). In Pench, chital had a lower average group size of 3.44 individuals when compared to 6.27 individuals in Nagarhole (Karanth & Sunquist, 1992) and was also found to be more 'solitary' than those in Nagarhole and Chitwan. Of all the chital sightings in Pench, 28% were of lone individuals, while in Nagarhole and Chitwan it was 14% and 18%, respectively. Moreover, chital groups in the study area were seen to forage around moist streams and small grass clearings surrounded by forests on three sides (pers. obs.), which probably rendered them more vulnerable to predation by tigers since it uses terrain, cover and habitat features for stalking its prey (Sunquist, 1981; Stander & Albon, 1993; Karanth & Sunquist, 2000).

Sambar formed the second most important prey species for tigers in our study site, and was consumed in excess of its availability only when the selectivity test was carried out using the density of individuals. When compared to studies from other areas, the predation rate on this species by tigers was relatively lower in Pench except at Kanha (Schaller, 1967) (Table 8). All the sites where predation on sambar was more than Pench indicate a correspondingly lower degree of chital predation by tigers. With the present data, we are unable to comment on the observed low, yet selective predation of sambar by tigers. Wild pig in the study area was preyed upon more than the availability, and is a regularly preyed upon species by tigers over most of its distribution. A recent study indicates that in one of the sites in the Sikhote-Alin mountain area of Russia, high overlap of habitat use between tigers and wild pigs (Miquelle *et al*., 1991) might have facilitated a high level of tiger predation on the wild pig. Information on habitat use of wild pig is needed from the Indian subcontinent to conclude whether a similar overlap in habitat use is influencing tiger predation on this species in the region. Though there was no indication that tigers killed gaur during the study period as evident from the scat analysis, there was a single sighting of a gaur kill from the western part of the PNP. The primary factor influencing predation rate on gaur in our study area is probably their low density. Apart from low abundance, the gaur population in the study area is also transient in nature and could be seen in larger numbers during the summer (M. K. S. Pasha & G. Areedran, pers. comm.). In Nagarhole, where gaur occur in much higher densities than Pench (Table 6), tigers are found to frequently prey upon gaur individuals (Karanth & Sunquist, 1995). The absence of nilgai remains in the tiger scats was probably due to the combined effect of their low density and habitat use. Nilgai are found mostly in open areas and relocated village sites that have a featureless terrain with little cover, a habitat highly unsuitable for tigers to hunt (Karanth & Sunquist, 2000). We consider the selective predation on chowsingha by tiger in the study area to be a rare event since this species is too small to be a profitable prey for tigers. It occurs in very low density and is patchily distributed in the park. The low occurrence of muntjac hair in tiger scats is probably a result of the infrequent predation of muntjac by tigers given the extremely low abundance of this species in the study area. The arboreal nature of common langur tends to explain its under-representation in the diet of tigers (Karanth & Sunquist, 1995). The presence of sloth bear hair in tiger scats is likely to be a result of occasional tiger predation on this species since sloth bears do not form a regular prey base for tigers. Though there was no livestock grazing in the study area, areas immediately outside the boundaries of the park are subjected to a high level of grazing. Since tigers are wide ranging in nature (Sunquist, 1981; Karanth & Sunquist, 2000), the observed occurrence of livestock remains in tiger scats during the study were possibly a result of predation outside the study area.

Tigers inhabit diverse forest types of varying altitudes, temperatures and rainfall regimes (Seidensticker, 1997; Miquelle *et al.,* 1999). To effectively use prey assemblages in these different ecosystems, a predator needs considerable behavioural plasticity. As is evident from an earlier study (Seidensticker & McDougal, 1993), large body size and flexibility of predatory behaviour releases tigers from the constraint of prey specificity and allows them to harvest large-bodied prey along with medium sized ones. Human activity has already modified all habitats where tigers occur, leading to a drastic reduction in the ungulate distribution and abundance (Sunquist *et al.,* 1999). In the face of such an onslaught, larger-bodied ungulates become more vulnerable because of their low turnover rates (Geist, 1974), eventually becoming extinct from those sites (Sunquist, 1981; Karanth & Sunquist, 1995). Thus, only in a few areas such as Nagarhole in South India, where the whole complement of ungulate species occurs in abundance (Karanth & Sunquist, 1992), are tigers able to substantially use the available biomass of large-bodied ungulates like gaur (Karanth & Sunquist, 1995). This also allows leopards to thrive in the same area without any behavioural and habitat segregation, thus maintaining the carnivore community intact (Karanth & Sunquist, 1995, 2000; Karanth & Nichols, 1998).

The tiger evolved from the *Panthera* stock following the Pleistocene radiation of large-bodied cervids and bovids in South-east Asia, which created a niche for a large-bodied forest-edge predator to hunt them. This evolutionary predisposition of tigers as a predator of the largest cervids and bovids of any assemblage should be taken into consideration and high priority should be given to the conservation of ungulate species along with that of the predator. Given the paucity of resources for conservation of tigers throughout its range, it is essential to prioritize areas where the probability of the tiger's survival is highest in the future (see Wickramanayake *et al.,* 1999 for a detailed discussion). These are areas where the tiger's basic need for a large unfragmented habitat and high-density prey populations are met (Karanth & Nichols, 1998). Pench is among those areas that still harbour high prey density with tigers mostly depending on wild prey rather than domestic livestock for food as in many other areas of the Indian subcontinent (Chundawat *et al.,* 1999). From the present study it can be concluded that Pench, because of its high density ungulate prey base, has the potential to accommodate a higher density of tigers, making it comparable to few of the best remaining tiger habitats of the Indian subcontinent (Karanth & Nichols, 1998). Thus, protection of the habitat along with regular monitoring of tigers and their prey population using comparable scientific methods is essential for Pench National Park to emerge as one of the most important areas for tiger conservation in Central India.

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