THE ECOLOGY OF THE DHOLE OR ASIATIC WILD DOG (*Cuon alpinus*) IN PENCH TIGER RESERVE, MADHYA PRADESH

Dissertation submitted to Saurashtra University, Rajkot, Gujarat, for the award of the Degree of Doctor of Philosophy in Wildlife Science

Submitted by:

BALEBAIL BHASKAR ACHARYA

Under the supervision of:

Dr. A. J. T. Johnsingh

Wildlife Institute of India
Dehradun

January 2007

19th January 2007

CERTIFICATE

This is to certify that the thesis titled "**The ecology of the dhole or Asiatic wild dog (*Cuon alpinus*) in Pench Tiger Reserve, Madhya Pradesh**" submitted for the award of degree of **Doctor of Philosophy** in **Wildlife Science** to Saurashtra University, Rajkot, is a record of original and independent research work carried out by **Mr. B. Bhaskar Acharya** under my guidance. No part of this thesis has been submitted in part or full to any other University/Institution for the award of any degree and it fulfils all the requirements laid down by Saurashtra University

Dr. A. J. T. Johnsingh
Ph. D. Supervisor
Ex-Dean,
Faculty of Wildlife Sciences
Wildlife Institute of India

Forwarded

Mr. P. R. Sinha
Director
Wildlife Institute of India
Dehradun

Director
Wildlife Institute of India
Dehradun

ACKNOWLEDGEMENTS

My sincere thanks to the Madhya Pradesh Forest Department for according the necessary permissions for this field study in Pench Tiger Reserve. I appreciate the support and trust by the Department by permitting the capture, radio-collar, and track dholes in Pench. In the former Field Director, Mr. R.G. Soni, I had someone who was constantly pushing me to achieve the maximum from this study. The current Field Director, Mr. N.C. Dungriyal, who joined in at a later stage of the study, quickly picked up from where Mr. Soni had left, and ensured the good work is not abated. Mr. L.K. Choudhury, the Deputy Director at the commencement of fieldwork, ensured every bit of logistics and staff support was given to me in field. His successor, Mr. Subharanjan Sen, not only ensured I got what I wanted from the staff, but was a close friend in field. Karmajhiri Range Officer Mr. Dondwe ensured my accommodation and local needs and logistics were in place at Karmajhiri Forest Camp. Foresters Mr. Gautam Soni, and Mr. Pathak (Karmajhiri), Mr. Damodar Patle (Turia), Mr. Thakur (Alikatta) served as eyes and ears within their circles, sending me word whenever necessary. I also thank Mr. Jarnail Singh, Field Director, Pench Tiger Reserve, Maharashtra, for granting immediate permission to monitor the radio-collared dhole that had crossed over to Maharashtra from Madhya Pradesh.

Special mention needs to be made of Jamtra Forester Mr. Tiwari, and his Forest Guard Mr. Katre, without whom I would not have been able to locate the dholes on several occasions. Other Forest Guards I an indebted to are Mr. Thomas (Kamrit), Mr. Rajput (Karmajhiri), Mr. Washington (Alikatta), Mr. Inwathe (Pivarthadi), Mr. Salame (Baagdev), and Mr. Pandey (Karmajhiri Territorial). Wireless operators Kaaru and the late Prakash provided valuable communication links for me. Dr. Akhilesh Mishra, Park Veterinarian, and WII researcher Mr. Karthikeya S. Chauhan are thanked for helping with the capture and radio-collaring operations.

No words can describe how much my field assistants Gurhan Lal Sirsham, Brij Lal Uike and Kaliram Inwathe have put in for the fieldwork. They bore the heavy burden of tracking through long odd hours, over difficult terrain and in inclement weather without a murmur of protest. Without them and the able driver Ramesh Marskole most of the fieldwork would not have been possible.

WII researcher Mr. R. Jayapal and his C.I.H. Bird Project Team were a constant and welcome presence in Pench. This study benefited in many ways from their support in times of need. I valued their company very much. Special thanks to Jayapal for tolerating me for such a long time.

Back in WII, former Director Mr. S.K. Mukherjee is deeply thanked for deftly removing the many obstacles in getting the project off successfully. His successors, Mr. Sawarkar, Mr. Singsit, and Mr. P.R. Sinha, ably supported the project to its completion. The All-India Tiger Monitoring Project (WII-Project Tiger) has been most kind to employ and support me during the analyses and write-up stage of this thesis.

I am most grateful to the scientists and staff of the Wildlife Institute of India. Dr. Jhala made the extra effort to help with the dhole captures. Drs. Goyal and Qamar Qureshi provided constant encouragement. Mr. Vinod Thakur's valuable assistance in the scat analyses is gratefully acknowledged. In the GIS Cell, Mr. Panna Lal helped a lot in the production of maps. Librarian Dr. M.S. Rana, and his staff ensured that I could put the library to its maximum use. Veerappan deftly sorted out many glitches I faced with the computers. Advait provided timely help with prey density estimation and with ArcView. I could not have done without the timely help from Priyadarshini, Yoganand and 'Brother' GopiGV at the time of thesis submission. Virender was quick and efficient with the printing and binding of this thesis.

I will never forget the love and affection of the Deshpande family in Nagpur, for providing me a home away from home. I thank all my friends who wrote to me by post (Priyadharshini, Gopisundar, Padhu, Antesh, Divya & Shridhar) when I was in field, and by email (Jayanti, Narendra Babu, Smitha, Yogish, Bindu, Bhatta, Tanushree, Meena, PriyaB, Raghu, Kashmira, and the Tuluva, Viveka, 5wildmess, flatpasunga email groups) during the analyses and write-up stage of this thesis. Anupama provided the much needed moral support to me whenever I was down. My brother Sudhir, despite his numerous protests, provided most of my material support. My little niece Anushka provided the smiles when I needed them most.

From my guide, Dr. Johnsingh, I learnt a lot more about life and values than about wildlife and dholes. It has been a privilege to be his student. A towering personality and an example to emulate, he continues to be an inspiration to many a wildlifer in India and elsewhere.

Dr. K. Sankar not only has been constantly 'guiding' me at WII all these years but also rescuing me from difficult situations on several occasions. Mrs. Sankar always treated me as another member of the family, making me feel I was not far from home.

I thank my father for putting the wildlife bug in me, and my mother, for being there, always!

CONTENTS

Contd..

LIST OF TABLES AND APPENDICES

contd...

~ * ~

LIST OF FIGURES

LIST OF MAPS

LIST OF PLATES

ABSTRACT

The Asiatic wild dog or dhole (*Cuon alpinus*) is one of the least studied social carnivores in the world. Even in many of the well-protected reserves, up-to-date scientific information on existing dhole populations remain negligible. It is most vital that a conservation strategy be evolved by collecting information on the biological and ecological requirements of dholes, and to identify the threats to the species at various levels. There is therefore an urgent need for in-depth, scientific research on dholes.

In order to gather such information on dholes, a four-year field research study on the dhole in Pench Tiger Reserve, Madhya Pradesh was initiated in May 2001. Pench Tiger Reserve in central India was chosen as the study site due to the relatively high and consistent presence of dholes, a large prey base, an existing logistic and research framework of the Wildlife Institute of India established at Pench, and relatively low biotic disturbances within this Reserve.

The objectives of this study in Pench Tiger Reserve, Madhya Pradesh, were to estimate the abundance of dhole prey species, to assess the diet of the dhole packs from their scats and kills, to determine ranging and movement patterns of dhole packs and to estimate dhole population size for the Tiger Reserve.

To collect information on the home range, habitat use, movement and activity patterns of dholes, three individuals from different packs were captured, immobilized, fitted with radio-collars and subsequently tracked for five to 12 months in this study. This study has the distinction of being the first long-term radio-telemetry study of dholes anywhere in their geographical range.

Systematic estimation of prey abundance was conducted on 19 permanently marked line transects and 10 un-marked GPS-based transects, averaging a length of 2.3 km each (1.2 - 3.5 km) for the dry seasons (Nov-June) from 2001 to 2003, using the Line Transect Method. Line transect sampling was carried out only within the approximate ranges of each radio-tagged pack, for the period November 2003 – June 2004. The transect lines covered an actual area of 85.2 km^2, which was ca. 29 % of the National Park area, and 11 % of the Tiger Reserve. Over the study period, the total annual length of transects in the study area averaged 41.2 km (27.3 – 51.0 km). Sighting angles and distances were

recorded accurately using a compass and a laser rangefinder respectively. The computer Program DISTANCE Version 4.1 Release 2 was used for analyses of line transect data, choosing the appropriate models with the lowest Akaike information criterion values, to yield density estimates of the different dhole prey species. The common langur data used was only from those individuals of a troop that were sighted on ground, to reflect what was available as prey to dholes.

It was found that data on abundances of gaur and nilgai, from line transects, was not adequate. The number of sightings from line transects was high for chital (n=449) and langur (n=261), medium for sambar (n=142), adequate for wild pig (n=70). Chital, followed by langurs on ground, were most encountered dhole prey species from both line transects and road counts.

Data regarding the encounter rates (numbers of animals sighted per km travelled) and group composition (group sizes, age-sex structure, etc.) of dhole prey species were also recorded using vehicle-based road counts from a four-wheel drive vehicle. A total of 660 km was travelled for the period 2001-2004.

Chital by far were the most numerous of the prey species in Pench. This species dominates the landscape in Pench in terms of both sheer numbers and biomass. Sambar, though, being the third-most numerous prey species in Pench, contribute the most in biomass next to chital. Their density in Pench is relatively on the high side, and this fact corroborates the great potential of Pench for large carnivores, as sambar is a keystone prey species.

Populations of both the two major prey species, chital and sambar, were dominated numerically by adult females, showing a clear female-biased sex ratio. In the case of chital, adult females constitute nearly half their population, whereas in sambar adult female form more than half the population. The adult sex ratios in the two prey species were: 50 males to 100 females in chital; 22 males to 100 females in sambar. The female: fawn ratio was 1: 0.27 for chital, and 1: 0.3 for sambar. Mean group size of chital was 22.58 (± 2.2 SE), while that of sambar was 3.15(± 0.2 SE).

Biomass densities of the different prey species were computed by multiplying the estimated mean numerical densities by the published average weights of the respective age/sex-classes of the species. From the population structure of the prey species obtained from the *ad libitum* counts, the biomass was corrected for the actual population structure.

Dhole scats (n= 725) and kills (n=137) were recorded whenever encountered, for dietary analyses to yield information on the prey species consumed, their age and sex class, and further on, biomass consumed. Only one scat was collected per site/pack per day to ensure scat samples were independent. Kills made by dholes were located by actively searching the study area for the same, or on an *ad libitum* basis.

The diet of dholes was estimated using standardised faecal analysis to determine the relative frequency of occurrence of prey species remains in scats, and also by recording the frequency of kills of particular prey species to determining age and sex class of prey killed. From these, prey selection by the dhole was arrived at.

Since prey distribution and abundance varies seasonally, wet and dry season diets and prey selection were compared between these seasons and focused on frequency of occurrence. Prey encounter rates obtained from line transects and road counts were used as indices of prey encounter by dholes. Percentage frequencies of different prey species in dhole scats was calculated by enumerating the number of scats with remains of a particular species out of the total number of scats with prey remains, depicted in the form of a percentage figure. Frequency of occurrence of a prey species was calculated as the number of occurrences of that prey species divided by the total number of scats analysed, also expressed as a percentage. Further, the relative numbers and biomass of different prey consumed by dholes and the relative biomass contribution of different prey species to the dhole diet was estimated.

Analysis of dhole scats and kills indicated that dholes consumed a minimum of seven prey types. Of the 725 dhole scats analysed, sambar remains were the most frequent prey item in dhole scats (nearly 50 %), followed by that of chital (38%). Significantly, 31 scats contained remains of langur. Around 6 % scats contained remain of more than one prey species. Analyses indicated that sambar was the only prey species preferred by dholes i.e. consumed more than their availability in the study area, while chital, langur and wild pigs were consumed less than their availability. Wet and dry season diets of dholes did not show any significant difference.

In total 137 dhole kills were assessed with respect to prey species, its age-sex class, and identity of dhole pack (if known). 53% of the dhole kills recorded were made in the morning, 27% in the evenings and 6.5% were kills around mid-day. Only one kill was recorded to have been made in the night. More than 80 % of the 137 dhole kills recorded for this period were that of chital, and around 13 % that of sambar. The age-sex class distribution of each major prey species in the kills data was compared with the corresponding population age-sex distribution recorded from road counts and *ad libitum* counts, to check if dholes were selecting for a particular age-sex class of their prey. There appears to be a significant sex-bias in dhole kills of chital, with more kills of adult stags compared to those of does. Adult chital stags and fawns were taken significantly more than their availability in the population, whereas adult chital does were taken significantly less than their availability. There was no significant selection for sub-adult chital by dholes Among chital stags killed by dholes, 65% were in ‘velvet’, and 35 % in ‘hard’ antler.

In the case of sambar, the juvenile age class (sub-adults and fawns) accounted for more than three-quarter (78%) of sambar killed by dholes, of which fawns alone formed half the number of kills. Dholes showed selection for age-sex classes of sambar too. Sub-adult sambar and fawns were taken significantly more than their availability in the population, whereas adult sambar does were taken significantly less than their availability. There was no significant selection for adult sambar stags by dholes.

The average weight of the major prey killed by dholes was 55.3 kg. Nearly 70% of the kills were that of the 26-100 kg size class, with the large (51-100 kg) prey size being the preferred weight class by dholes. There was no significant correlation between dhole pack size and the prey weight. Average meat available for consumption per dhole per kill amounted to 7.54 kg.

In all, sambar and chital constituted by far the main prey of dholes, with just these two species making up about 95 % of all kills and scats recorded in this study.

The radio-telemetry study revealed that home range sizes of radio-collared dholes in Pench covered 66.4 km^2 to 202.8 km^2 (95% MCP). Seasonal home range size averaged 77.58 (± 26.6 SE) km^2, while core areas of dhole packs averaged 57.5 (± 18.8 SE) km^2 (80% ADK). Activity centres of dholes averaged 32.2 km^2 (18–57 km^2) (65% HMM). Dhole packs restricted themselves to a small area (15-20 km^2) during the denning and nursing season (winter: Nov-Feb).

Ranges increased (30-60 km^2) gradually during post-denning (pup-rearing) season (spring-summer: Mar-June). A great increase in home range sizes (< 100 km^2) occured during the dispersal & pre-denning season (monsoon: July-Oct). Based on intensive tracking of an optimal pack of 14 dholes, it was conclude that 60-70 km^2 would constitute the ideal home range area required for a dhole pack, with a smaller activity centre of ca. 20 km^2. Thus, the dhole density in Pench would be 0.2-0.23 dholes/km^2 or 1.43-1.66 packs/100 km^2. Monthly range sizes of the radio-collared dholes ranged from a minimum of 1.5 km^2 to a maximum of 92. 6 km^2. On an average, monthly ranges covered around 38 km^2.

Mean daily distance (inter-day distance) moved by dholes in Pench spanned 2.96 km (± 0.16 SE) whereas mean travel speed of dholes packs was 2.54 km h^{-1} (± 0.36 SE), with a maximum travel speed of 16.1 km h^{-1} in one session.

Based on the monthly range sizes and corresponding pack sizes of the three dhole packs, it was found that mean density of dholes in Pench was 0.29 (0.08 ± SE) dholes km^{-2}, or 2.9 dholes per 10 km^2. This density ranged from a minimum of 0.02 to a maximum of 1.34 dholes km^{-2}. If one of the study packs, ♀44 + 13 dholes, with a home range of 60-70 km^2 were to be considerd as the ideal dhole pack, then the density would be 0.2-0.23 dholes km^{-2} or 1.43-1.66 packs per 100 km^2.

Chapter 1. INTRODUCTION

1.1. Introduction

The dholes or Asiatic wild dogs (*Cuon alpinus* Pallas 1811) are one of the most remarkable carnivores in the Asian jungles. The term 'dhole' is reported to have an ancient Asiatic origin signifying "recklessness and daring" (Mivart 1890). Dholes are group-living canids, in many ways resembling the wolves (*Canis lupus*), the African wild dogs (*Lycaon pictus*), and the South American bush-dog (*Speothos venaticus*) in their life history traits (see Johnsingh 1982b). Like wolves, dholes run down their prey, biting as they chase, and feeding while the prey is still alive. As expected, this behaviour has led to unjustified revulsion and calls for their extermination, and were highly persecuted in the past.

Within peninsular India, dholes are encountered specifically in dense forests and thick scrub jungles (Krishnan 1972, Davidar 1975), making them difficult animals to find and to observe, unlike the wild dogs of the African savannah. The prime factors that determine dhole habitats are prey abundance, water availability, interspersion of forests with grassy openings, minimum human disturbance, and potential den sites (Johnsingh 1985). Dholes are extremely fond of water and are often seen resting or playing in shallow waters in the hot season, particularly after hunts. In fact, dholes are excellent swimmers.

A dhole pack is an extended family unit as in wolves (Mech 1970) and African wild dogs (Malcolm 1989), and it usually includes the nuclear family and possibly the non-reproductive siblings of the adult breeding pair. Dhole packs exhibit a remarkable degree of co-operation in hunting down prey. However, on rare occasions, hunting by lone individuals or a pair has been observed. Hunting strategies and methods may vary depending on hunting pack size, prey type, and habitat conditions. Dholes are predominantly diurnal in habit, hunting mainly in the mornings and evenings (Johnsingh 1983). As a prelude to a hunt, dholes perform a 'pep rally' involving vigorous activities such as aggressive play, mock chases, etc. Once suitably ‘stimulated’, the pack usually moves in single file, trotting at a gradual pace, often on roads, tracks or forest paths, sniffing and scanning the surrounding area for potential prey. Most chases do not last long, as the dholes use a combination of speed and teamwork to bring their prey to bay. Small animals are swiftly dealt with, while large prey is attacked from the rear.

The injured prey eventually dies of severe shock and loss of blood. Dholes are rapid and voracious feeders.

Dholes locate prey mainly through their keen sense of smell (Jerdon 1874, Prater 1980). Once the prey is flushed and flees, the visual and auditory senses of dholes help them chase the prey. Dholes have distinct 'latrine sites' on paths, roads or intersections, where the whole pack may defecate communally. A unique feature of dholes is a characteristic whistle, repeated at intervals, which they use as a contact call when they are unable to sight other pack members, and wishes to reassemble after a hunt or re-group after separation (Phythian-Adams 1927).

1.2. General Description

Adult male dholes weigh between 15 to 20 kg, standing around 50 cm at the shoulder. The total body length comes to around 130 cm, including the 40-45 cm long tail. Females are slightly smaller than the males (Prater 1980). Dholes are uniformly-marked and there is little variation between the members of a pack. Since they are more-or-less monomorphic, it is not very easy to distinguish sexes, and individual recognition in field is extremely difficult.

The term ‘wild dog’ is in fact a misnomer, as dholes are generically distinct from the true dogs. The ears are slightly rounded and furrier. The muzzle, viewed from the side, is slightly convex and shorter than typical dogs. In contrast to other the canids, the dholes have extremely well-developed jaw muscles, which gives their angular head an almost hyaena-like appearance. The teeth on the lower jaw are fewer (six molars) than in typical dogs (seven molars), the last molar being absent. However, the teats in females are more numerous (12-14) than the typical dog number (i.e. 10) (Prater 1980). The coat colour is usually bright rust-red, paler ventrally. Some races however may have a duller pelage, tending to brownish-grey. Dhole pups are born with a sooty-brown coat, progressively turning russet-red with age Fox (1971). Wagging of the tail, a sign of pleasure or happiness, typical of domestic dogs, is common in dholes too. Unlike domestic dogs, the tail is straight, usually held slightly lower than horizontal. The black tail is bushier than in wolves and jackals. In some individuals, the tail has a pronounced white or grey tuft of hair at the extreme tip (Brander 1923).

1.3. Geographical Distribution

India, like most tropical countries, harbours a large number of mammalian carnivores, 55 in all, within its limits (Corbett and Hill 1992), many of which are sympatric within protected areas (Johnsingh 1986). The dholes have a geographical range stretching from Siberia in the north, India in the west, Java in the south, and China in the east (Fox 1984, Johnsingh 1985). Oddly, dholes occur on the islands of Sumatra and Java, but not on those of Japan, Sri Lanka or Borneo (Pocock 1936, Ellerman and Morrison-Scott 1951). In effect, dholes are the most widespread canids of the Indian, the Indo-Malayan and the Indo-Chinese sub-regions of the Oriental region. Currently however, dholes are either extinct or extremely rare in China (Haibin and Fuller 1996). Such a problem of rarity or extinction is evident from many other parts of their range, such as Siberia. A major stronghold of the dholes still remains in the forests of south and central India, and probably Myanmar too (Johnsingh 1985).

Among the South Asian sub-populations, Johnsingh (1985) reported *C. a. dukhunensis* to be frequently seen in many of the protected areas south of the river Ganga with the forests of the Central Indian Highlands having the largest population of dholes, followed by the Western and the Eastern Ghats of southern India. Small groups of *C. a. primaevus* are occasionally seen in places like Corbett Tiger Reserve (Israel and Sinclair 1987), but rarely encountered in Himachal Pradesh. This subspecies is rarely seen in Chitwan (Stewart 1993), Royal Bardia (Israel and Sinclair 1987) and Langtang (Green 1981) National Parks of Nepal. The Tibetian dhole *C. a. laniger* in Ladakh, is also rare. Some of the north-eastern states of India have shown a decline in dhole sightings. But dholes are frequently seen Arunachal Pradesh and the subspecies in Namdapha Tiger Reserve would be *C. a. adustus*, which is also found in Myanmar. In Bangladesh, dholes occurred in the past in the hill tracts of Chittagong and Sylhet. Dholes (both *C. a. adustus* and *C. a. infuscus*) may be common in most of the forested tracts of Myanmar, though the geographical limits of these two subspecies are unknown, compounded by the negligible ecological information emanating from Myanmar. One also has to keep in mind that hunting of ungulate prey is rampant here.

Among the South Asian sub-populations, Johnsingh (1985) reported *C. a. dukhunensis* to be frequently seen in many of the protected areas south of the

river Ganga with the forests of the Central Indian Highlands and the Western Ghats having the largest populations of dholes, followed by the Eastern Ghats of southern India.

1.4. Conservation Status

Dholes have had a long history of persecution by humans (Fox 1984), particularly well documented in India, where bounties were arranged for killing them (reviewed by Davidar 1968). The systematic killing of dholes was in fact promoted citing them as competitors to human (sport) hunters who accused dholes of wiping out entire populations of 'game' (Burton 1899, Phythian-Adams 1939, 1949). This line of thought completely ignored the fact that dholes, their prey, and also their co-predators, have co-existed sympatrically for ages (Krishnan 1972). Dhole kills were often poisoned with strychnine (Burton 1899, Witt 1907). This persecution was eventually stopped only when dholes were brought under the legal protection of the Indian Wildlife (Protection) Act of 1972 (Ginsberg and Macdonald 1990). Though this has helped to check the drastic decline of the dhole in many reserves within India, the trend has not halted overall, particularly in places where dholes frequently prey on livestock.

Dholes are listed as 'threatened' according to the Indian Wildlife (Protection) Act of 1972 (Schedule II) and 'vulnerable' by the IUCN (Appendix II of CITES). However this status has been accorded to the species without taking into consideration the almost extinct status of some of the dhole sub-species and their uncharted distributions. Such information on their status, abundance, and distribution of sub-populations throughout their geographical range, especially in Myanmar and China, is vital for the conservation of this species.

1.5. Threats

Throughout the world, the major cause of mortality of wide-ranging large carnivores is conflict with humans on the edges of protected areas. Because of their high energy requirement, the territories of these carnivare large and they are therefore exposed to threats at reserve boundaries. Carnivores are killed through hunting and poisoning, collisions with vehicles, and diseases from domestic animals (Woodroffe and Ginsberg 1998).

Dholes have been facing a variety of threats from humans. Encroachments by humans into its forested habitat for agriculture, stealing of kills, cattle grazing, fodder, fuel-wood, and non-timber forest products collection, have pushed the dhole to high degree of isolation and even local extinction (Johnsingh 1984). More so, increasing cases of poisoning of kills, den digging and killing of pups, diseases, poaching and resultant prey depletion may have contributed greatly to hasten the dholes' decline (Fox 1984), making it go the way of the African wild dog (*Lycaon pictus*).

1.6. Study Justification

Dholes are one of the least studied social carnivores in the world (Fox 1984). Even in many of the well-protected reserves, up-to-date scientific information on existing dhole populations remains negligible. Very few specific long-term studies have been conducted on this species (Johnsingh 1982a, Venkataraman et. al. 1995). More urgently, the steady decline in their numbers due to reduction in prey base, habitat destruction, and other human mediated threats, have made dholes either rare or absent in many parts of their supposed range. It is most vital that a conservation strategy be evolved by collecting information on the biological and ecological requirements of dholes, and to identify the threats to the species at various levels (Ginsberg and Macdonald 1990). For instance, the requirements of dholes in terms of space and food, the risks of disease outbreaks, the impacts of their predation on prey populations, and the factors that control the amounts of food consumed by a pack need to be known. Some important parameters associated with hunting strategies in relation to pack size have not been looked into. To supplement the basic information given by earlier studies (Johnsingh 1983; Karanth and Sunquist 1995), more information on inter-specific relationships, competition and niche separation between the dhole and other sympatric large carnivores, such as tiger and leopard, would be of relevant conservation value. In the absence of radio-telemetry studies on dholes, causes of mortality of pups and sub-adults have not yet been tracked with certainty. It is essential to acquire more information on the dispersal or philopatric patterns of dhole individuals and pack formation, as this would throw light on dhole social and population dynamics, colonising ability, mortality rates, and inbreeding risks. Being top predators, dhole abundance and distribution may provide important indicators of prey abundance and habitat quality in general, thus qualifying to be considered a flagship species. There is therefore an urgent need for in-depth, scientific research on dholes. Only with this knowledge, can initiatives to conserve this fascinating species succeed.

In order to gather such information on dholes, a four-year field research study on the dhole in Pench Tiger Reserve, Madhya Pradesh was initiated in May 2001, involving radio-telemetry. Radio-telemetry can help in collecting accurate data on the movement patterns, feeding and habitat use, breeding, dispersal and mortality of dholes. The data collected on dholes and allied mammals in Pench TR would have most relevant management applications pertinent to protected areas and for further research in the other locales in the range of the dholes. These efforts are oriented ultimately towards planning a conservation plan for dholes.

1.7. Why Central India?

Pench Tiger Reserve in central India was chosen as the study site due to reports of consistent presence of dholes, a large prey base, an existing logistic and research framework of the Wildlife Institute of India established at Pench, and relatively low biotic disturbances within this Reserve. Many of the requirements and limitations of dholes can be much easily identified here. The mammalian fauna is also rich, with relatively high densities of mammalian carnivores (tigers, leopards, dholes) and their prey species (chital, sambar, nilgai, gaur, wild pig, barking deer, common langur and the four-horned antelope).

1.8. Study Objectives

- To estimate the abundance and population structure of dhole prey species in Pench Tiger Reserve.
- To ascertain the predation patterns of the dhole packs on the different prey species.
- To determine range sizes and movement patterns of dhole packs.
- To compare the findings from this study with earlier studies on dholes.

1.9. Organization of the thesis

The thesis is organized into six chapters, each chapter consisting of an introduction of the topic, elaboration of methods used, results arrived at, and discussion of the results and comparisons with earlier studies.

This introductory chapter that elaborates on the study species, the dholes, and the scope of the study.

Chapter 2 gives a descriptive account of the study area viz. the Pench Tiger Reserve, Madhya Pradesh.

Chapter 3 reviews the information available on dholes and refreshes current knowledge about aspects touched upon by this thesis.

Chapter 4 deals with the prey species of dholes in Pench Tiger Reserve; their abundance, biomass and population structure, essentially representing what and how much is available as prey to dholes within the study area.

Chapter 5 looks at the food habits and prey selection to see how dholes use the different prey species available to them in the study area.

Chapter 6 covers various aspects of the ranging and movement patterns of radio-collared dholes in Pench Tiger Reserve.

Chapter 2. REVIEW OF LITERATURE

2.1. Introduction

Dholes famously appear in Rudyard Kipling's stories for children e.g. 'Red Dog' and in 'The Second Jungle Book' as a threat to Mowgli's wolf pack.

Dholes are still relatively less studied animal in the wild. The scientific world for long has depended only on anecdotal notes on dholes chiefly by officers of the British Army in India (e.g. Burton 1940), Indian aristocrats, or as incidental observations. However with elaborate scientific reviews such as Cohen's (1977 and 1978) followed by Johnsingh's (1982b) two-year study specifically on the dholes in Bandipur Tiger Reserve, in southern India, there was a gradual increase in the scientific knowledge on dholes. Johnsingh's study provided quantitative data on the dhole feeding ecology, focussing on prey selection (Johnsingh 1992), spatial use patterns, social dynamics, and reproductive behaviour (Johnsingh 1982a). This was followed by a similar four-year study on two dhole packs in the adjoining Mudumalai Wildlife Sanctuary (Venkataraman *et al.* 1995), adding to the knowledge of pack dynamics, range use and prey selection by dholes.

2.2. Evolution and Systematics

Mammalian carnivores are thought to be descended from small civet-like animals called 'miacids', which lived in the time of the dinosaurs (Eocene period - 50 million years ago) (Ginsberg and Macdonald 1990). After the dinosaurs became extinct, the miacids evolved into the various families of mammalian carnivores. Each family represents an adaptation to a characteristic way of life. Of these, the canids first evolved about 38 to 54 million years ago in the Eocene, and some ancient canids were long-bodied and short-limbed resembling modern-day civets.

Thenius (1954) discussed the possible origins of dholes using fossil remains. According to him, the genus *Cuon* is post-Pleistocene in origin, once widespread across North America, Europe and Asia. Based on the numerical analyses of 90 morphological, ecological and behavioural characteristics of 37 canid species, Clutton-Brock *et al.* (1976) opined *Cuon* is more similar to *Canis*, *Dusicyon* and even *Alopex*, than to either *Speothos* or *Lycaon*. However, when only skull and dental characters are considered, *Cuon* resembles *Speothos* and *Lycaon* most. As suggested by Seal (1975), molecular genetic studies (e.g. Girman *et al.* 1993 for *Lycaon*, Gottelli *et al.* 1994 for *Canis simensis*) are required to get a true and conclusive picture of genetic and taxonomic affinities of these three species within Canidae. Recent molecular phylogenetic analyses (e.g. Wayne *et al.* 1997) have placed *Cuon* as an early divergent within the wolf-like canid group along with the grey wolf (*Canis lupus*), the coyote (*Canis latrans*), the Ethiopian wolf (*Canis simensis*), and some jackals (*Canis aureus, Canis mesomelas*).

Mivart (1890) split the genus *Cuon* into two species, *C. javanicus* and *C. alpinus*, on the basis of body size and molar dentition. Ellerman and Morrison-Scott (1966), however, recognised nine subspecies. According to Ginsberg and Macdonald (1990), currently there exist 11 subspecies, of which, three subspecies occur within India viz. *C. a. dukhunensis* Sykes 1831, found south of the river Ganga, *C. a. primaevus* Hodgson 1833, seen in Kumaon, Nepal, Sikkim and Bhutan, and *C. a. laniger* Pocock 1936, occurring in Kashmir and Ladakh. *C. a. adustus*, a subspecies found in northern Myanmar, may range into adjacent parts within India. *C. a. infuscus* is the other subspecies found in Myanmar that may occur within Indian limits.

2.3. Prey species of dholes

Several long-term studies have been conducted on wild herbivores in the Indian sub-continent, notable among them being those of Schaller (1967), Eisenberg and Lockhart (1972), Berwick (1974), Dinerstein (1979), Mishra (1982), Balakrishnan and Easa (1986), Green (1987), Karanth (1992), Haque (1990), Khan (1993), and Sankar (1994). A lot of information has also been generated from the Thai sambar population (e.g. Ngampongsai 1987) and studies on sambar introduced into Texas (e.g. Richardson II 1972), Florida (e.g. Shea *et al.* 1990), and; chital introduced into Hawaii (e.g. Graf and Nichols 1966), Texas (Ables 1974), and nilgai in Texas (e.g. Sheffield *et al.* 1983). Newton (1984) conducted a pioneering study on the ecology of common langurs and their association with chital, in central India.

Distance sampling, and line transect sampling in particular, is practical, efficient and relatively inexpensive method for sampling many biological populations. This method has been successfully used to estimate ungulate densities within the Indian sub-continent (Karanth and Sunquist 1992, 1995; Varman and Sukumar 1995, Khan *et al.* 1996, Raman *et al.* 1996, Karanth and Nichols 1998). The Line Transect method has also been used to estimate primate densities (Brockelman and Ali 1987).

Prey of dholes vary from place to place within the latter's distributional range. Brander (1923) was of the opinion that nearly every species of forest animal within the dholes' range has at one time or other served as their prey. Chital and sambar are considered the principal prey of dholes within India (Davidar 1975, Johnsingh 1992, Venkataraman *et al.* 1995). Not only for dholes, these two major wild herbivores together form the bulk of the prey base for all large carnivores of the Indian sub-continent such as the tiger, the Asiatic lion (*Panthera leo*), and the leopard.

2.4. Feeding and predation ecology

Dholes are primarily and predominantly carnivorous, hunting communally or alone, depending on the size of their prey (Fox and Johnsingh 1975, Johnsingh 1983). In Mudumalai, small prey such as ungulate fawns or hares were often killed by a solitary dhole, but for larger prey (adult ungulates), hunting packs of five dholes were common (Cohen *et al.* 1978).

Two long-term studies, the one in Bandipur (Johnsingh 1983 and 1992) and the other in Nagarahole (Karanth and Sunquist 1995) have attempted to compare prey selection by dholes, tigers (*Panthera tigris* Linnaeus), and leopards *P. pardus* Linnaeus, by using faecal (scat) analyses, kill data, and corresponding prey abundance estimates. Both studies indicated that the size of the major prey was positively related to the size of the predator. Karanth and Sunquist (1995) found that dholes usually focussed on prey in the 31-175 kg size class. Dholes in Nagarahole preyed more upon adult male than adult female chital. Re-analysis of Johnsingh's (1982b) Bandipur data showed that dholes appear to select the medium-sized ungulate prey species (chital) and proportionally more male chital were killed (Patel 1992). This was attributed to the fact that male deer tended to range more widely during the rut, and were often solitary, possibly increasing their vulnerability to predation. The same pattern was observed with respect to sambar males, attributed to their solitary habits making them more prone to dhole predation (Johnsingh 1992). Dholes in Bandipur also preferred to kill chital males that had longer antlers, possibly because stags with large antlers may be hampered when running through dense vegetation and are easily killed (Johnsingh 1983). Juvenile animals (excluding gaur calves) appear to have been taken non-preferentially by all three predators (Karanth and Sunquist 1995).

Johnsingh’s (1983) study estimated that an adult dhole (15-17 kg) consumed 1.86 kg meat per day, or 0.103kg per kg of it’s body weight.

Venkataraman et. al. (1995) specifically compared prey selection in two dhole packs within Mudumalai. They found that, both packs preferred chital; one pack preferred sambar while the other took sambar in proportion to the latter's availability. Most of the ungulates killed were young individuals. As was the case in Bandipur (Johnsingh 1992) and Nagarhole (Karanth and Sunquist 1995), adult male chital were preferred. However, sambar were killed without any apparent preference for either sex class.

The Mudumalai study (Venkataraman *et al.* 1995, Venkataraman 1998), while examining communal hunting in the dhole, found no relation between adult pack size and weight of the prey killed. However, in the dense habitats, it was not always possible to determine the size of the hunting group responsible for a particular kill. Re-analyses of Johnsingh's (1982b) data revealed a negative relation between per capita food intake and pack size. From these results, it was suggested that co-operative hunting might not be the main function of dholes’ sociality (Venkataraman *et al.* 1995). They suggested a possible function of communal living is for defence against other large predators. The dhole has been observed to group together to counter a tiger, and to "tree" leopards very often (Venkataraman 1995). When competition with other predators is high, large hunting sizes may help greatly in procuring regular prey requirements. This possible function of sociality remains to be investigated. Interestingly, Keller (1973) observed that hunting pack sizes in Kanha were larger in the morning than in the afternoon and evening, and a hunting success of 20 % for dhole packs in Kanha.

2.5. Spatial Ecology

Over the years, the field of wildlife telemetry has developed to such a great extent that in-depth information on diverse facets of an animal’s biology, such as movements, activity patterns, home ranges, space use patterns, survivorship, mortality, physiology etc., can be obtained remotely, reliably and accurately. This has encouraged the deployment of radio-collars and other such transmitters on to a host of study animals.

Until date, the only published account of capture and immobilization of dholes is that of Kotwal (1981) in Kanha Tiger Reserve, central India, in the year 1980. He used a combination of Fentanyl and Droperidol for a male dhole darted using a blowgun rifle from elephant-back.

Estimation of size and shape of home ranges is the norm in studies of territory and spacing patterns of animals (McNab 1963, Harestad and Bunnell 1979). From past studies in the Indian forests, it appears that the dhole requires a relatively smaller range than that used by other pack-hunting canids such as the wolf (Mech 1970, Jhala 2000) or the African wild dog (Fuller and Kat 1990), probably due to sedentary nature and high biomass of prey species (Johnsingh 1982b). A single dhole pack in Bandipur held an exclusive territory over a range of around 40 km^2 with 99% of the sightings within a 20 km^2 core, which was possibly defended. During the denning season the hunting home range shrunk to 11 km^2. This study suggested that inter-specific competition, capture efficiencies, prey size and prey biomass may determine dhole pack sizes (Johnsingh 1982b).

In the case of the Mudumalai study, the individual home ranges of two dhole packs appeared to be larger that that of Bandipur - 53km^2 and 84 km^2 respectively (Venkataraman *et al.* 1995). However unlike the Bandipur study, in this study core areas were not delineated. Range sizes were smaller during the dry season than the wet season, probably an effect of the distribution of water resources on prey abundance. However, unlike in Bandipur, hunting ranges of packs during denning season did not shrink in the Mudumalai study. This study also found that a dhole pack visits prey resource patches (e.g. chital herds) cyclically, in a specific sequence that seemed largely pre-determined and uni-directional. In effect, the pack moves in a circle, predictably in the forward direction and less predictably on the return. Karanth and Sunquist (2000) reported a home range size of around 23 km^2 (95% Minimum Convex Polygon) for a dhole pack in Nagarahole, also in southern India.

2.6. Population Ecology

Dhole populations have been known to fluctuate sharply (Burton 1940). This is particularly true for central India where, during his pioneering 14 month study in Kanha, Schaller (1967) could not record any direct observations of dholes, but years later, during a study led by Keller (1973) in Kanha, dholes were commonly sighted there. Density estimates from studies in southern India vary from 0.1 km^{-2} in Bandipur (Wesley 1977) to 0.22 dholes km^{-2} in Mudhumalai (Venkataraman *et al.* 1995). Dispersal, and conversely philopatry (staying back with natal pack), could play a major role in determining pack sizes in dholes. In the studies in southern India, it was noticed that pack sizes fluctuated widely, due to individual migrations from and to other packs, dispersal or mortalities (Johnsingh 1983, Venkataraman *et al.* 1995). The largest pack size reported, among these three studies, was 25 (Venkataraman et. al. 1995), but much larger packs have been observed elsewhere (40 by Davidar 1975, 26 to 28 - Ramanathan 1982), which may occur through temporary fusion of packs (Fox 1984) or philopatry. Fox (1984) also mentions that neighbouring packs with recently shared genealogies may fuse and re-form for hunts. Johnsingh (1982b) suggested that interspecific competition, capture efficiency, prey size, and prey biomass may determine dhole pack size. Surprisingly however, per capita meat consumption decreased with increase in pack size (Venkataraman *et al.* 1995).

In the Mudumalai packs (see Venkataraman 1998) there was considerable variance in the proportion of sub-adults dispersing from both the packs. Dhole packs in both Bandipur (Johnsingh 1982) and Mudumalai (Venkataraman 1998) had males outnumbering the females, as is the case with the African wild dog *Lycaon pictus* (Malcolm and Marten 1982), due to a combination of female dispersal and male philopatry (Frame and Frame 1976). Males may delay dispersal and co-operate within their natal packs because of a variety of reproductive strategies they could pursue within it (Venkataraman 1998). The study felt that a combination of ecological constraints and difficulties of achieving breeding status within non-natal packs might make early dispersal and independent breeding less beneficial. The disappearance or appearance of particular individuals was usually unaccounted for in these studies.

2.7. Sympatric carnivores

Throughout most of their range, dholes are sympatric with tigers and leopards, competing and coexisting for thousands of years through subtle ecological and behavioural mechanisms such as differential prey selection and spatio-temporal use of the habitat (Johnsingh 1992, Karanth and Sunquist 1995).

Most of the encounters of dholes with their main co-predators, i.e. tigers and leopards, are chance occurrences. Although there exist accounts of dholes attacking tigers (Connell 1944, Khajuria 1963), dholes and tigers maintain a safe distance from each other. With leopards however, dholes behave aggressively, usually driving the former up a tree ('treeing') for substantial lengths of time (Wright 1890, Venkataraman 1995), even killing them on occasion (Morris 1933b). Dholes are also known to rob leopards of their kills (Morris 1933a). However, a large male leopard can resist attack or defend its kill from small dhole packs (Burton 1925). This legendary antagonism towards leopards could be an apprehensive strategy to thwart potential attacks by leopards on isolated individual dholes (Venkataraman 1995).

2.8. Unstudied Topics

All earlier studies have not been able to monitor dhole packs on a systematic basis. Without telemetry, the methods they used were relatively inefficient in terms of observer effort, which could produce biased estimates. Accurately collected estimates are essential to determine food and space use requirements.

It has to be pointed out here that all three existing long-term studies on dholes have been conducted in geographically connected (all located within the Nilgiri Biosphere Reserve) and similar habitats. There is a great need for further ecological data on dholes from other ecological zones.

Mechanisms of breeding system, the method of dispersal, territoriality, population regulation, and reproductive suppression in dholes have yet to be determined. These processes would help determine the viability of small populations. Earlier studies (Fox and Johnsingh 1975) indicates that dholes may possibly be regulating prey numbers, prevent prey population booms, the resulting over-grazing, and the inevitable crash in numbers of all prey and their predators in turn. This possibility needs to be investigated to come to a definite conclusion.

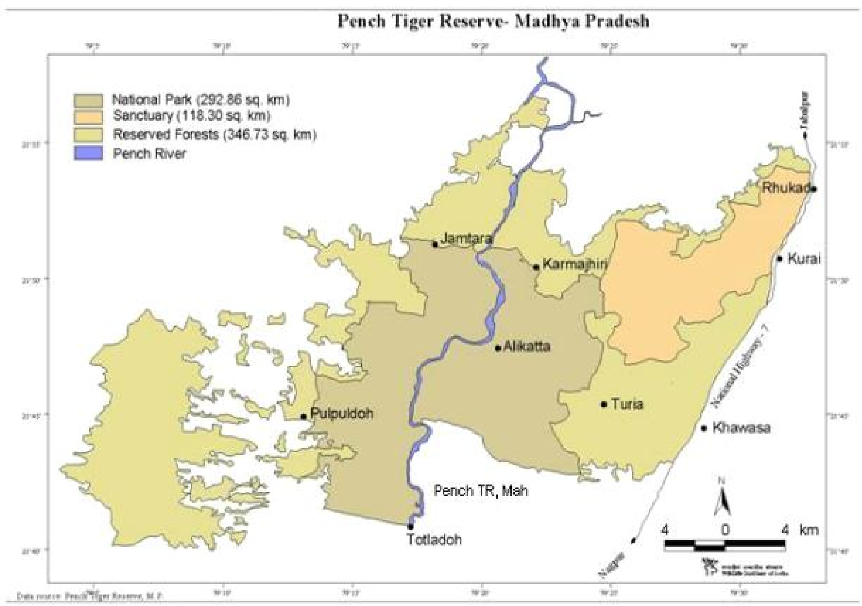
Fecundity and mortality patterns and factors in dholes have not yet been studied. The presence, virulence and transmission of known canid diseases have not been assessed, though disease is believed to have decimated dholes in some regions (Johnsingh 1985).

There have been no quantitative assessments of the use of different habitats by dholes, especially habitats with anthropogenic presence. Until such information is recorded, assessment of threats to existing dhole populations, and remedial action, would be greatly handicapped.

Chapter 3. STUDY AREA

The field study on dholes was conducted in the Pench Tiger Reserve (77° 55' E to 79° 35' E and 21° 08' S to 22°00' N), located in the Seoni and Chhindwara districts, southern Madhya Pradesh, central India (Map 1). The field study in Pench commenced in May 2001.

Map 1. Map of Pench Tiger Reserve, Madhya Pradesh, showing administrative zones and major locations.



3.1. Location

The Reserve gets its name from the Pench River that flows through it, North to South, covering a distance of about 74 km through the Reserve. The Reserve lies in the southern lower reaches of the Satpura Hill Range on the southern border of Madhya Pradesh. The total area of the Reserve is 757.89 km² of which, the Indira Priyadarshini Pench National Park, forming the core zone of the Reserve, covers 292.85 km², and the Mowgli Pench Wildlife Sanctuary is 118.30 km² in area. A Buffer Zone constituted by Reserved Forests, Protected Forests and Revenue land, occupies 346.73 km². The habitat is contiguous on the south with the 257.26 km² of the Pench Tiger Reserve, Maharashtra, both of which have been included in the Tiger Conservation Unit – 31 (Kanha-Pench TCU) (Wikramanayake *et al.* 1998). The adjoining forests to the west and north-west of the Tiger Reserve come under the East Chhindwara and South Chhindwara Territorial Forest Divisions respectively. The Forest tract to the north and north east of the Reserve comes under the South Seoni Territorial Forest Division.

3.2. General Information

This area was described as extremely rich and diverse in wildlife from the earliest records available on the 16th century Deogarh kingdom (Kumar 1989). The scenic beauty and the floral and faunal diversity of the Central Indian Highlands have been well documented by the British since the late 17th century e.g. Forsyth's (1919) "Highlands of Central India" (first published in 1871). Thereafter, Sterndale (1887) and Brander (1923) have added to the knowledge on the distribution of the flora, fauna and the local inhabitants of this tract. The popular fictional works of Rudyard Kipling "The Jungle Book" and "The Second Jungle Book" too have their stories set around this region.

During the 17th Century the Gond rulers of this region cleared large tracts of forests for cultivation and dwellings. This onslaught continued up to 1818, through the rule by the Marathas and later under the British. It was not until 1862 that efforts were made to control the indiscriminate destruction and the forests were declared reserved (elaborated in Kumar 1989).

The Pench Sanctuary was notified in September 1977, with an initial area of 449.39 km^2. The Pench National Park, recently renamed as Indira Priyadarshini Pench National Park, was created in 1983, carved out of the Sanctuary. The Tiger Reserve, 19th in the series, was formed under the Project Tiger scheme in November 1992. The Pench River bisects the Pench Tiger Reserve into two nearly equal parts, the 147.61 km^2 of the Western Block which falls in the Gumtara Range of the Chhindwara Forest Division and the 145.24 km^2 of the Eastern Block in the Karmajhiri Range of the Seoni Forest Division (Map 1). Administratively, the Tiger Reserve is divided into three Forest Ranges (Karmajhiri, Gumtara, and Kurai), nine Forest Circles (Alikatta, Dudhgaon, Gumtara, Kamreet, Karmajhiri, Kurai, Murer, Rukhad, and Pulpuldoh), 42 Forest Beats, and 162 Forest Compartments. The

National Highway NH 7 that runs between Nagpur and Jabalpur forms the eastern boundary of the Tiger Reserve for an extent of around 10 km.

3.3. Physical Features

The general topography of Pench Tiger Reserve is mostly undulating, characterised by small ridges and hills having steep slopes, with a number of seasonal streams and nullahs carving the terrain into many folds and furrows, a result of the folding and upheavals of the past. The topography becomes flatter close to the Pench River. Most of the Tiger Reserve area falls under flat to gentle slope category (0-22 °) (Sankar *et al.* 2000b). The mean altitude is around 550 m above M.S.L. The geology of the area is mainly comprised of gneisses and basalt (see Shukla 1990 for details).

3.4. Climate

The Central Indian Highlands have a tropical monsoonal continental climate, with a distinct monsoon (July to September), winter (November to February) and summer (April to June).

The mean annual rainfall is around 1400 mm, with the south-west monsoon accounting for most of the rainfall in the region. For the dry season (November to May), the mean rainfall was 59.5 mm, and the temperature varies from a minimum of 0° C in winter to 45° C in summer (Sankar *et al*. 2000).

3.5. Hydrology

On the extreme southern boundary of the Tiger Reserve, a dam (Pench Hydroelectric Project) has been constructed on the Pench River. This dam forms the State boundary between Madhya Pradesh and Maharashtra. Because of this dam's reservoir, a sizeable proportion (54 km^2) of the Tiger Reserve on the Madhya Pradesh side has come under submergence of the resulting water body (reservoir) after the monsoonal rains. As summer approaches, these areas, from where the water gradually recedes downstream, become lush green meadows attracting high numbers of wild herbivores. During summer, the Pench River dries out leaving small pools of water locally known as "doh" or "khassa", which, besides the Pench reservoir, are the most important sources of water for the animals during this period. Artificial sources of water such as earthen tanks and check-dams (anicuts) too tend to dry out before the month of March, due to the inherent low water retention capacity of the soil. The Reserve management has also set up many hand-pumps and artificial water holes throughout the Reserve to serve as minor sources of water during the pinch summer months.

3.6. Vegetation

Pench Tiger Reserve belongs to the Indo-Malayan phyto-geographical region. Ecologically, Wikramanayake *et al.* (1998) categorized Pench as a tropical moist deciduous (TMD) tiger habitat. Floristically, the Tiger Reserve can be classified, according to Champion and Seth (1968), as:

I. TROPICAL MOIST DECIDUOUS FORESTS:

i. TYPE $3B/C_{1c}$ Slightly moist teak forests

II. TROPICAL DRY DECIDUOUS FORESTS:

i. TYPE $5A/C_{1b}$ Dry teak forests

ii. TYPE $5A/C_{3}$ Southern dry mixed deciduous forests

Teak is a ubiquitous species in the region, with a presence ranging from a sporadic distribution in most parts of the study area to localized teak-dominated patches. Teak (*Tectona grandis*), and associated species such as *Madhuca indica*, *Diospyros melanoxylon*, *Terminalia tomentosa*, *Buchanania lanzan*, *Lagerstroemia parviflora*, *Ougeinia dalbergoides*, *Miliusa velutina* and *Lannea coromandalica*, occur on flat terrain. The undulating terrain and hill slopes have patches of Mixed Forest dominated by *Boswellia serrata* and *Anogeissus latifolia*. Species like *Sterculia urens* and *Gardenia latifolia* are found scattered on rocky slopes. Bamboo forests occur in the hill slopes and along streams. Some of the open patches of the Park are covered with tall grasses interspersed with *Butea monosperma* and *Zizyphus mauritiana*. Evergreen tree species like *Terminalia arjuna, Syzygium cumini* and *Ixora parviflora* are found in riparian vegetation along nullahs and river banks. *Cleistanthus collinus* dominant patches are also found in some parts of the Tiger Reserve.

The tracts that previously formed pastures of villages (subsequently relocated outside the National Park limits) now constitute open grassy meadows much favoured by the gregarious herbivores. With the approach of summer, the extent of open areas of the Reserve gradually increases with the recession of reservoir's waters.

3.7. Fauna

Zoogeographically, the Reserve falls in Oriental region. The carnivore fauna is represented by the tiger (*Panthera tigris* Linnaeus), leopard (*Panthera pardus* Linnaeus), dhole (*Cuon alpinus* Pallas), jungle cat (*Felis chaus* Gueldenstaedt), and small Indian civet (*Viverricula indica* Rasse). Wolf (*Canis lupus*) occurs on the fringes and outside the Reserve limits. Striped hyena (*Hyaena hyaena*), sloth bear (*Melursus ursinus* Shaw), jackal (*Canis aureus*), and common palm civet (*Paradoxurus hermaphroditus*) make up the rest of the carnivore fauna of the Reserve.

Chital (*Axis axis* Erxleben), sambar (*Cervus unicolor* Kerr), gaur (*Bos frontalis* Lambert), nilgai (*Boselaphus tragocamelus* Pallas), wild pig (*Sus scrofa* L.), barking deer (*Muntiacus muntjac* Zimmerman) and chowsingha (*Tetraceros quadricornis* Blainville), are the wild ungulate species found in the study area. Chital, sambar, nilgai and wild pigs are found all over the Tiger Reserve. With the distribution of water governing their movement patterns to a great extent, gaur migrate down from the hills during the dry season and occupy the forests along the Pench River and other sources of water, and migrate back to the hill forests during the monsoon. Nilgai are found mostly in a few open areas, along forest roads, scrub jungles and fringe areas of the Reserve. Chowsingha are more localized to the greatly undulating areas of the Reserve. Barking deer are seen infrequently in moist riverine stretches. Chinkara (*Gazella bennetti* Sykes) are infrequently seen on the open areas bordering and outside the Buffer Zone of the Reserve (e.g. Turia, Telia, and Dudhgaon).

The common langur (*Semnopithecus entellus* Dufresne) and rhesus macaque (*Macaca mulatta* Zimmerman) represent the primate fauna of the area. The Indian porcupine (*Hystrix indica* Kerr), two species of mongoose *viz.* common mongoose (*Herpestes edwardsii*) and ruddy mongoose (*Herpestes smithii*), and black-naped hare (*Lepus nigricollis nigricollis*) also occur in this Tiger Reserve.

3.8. People

Currently there are no human settlements within the core zone (National Park) of the Tiger Reserve, with the last two forest villages, Alikatta and Chhendia, relocated out in 1992 and 1994 to Durgapur and Khairanji respectively. Villages, inhabited by people of the Gond tribe, small farmers, and labourers, surround the Reserve. The Gond tribals, being forest dwellers, hold great respect for the forest and its fauna, many of which are worshipped. Domestic livestock such as cattle, buffaloes and goats owned by these people frequent the areas adjacent to the Tiger Reserve, many a times falling prey to the wild carnivores of the region.

3.9. Research in Pench

Long-term research in Pench was initiated by the study on the interactions between wild animal and their habitat in the Pench Sanctuary by Shukla (1990). This was followed by a tiger-prey estimation study by Karanth and Nichols (1998). Since 1995 the Wildlife Institute of India has initiated a series of studies beginning with an long-term radio-telemetry study on the gaur (*Bos frontalis*) (Sankar *et al.* 2000a), followed by the creation of a spatial mapping database for the Tiger Reserve (Sankar *et al.* 2000b).

Short-term Master’s studies from the Wildlife Institute of India increased the knowledge on avifauna (Jayapal 1997), wild herbivores (Acharya 1997), and tiger food habits (Biswas and Sankar 2002) in Pench. Pasha *et al.* (2004) have given a description on the diversity and distribution of the avifauna of Pench Tiger Reserve.

Chapter 4. DHOLE PREY

4.1. Introduction

The distribution and abundance of organisms in space and time is one of the fundamental focuses of ecological research (Buckland *et al.* 1993). The study of the biotic and abiotic factors that influence the distribution and abundance of animals has become all the more vital not only for their conservation and management, but also for those species dependent on them.

Prey distribution, density and biomass within a given area represent measurable amounts of energy potentially available as food to carnivores, with herbivore density and biomass inextricably determining food (or energy) available to the predators (Sunquist and Sunquist 1989, Carbone and Gittleman 2002).

The knowledge on the type of prey available within a given area and their distribution in space and time is the basis for any carnivore study. Prey assemblages, in particular their diversity, structure and abundance, are mediated through vegetation structure, productivity of the habitat, and to what extent humans have altered and impacted the habitat. The relative availability of different age- and size classes of potential prey could determine the distribution and abundance of large mammalian carnivores, especially in tropical forests. Most of prey species here, being generalist feeders or grazers, contribute to the overall larger percentage to terrestrial mammalian biomass in any given habitat (Eisenberg and Seidensticker 1976).

More significantly, the distribution of prey in space and time influences the intra-specific and inter-specific spacing of carnivore populations dependent on the prey, and ultimately the carnivore density and biomass in a given area (Sunquist and Sunquist 1989). Therefore, population status (i.e., numbers, density, or trend) of prey needs to be determined and monitored accurately and regularly for the proper management of prey, and in turn, the predators (Eisenberg and Seidensticker 1976). In this context, a thorough knowledge of the prey base of dholes, a major carnivore species of south Asia, is essential to predict the viability and persistence of dholes in their current range and to plan for their conservation in future.

In order to collect basic information on the prey species of dholes, this study aimed to estimate the density, encounter rates, biomass, and the population structure and composition of the major prey species within the study area. Eventually, this data would represent prey available to predators – in numbers, proportions, or sizes. This information obtained on prey in Pench could be compared with earlier dhole studies in India, since the prey compositions would be fairly similar.

The prey community in Pench is made up of essentially three large (gaur, average weight 550 kg; sambar, 200 kg; nilgai, 170 kg), two medium (chital, 50 kg; wild pig, 40 kg), and three small-sized prey species (barking deer, 20 kg; chowsingha, 20 kg; common langur, 12 kg). Within the Tiger Reserve, these prey species differed greatly in their spatio-temporal distribution.

4.2. Methods

The estimation of large herbivore abundance, biomass and population structure is a process that is central to wildlife conservation and management, essentially with respect to long-term wildlife monitoring and prey-predator relationships.

Direct enumeration of herbivores in tropical forests is difficult mainly because of the dense vegetation cover, poor visibility and relatively low density of these populations, resulting in inadequate sample sizes for statistically precise results. With the development of sophisticated statistical methods of sampling animal densities (Burnham *et al.* 1980), this difficulty has been largely reduced, especially in India (reviewed by Rodgers 1991). The most common method of estimating animal densities is the Line Transect Sampling method (Eberhardt 1968; Anderson *et al.* 1979; Burnham *et al.* 1980; Buckland *et al.* 1993).

Encounter rates of prey along roads have also been used as a measure of prey encounter by carnivores (Krüger *et al.*, 1999).

A commonly expressed version of density in terms of total biomass is the biomass density. This is calculated by multiplying the density of prey species by their average individual weights. The average body weight of each prey species required for biomass calculation was taken from available literature (Schaller 1967; Prater 1980 ; Karanth and Sunquist 1995).

4.2.1. Line Transects

The line transect method essentially involves establishing a set of randomly located lines in field, and distances are measured to those animals detected by walking the line. It is based on the idea of the detection probability function, which acknowledges that the probability of detecting an animal decreases as the distance between the observer and the animal increases. This method allows for the fact that some of the animals will go undetected and that there is a tendency for detectability to decrease with increasing distance from the transect line. The strength of this method therefore lies largely in its ability to take into account non-detectability of animals and their non-random distribution, by incorporating the appropriate detection functions (Karanth and Nichols 1998). The density estimates are accordingly adjusted for non-detection bias under the hypothesis that detection probability is related to the distance between the sampled object and the point of observation.

Unbiased estimates of density can be obtained using this method if certain critical assumptions are fulfilled, such as, animals are detected at their initial location prior to any movement, distances and angles are measured accurately, animals are spatially distributed in the area in such a way that they are random with respect to the transects, etc.

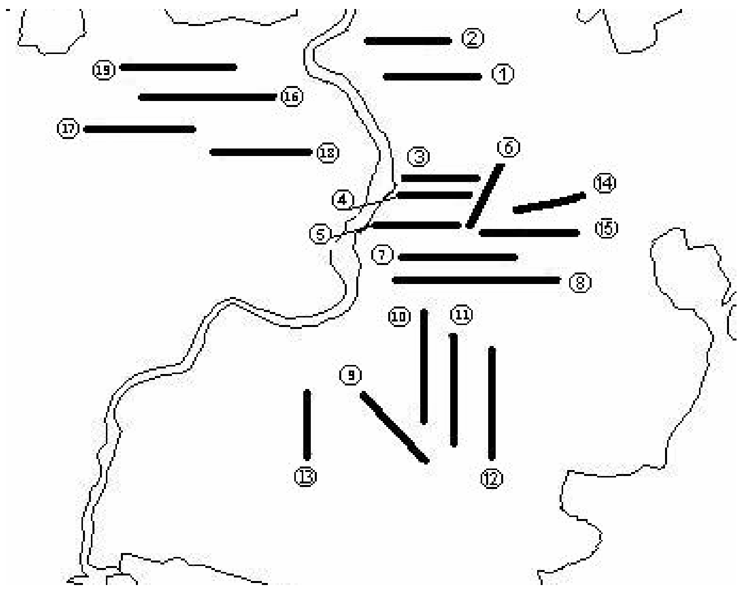
Table 3. Details of line transects sampling for estimation of major dhole prey species in Pench T.R., Madhya Pradesh (2001-2004).

Year	No. of transects	Total transect length (km)	Avg. transect length (km)	Total length walked (km)
2001-2002	12	27.3	2.2	218.4
2002-2003	19	45.5	2.2	140.4
2003-2004	20	51	2.5	72.8
All years	-	-	2.3	431.6

One of the main assumptions of the Line Transect Method is that objects on the line are seen with probability one ($g(0) = 1$), and this probability $g(x)$ decreases in a particular way as objects are sighted away from the line (x = distance of object from the line). The way this probability decreases is known as the probability density function (PDF) (Burnham *et al.* 1993) having a particular shape. Several flexible models or key functions (e.g. Half-Normal, Hazard-Rate, Uniform and Negative Exponential) are available to fit this shape in order to estimate the density of the objects on the transect.

Systematic estimation of prey abundance was for the dry seasons (Nov-June) from 2001 to 2003 (see table 3 and Map 2). For the period Nov 2003 – June 2004, line transect sampling was carried out only within the approximate home ranges of each radio-tagged dhole pack.

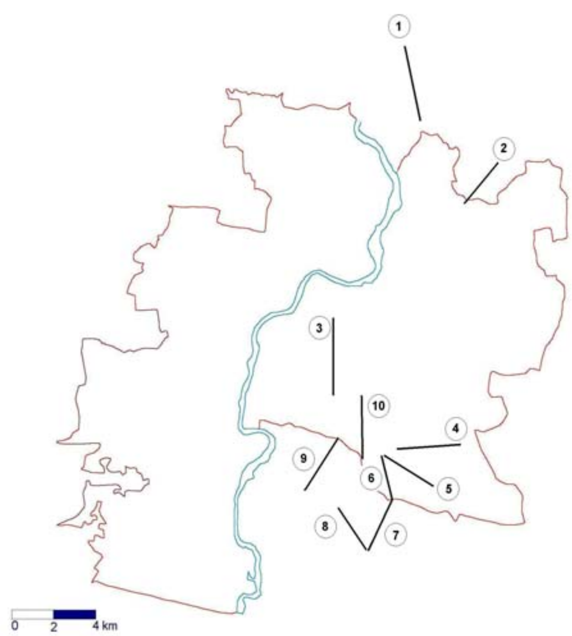
Map 2. Location of permanent transects lines within the Pench N.P., Madhya Pradesh.



Transect No.	Transect name	Transect No.	Transect name	Transect No.	Transect name
1 -	Singungarh	8 -	Bison Camp	14 -	Baara Mod
2 -	Jamun Nala	9 -	Pivarthari	15 -	Jandi Pahad
3 -	Khairbanmatta	10 -	Joda Munhara	16 -	Rohni
4 -	Badjodi	11 -	25 Number	17 -	Gumtara
5 -	Kasai	12 -	Seewan Nala	18 -	Chita Pahad
6 -	Mannutalab	13 -	Kala Pahad	19 -	Naagdev
7 -	GurluTek				

Transects were laid throughout the intensive study area in such a way that the various habitat types within the study area were adequately represented. However, only three forest types viz. teak dominant forest type, *Anogeissus-Boswellia* mixed forest type, and miscellaneous forest type, were found to have large contiguous areas fit for laying adequately long (> 2 km) transect lines. The riverine forests formed a linear habitat that precluded the random distribution of animals with respect to the transect line, a pre-condition for this method. The scattered bamboo forests, and the *Cleistanthus collinus* dominant forest type were found to be too small in size for laying transect lines of adequate length within them.

Map 3. Location of GPS-based transects sampled in and around Pench N.P., Madhya Pradesh.



Transect No.	Transect name	Transect No.	Transect name
1 -	DEVI SHRINE	6 -	CHIKLAKARI
2 -	GARRAKOL	7 -	BHIMSEN-CHIKLAKARI
3 -	SAPAT	8 -	BHIMSEN-SADDLE DAM
4 -	KALACHOPUN	9 -	NAGDEV
5 -	MARKA KHASSA	10 -	BOUNDARY

Almost all of the 54 km² area of the submergence zone of the Pench reservoir was not available for sampling in winter, as it was invariably under submergence till the end of February every year, when the waters gradually recede. Therefore, it was not possible to lay line transects in this special habitat.

Within the three major forest types, a total of 19 permanent transects averaging a length of 2.3 km (1.2-3.5 km) were laid in a fashion that ensured the random distribution of animals with respect to the transect lines (table 3 and map 2). In a similar way, 10 unmarked non-permanent transects, walked with the help of GPS navigation, were sampled within the ranges of known dhole packs (map 3), for the period 2003-2004. The orientation angle (bearing) of each transect line was recorded. Geographical locations i.e. latitude-longitude of the starting and ending points of each transect were recorded on a Global Positioning device (GPS Receiver - Garmin® GPS 12XL, Garmin International Inc., Kansas, USA). It was ensured that these respective points were located near forest roads to facilitate easy drop off and pick up of the transect team by vehicle. The course of the transect line was marked with red paint on trees or other objects at eye-level. Transect length was measured using a 50-m rope and every 100 metre points was tagged with corresponding km reading. The route line was cleared just enough to facilitate proper enumeration of prey animals without biasing the latter towards or away from the line. Over the study period, the total annual extent (length) of transects in the study area averaged 41.2 km (27.3 – 51.0 km).

Prey abundance data was collected by direct sightings using the Line Transect Method (Anderson *et al.* 1979). Transect walks were optimised by first saturating the number of replicates possible (e.g. 19 for period 2002-2003) and then using repetitions i.e. pseudo-replicates (repeated walks). In this way, each transect was walked 1-2 times in a season. Transects were sampled both in the mornings and evenings, in such a way that morning transects were initiated one hour after sunrise and evening transects terminated one hour before sunset, coinciding with the periods of highest herbivore activity. The transects were walked by a team consisting of an observer and a recorder. The utmost care was taken while walking the transects to maximize detection of animals from the transect before they are flushed.

For each detection, the exact time, species, group size, group composition (age classes and sex, whenever possible), compass bearings and the sighting (radial) distance of the animals from the observer were recorded. Compass bearings were recorded using a liquid-filled see-through compass (Suunto KB 20, Vantaa, Finland). Sighting angles were derived from the bearings (orientation) of the respective transects. Sighting distances were measured accurately using a laser rangefinder (Yardage Pro 400, Bushnell, Kansas, USA), thus preventing a bias in the density estimation process due to heaping (Buckland *et al.* 1993). Additional information such as topography and vegetation type of the animal location was noted for each sighting.

In order to estimate the total spread of area that fell within the ambit of transects, that would represent the actual area sampled from transects, a 100% minimum convex polygon with a 100 m buffer was constructed around the transect locations, using the GIS software program ArcView GIS 3.2 (ESRI 1999).

4.2.2. Road Transects

Data regarding the encounter rates (numbers of animals sighted per km travelled) and group composition (group sizes, age-sex structure, etc.) of dhole prey species were recorded using vehicle-based road counts (Hirst 1969) from an open four-wheel drive vehicle while driving at a constant speed of 20 km h^{-1}. A total of 660 km was travelled for the period 2001-2004. These road transects (average length 5.2 km) were sampled during the two hours after sunrise and two hours before sunset. Two observers carefully scanned either side of the roads for prey species. For each sighting, the species, group size, and group composition (age classes and sex) were recorded. Ancillary information such as time, kilometre reading, vegetation type, etc, were also recorded. Age-sex classes of the dhole prey species were designated based on size, antlers, horns, etc., using earlier long-term studies on these species, such as Schaller (1967), Johnsingh (1983), and Karanth and Sunquist (1992) as references for such classifications (see table 5). Adult stags of chital and sambar were classified as ‘hard’ or ‘velvet’ antlers, with stags in shed antlers being included in the ‘velvet’ category. For some of the prey species such as langur, wild pigs and barking deer, since the sub-adults were not discernable with certainty, only male-female-juvenile categorization was followed. From December 2003 to June 2004, road counts were carried out only within approximate dhole pack home ranges.

4.2.3. *Ad libitum* counts

In order to obtain accurate information on the population structure of dhole prey species, data regarding their group size and group composition were recorded *ad libitum* when it was confirmed that the whole group was clearly visible for enumeration (total count). Age-sex classes of the dhole prey species sighted were assigned in the same way as was done in the road counts. Prey animals were categorized as small (<25 kg), medium (26-50 kg), large (51-100 kg) and very large size (>100 kg) prey following Johnsingh (1992).

4.3. Analyses

4.3.1. Prey Densities

The computer Program DISTANCE Version 4.1 Release 2 (Thomas *et al.*, 2004) was used for analyses of line transect data to yield density estimates of the individual dhole prey species. The program also checked for size-bias in detections of prey species on transects, and corrected for the same. In the case of langurs, data for only those individuals of a troop that were sighted on ground was taken for analysis, to reflect what was available to dholes.

Data from all temporal replicates (pseudo-replicates) for a transect were pooled and treated as one sample for that year. The sample size, therefore, equalled the number of transect replicates for that year (e.g. 19 for the period 2002-2003). The output is a pooled density estimate with an empirical variance. In this way, a density estimate was obtained for each prey species, for each year.

To obtain the model that best fit the data, the Half-Normal, the Uniform and the Negative Exponential detection function (key) models were used on the transect data. For each of these models, the best key function (with the appropriate adjustment term, where necessary) was selected using the criterion of lowest AIC (Akaike's Information Criterion) value (Buckland *et al.* 1993). For those prey species for which the sample size was too small to reliably estimate densities from distance sampling, the encounter rates were presented. The effective strip width (ESW) or the distance from the transect line within which individuals can be reliably observed, probability density function of detected distances from the line evaluated at zero distance ($f_{(0)}$), the detection probability ($\hat{p}$) were also generated for each prey species by Program DISTANCE.

4.3.2. Encounter Rates

Encounter rates for each of the prey species was estimated by dividing the total number of animals of a particular species sighted by the total length of road transects travelled in a given year, to generate annual and one composite encounter rate for that species. The figures are presented as the number of individuals observed per 10 km.

4.3.3. Biomass

Figures for average weights (table 5) were assigned to the respective age/sex-classes of dhole species based on subjective estimation and from published figures for the same species from earlier studies (Schaller 1967, Tamang 1982, Karanth and Sunquist (1995). From the population structure of the prey species obtained from the *ad libitum* counts, the proportional representation of individual age-sex classes of each prey was computed. Using these proportions, the average unit weight of each prey species was calculated that was weighted by the proportions of each age-sex class of that species. Thus, a corrected biomass figure (unit weight) representing actual population structure for each prey species in the study area was obtained. Using the encounter rates from road counts and population structure from *ad libitum* counts, the proportions of the different weight classes of prey species was also calculated.

Biomass densities of the different prey species were computed by multiplying the estimated mean individual densities (pooled for all years) by these respective unit weights. Total biomass contributed by each species in the study area was also calculated by extrapolating biomass densities for the intensive study area. Since, prey abundance estimation as carried out only within the National Park limits of the Tiger Reserve, this total biomass figure would only represent this region.

Table 5. Body weight estimates assigned to different age-sex classes of major dhole prey species in Pench T.R., Madhya Pradesh, based on literature and field data.

Prey Species	Age class	Age	Sex class	Weight (kg)
Chital	Adult	> 2 years	Male	70
	Adult	> 2 years	Female	50
	Yearling	1- 2 years	Male	50
	Yearling	1- 2 years	Female	40
	Fawn	< 1 year	-	20
Sambar	Adult	> 2 years	Male	320
	Adult	> 2 years	Female	200
	Yearling	1- 2 years	Male	160
	Yearling	1- 2 years	Female	130
	Fawn	< 1 year	-	45
Langur	Adult	> 1 years	Male	18
	Adult	> 1 years	Female	12
	Infant	< 1 year	-	5
Wild pig	Adult	> 1 year	Male	60
	Adult	> 1 year	Female	40
	Piglet	< 1 year	-	15
Nilgai	Adult	> 2 years	Male	240
	Adult	> 2 years	Female	170
	Yearling	1- 2 years	-	100
	Calf	< 1 year	-	30
Barking Deer	Adult	> 2 years	Male	22
	Adult	> 2 years	Female	20
	Fawn	-	-	10
Gaur	Adult	> 2 years	Male	745
	Adult	> 2 years	Female	550
	Yearling	1- 2 years	-	250
	Calf	< 1 year	-	75

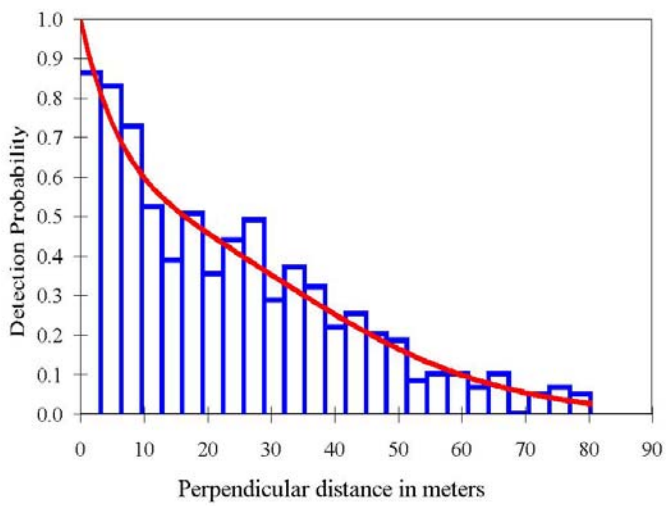
4.4. Results

4.4.1. Prey Abundance Estimates

Transects

Since all the transects were located in the highly protected core zone of the Tiger Reserve, there were no sightings of domestic livestock on any of the transect walks. Sighting data on abundances of gaur and nilgai, from line transects, was not adequate to produce reliable density estimates. Nilgai were sighted on transects 28 times and gaur 20 times. These numbers were much below the 40 sightings recommended by Buckland *et al.* (1993). Therefore, prey species that were sighted less than 20 times on transects were excluded from analyses. Fortunately, the number of sightings from line transects was high for chital (n = 449) and langur (n = 261), medium for sambar (n = 142), and adequate for wild pig (n = 70).

Figure 1. Detection probability plot of chital detections from line transect sampling in Pench T.R., M.P. (2001-2004). Model selected: Negative Exponential-Cosine.



The results of the density estimation analyses using Program DISTANCE showed that chital (ca. 115 individuals km^{-2}) and langur (ca. 66 individuals km^{-2}) are the prey species with the highest density in Pench (table 6). Wild pig and sambar had densities of 20 individuals km^{-2} and 12 individuals km^{-2} respectively. The total density of prey aggregated 215 individuals km^{-2}. Based on the criterion of lowest AIC value, the Negative Exponential key function fit the chital and sambar sighting data (figures 1 and 2).

Figure 2. Detection probability plot of sambar detections from line transect sampling in Pench T.R., M.P. (2001-2004). Model selected: Negative Exponential-Cosine.

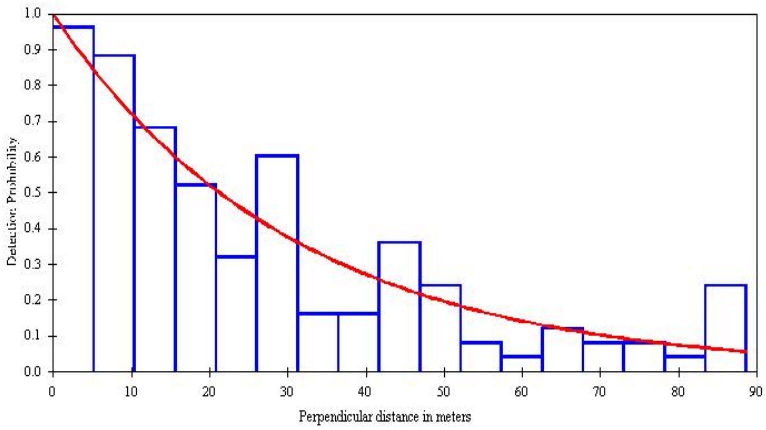


Table 6. Estimates of density for major prey species in Pench T.R., Madhya Pradesh, from analyses of line transect data using Program DISTANCE, Nov 2001 – June 2004.

Prey species	n	D_g	CV D_g %	SE D_g	D_i	CV D_i %	SE D_i	95 % C. I. Lower	95 % C. I. Upper
Chital	449	**21.3**	16.8	3.6	**115.6**	17.5	20.2	76.7	174.0
Sambar	139	**5.5**	19.1	1.1	**12.2**	19.9	2.4	7.0	21.0
Langur	261	**13.8**	35.7	4.9	**65.8**	36.2	23.8	17.2	251.9
Wild pig	70	**3.4**	23.4	0.7	**20.3**	26.7	5.4	11.2	36.6
Nilgai	28	**1.6**	41.8	0.3	**0.9**	43.4	0.7	0.5	4.7
Gaur	20	**1.1**	34.7	0.1	**0.4**	43.3	0.5	0.4	3.3
Prey	967	**46.7**			**215.2**				

N – number of sightings or detections
Dg - groups/km^2
D_i - indivs/km^2
SE – standard error on mean
CV – coefficient of variation

The mean group sizes of chital and sambar estimated from transects were 5.42 and 2.2 respectively, while the encounter rates were 5.6 chital and 0.7 sambar for one kilometre of transect walked (table 7).

Table 7. Ancillary abundance parameters for major prey species in Pench T.R., Madhya Pradesh, from analyses of line transect data using Program DISTANCE, Nov 2001 – June 2004.

Prey species	n	GS ± SE	ESW ± SE (m)	$f_{(0)}$	$\hat{p}$	Enc(G) km^{-1}	Enc(I) km^{-1}
Chital	449	5.42 ± 0.3	24.39 ± 2.7	0.041	0.304	1.040	5.638
Sambar	139	2.20 ± 0.1	29.05 ± 2.7	0.034	0.328	0.322	0.709
Langur	261	4.75 ± 0.2	21.85 ± 1.7	0.046	0.302	0.605	2.875
Wild pig	70	6.03 ± 0.8	24.07 ± 3.6	0.042	0.354	0.162	0.978
Nilgai	28	1.75 ± 0.2	35.92 ± 8.1	0.028	0.416	0.065	0.114
Gaur	20	2.95 ± 0.8	60.36 ± 0.0	0.017	1.000	0.046	0.137

n – number of sightings or detections
GS – group size
ESW – effective strip width
$f_{(0)}$ – probability density function at zero
$\hat{p}$ - detection probability
Enc(G) – Encounter rate of groups
Enc(I) – Encounter rate of individuals
SE – standard error on mean.

The annual density of chital ranged from a minimum of 79 individuals km^{-2} in 2001-2002 to a maximum of 175 individuals km^{-2} in 2002-2003. A break-up of annual density estimates, group sizes, and transect-related parameters of the two major dhole prey species, *viz.* chital and sambar, for the three individual years of the study period is given in table 8. Annual density figures were not statistically compared between years since the transects, sampled areas and effort varied each year of the study.

Even within individual home ranges of the dhole packs, chital had the highest densities (see table 8), followed by langur (on ground only), and sambar.

Table 8. Annual density estimates of chital and sambar in Pench T.R., Madhya Pradesh, from line transects, for three years.

Period	Length (km)	Prey Species	N	D_i	CV D_i %	Group size
2001-2002	218.4	Chital	193	78.97	13.9	5.02
		Sambar	54	6.62	23.3	2.13
2002-2003	140.4	Chital	193	175.10	16.0	5.77
		Sambar	55	15.32	19.1	2.38
2003-2004*	72.8	Chital	73	99.25	20.8	5.6
		Sambar	30	11.95	29.6	2.0

D_i - Density Estimate (no./km^2) ; CV D_i - coefficient of variation on D_i

* - included transects within Pench MH.

Table 9. Density estimates of major prey species in Pench T.R., Madhya Pradesh, from transects exclusively within dhole pack ranges, 2003-2004.

Pack Range	Prey Species	D_i	CV D_i %	Df
Pack A	Chital	67.95	28.73	15.34
	Sambar	9.89	26.57	17.85
	Langur	29.92	35.65	11.08
Pack B	Chital	96.77	26	22.72
	Sambar	8.53	28.29	19.89
	Langur	71.12	17.15	66.66

From the 100% MCP that was constructed around the transect locations, the actual area sampled from the transects encompassed 85.2 km^2, which would represent the actual area sampled for prey abundance from line transects. In terms of fractions, this accounts for almost 29% of the intensive study area (National Park), and 11% of the Tiger Reserve.

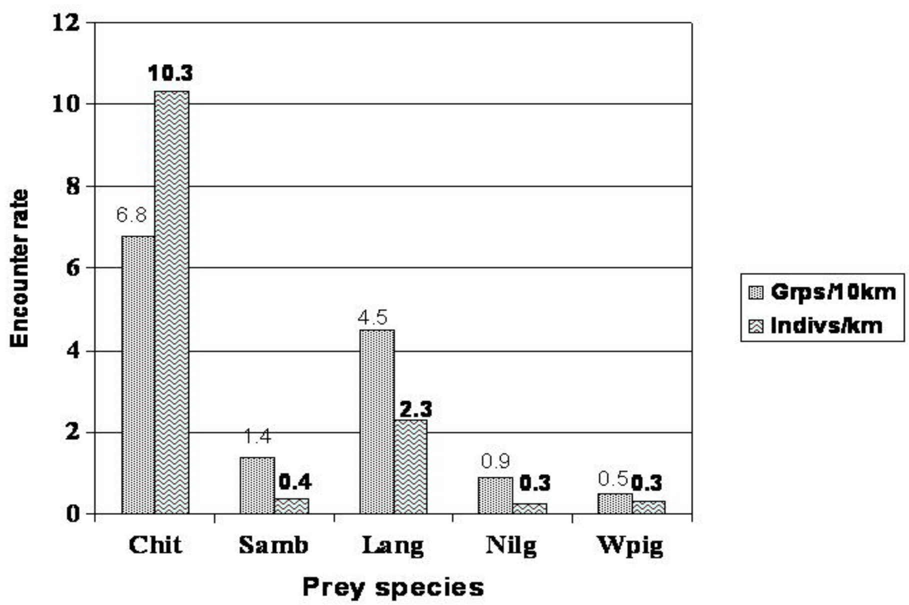
Vehicle Counts

The most encountered dhole prey species from road counts was chital (10.3 chital km^{-1}), followed by langur on ground (2.3 langurs km^{-1}) (see table 10 and figure 3). Sambar had an encounter rate of 0.4 sambar km^{-1}. The mean group sizes of chital and sambar estimated from vehicle counts were 15.2 and 2.8 respectively. Interestingly, wild pigs were encountered more often than sambar within the range of pack B than that of pack A.

Table 10. Encounter rates of major prey species in Pench T.R., Madhya Pradesh, from road counts (660 km), 2001-2004.

Prey Species	No. groups	No. indivs	Encounter Rates (no./km)	Encounter Rates (groups/km)	Group size
Chital	440	6691	10.31	0.68	15.2
Sambar	92	259	0.40	0.14	2.8
Langur	291	1489	2.30	0.45	5.1
Wild pig	32	214	0.33	0.05	6.7
Nilgai	61	165	0.25	0.09	2.7

Figure 3. Encounter rates (groups and individuals) of major prey species in Pench T.R., Madhya Pradesh, from road counts (660 km), 2001-2004.



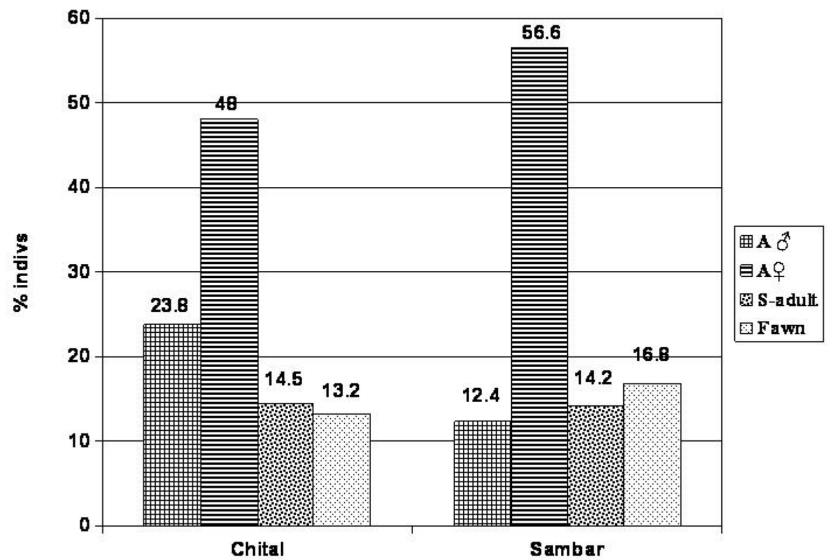
4.4.2. Population Structure

The population structure of the two major prey species of dholes including proportional representation of the different age-sex classes in the population, and other population parameters, obtained from road counts and *ad libitum* counts is summarised in table 11 and figure 4. The adult sex ratios in the two major prey species were: 50 males to 100 females in chital; 22 males to 100 females in sambar. The female: fawn ratio was 1: 0.27 for chital, and 1: 0.3 for sambar. Overall, chital also showed fairly large mean group size of around 22 individuals per group, while the mean group of sambar was only around 3 individuals.

Table 11. Group structure and composition of chital and sambar in Pench T.R., Madhya Pradesh, from *ad libitum* counts and road counts, Nov 2001 – June 2003.

Prey Species	No. groups	No. indivs	Group size	Age / Sex Class	No. individuals	%	♀:♂	♀:fawn
Chital	391	8827	22.58 (± 2.2 SE)	A. male	2108	23.8	1: 0.50	1: 0.27
				A. female	4237	48		
				S-adult	1276	14.5		
				Fawn	1165	13.2		
Sambar	219	654	3.15 (± 0.2 SE)	A. male	81	12.4	1: 0.22	1: 0.30
				A. female	370	56.6		
				S-adult	93	14.2		
				Fawn	110	16.8		

Figure 4. Group structure and composition of chital (n=8827) and sambar (n=654) in Pench T.R., Madhya Pradesh, from road counts, Nov 2001 – June 2004



4.4.3. Biomass

Table 12 depicts the proportional biomass contribution of individual age-sex classes, and their unit weights representative of the actual population structure. The unit weights of chital and sambar calculated were 49.1 kg and 193.2 kg respectively.

Table 12. Proportional biomass and unit weights of chital and sambar in Pench T.R., Madhya Pradesh.

Species	Age class	Sex class	Weight (kg)	% in pop	Prop wt (kg)	Unit wt (kg)
Chital	Adult	♂	70	23.8	16.7	49.14
	Adult	♀	50	48	24.0	
	Yearling	-	40	14.5	5.8	
	Fawn	-	20	13.2	2.6	
Sambar	Adult	♂	320	8.8	39.7	193.18
	Adult	♀	200	59.2	113.2	
	Yearling	-	160	16	18.5	
	Fawn	-	45	15.7	21.8	

Prey animals in the medium size (26-50 kg) weight class formed 46% of prey population, while small size (<25 kg) prey formed 40%, while large size (51-100 kg) prey formed 11 % of the population. Very large size (>100 kg) prey formed only 3% of the prey population.

Estimates of prey biomass (table 13) showed that chital formed the bulk of the prey (60%) in Pench. Sambar (24%), despite lower densities, ranked higher than langur (5%) in terms of biomass density and contribution to prey biomass, by virtue being nearly 30 times larger than langurs. Total prey biomass density was 9607 kg km^{-2} out of which the wild ungulate biomass density was 9080 kg km^{-2}. Total biomass contributed by each species in the study area is also tabulated.

Table 13. Biomass density and total biomass estimates of major dhole prey species for 292.85 km^2 of Pench N.P., Madhya Pradesh.

Prey species	D_i	Unit weight (kg)	Kg/km^2	Total Biomass (kg)	Biomass %
Chital	115.6	49.1	5,680.6	16,63,559	59.1
Sambar	12.2	193.2	2,356.8	6,90,187	24.5
Wild pig	20.3	34	690.2	2,02,125	7.2
Nilgai	0.9	170	153	44,806	1.6
Gaur	0.4	500	200	58,570	2.1
Ungulates	149.4	189.3 *	9080.6	26,59,253	94.5
Langur	65.8	8	526.4	1,54,156	5.5
Major Prey	215.2	159.1 *	9607	28,13,409	-

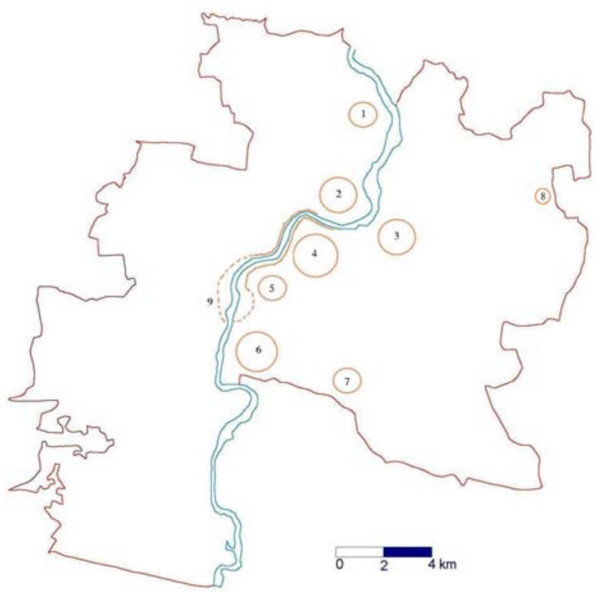
* - averages

4.5. Discussion

Chital

Chital by far were the most numerous of the prey species in Pench. This species dominates the landscape in Pench in terms of both sheer numbers (density 115 km^{-2} and encounter rate 10.3 km^{-1}) and biomass (60% of all prey species). Except for the hill-tops, they were found almost everywhere in the Reserve, occasionally forming large herds (Map 4), especially in the dry months when the grassy patches on the Pench reservoir beds were sprouting new shoots. Being generalist feeders tending to be grazers, chital find the habitat interspersion and resultant vegetation in Pench ideal. The density of chital in Pench (115 chital km^{-2}) is extremely high, compared to other dhole sites such as Mudumalai - 18.6 chital km^{-2} (Venkataraman *et al.* 1995), Bandipur - 40 chital km^{-2} (Johnsingh 1983) or Nagarahole – 49.1 chital km^{-2} (Karanth and Sunquist 1995). Chital density for a fraction of the same sampled area of transects in Pench from an earlier study (Biswas and Sankar 2002) was 80.7 chital km^{-2}, while another study (Acharya 1997) recorded a density of 107.7 km^{-2} chital km^{-2} within the miscellaneous forest type of the National Park during summer.

Map 4. Locations of known sites of aggregations of chital (*Axis axis*) in Pench NP, Madhya Pradesh (2001-2005).



No.	Location	No.	Location
1 -	Chendia Maidaan	6 -	ChhindiMatta submergence zone
2 -	MahadevGhat Maidaan	7 -	Pivarthadi Maidaan
3 -	Alikatta Maidaan	8 -	BodaNala Tank-bed
4 -	Daudikund submergence zone	9 -	Pench River banks
5 -	Sapaat Maidaan		

Naturally, their corresponding biomass density of chital in Pench (5680 kg km^{-2}) is also overwhelming, compared to the chital biomass density in other dhole sites such as Mudumalai - 961.5 kg km^{-2} (Venkataraman *et al.* 1995), Bandipur - 1648-1730 kg km^{-2} (Johnsingh 1983) or Nagarahole – 2379 kg km^{-2} (Karanth and Sunquist 1992).

Sambar

Sambar is most widely distributed dhole prey species in Pench. Despite being the third-most numerous prey species in the study area, sambar contribute the most to the prey biomass (24%) next to chital. Similar to chital, their density and biomass density in Pench (12.2 sambar km^{-2} and 2356 kg km^{-2}) is also relatively high, compared to other dhole sites such as such as Nagarahole - 3.4 sambar km^{-2} and 736 kg km^{-2} (Karanth and Sunquist 1992), Mudumalai - 5.2 sambar km^{-2} and 743.5 kg km^{-2} (Venkataraman *et al.* 1995), or Bandipur - 7 sambar km^{-2} and 1244-1399 kg km^{-2} (Johnsingh 1983). An earlier study by Biswas and Sankar (2002) recorded a sambar density of 6.1 individuals km^{-2}. This fact corroborates the great potential of Pench for large carnivores, as sambar is a keystone prey species.

Wild pig

Wild pigs in Pench contribute sizably to the prey biomass (7.2 %). Due to their smaller size and shorter stature, it was very difficult to count the exact number of individuals in a wild pig sounder from transects within dense forests. Therefore, wild pig numbers, densities, and biomass figures cited above are gross underestimates. Despite this fact, the wild pig densities in Pench (20.3 wild pigs km^{-2}) were much higher than that in Nagarahole (3.4 wild pigs km^{-2}) (Karanth and Sunquist 1995).

Langur

Langurs were the second-most numerous prey species in Pench (ca. 66 langur km^{-2}), but contributed lesser in terms of prey biomass as compared to sambar and chital. The langur density for Nagarahole was much lower at 25 langur km^{-2} (Karanth and Sunquist 1995). However, it has to be reiterated here that the estimates presented here refer to data of only langurs sighted on ground, deemed available to dholes. Therefore, these figures for langurs, especially of density, encounter rates, and biomass, are a gross underestimation of actual contribution of langur as a prey species. Further analyses of langur data with the inclusion of the counts of arboreal individual of langurs may reveal that langurs are indeed the most numerous prey species in Pench. This would be essential information in relation to predation by their main predator, the leopard.

Nilgai

Nilgai are localized to select areas of the Reserve that have wide open spaces (e.g. submergence zones of the Pench river such as Daudikhund and Sapaat) or scrub vegetation (e.g. Kaamrit, Awarghani). These habitats were not adequately sampled on transects and hence nilgai showed lower densities than actual. A similar situation was found with the locally migratory gaur. This does not understate the importance or contribution of these two species to the herbivore fauna and prey biomass of Pench.

Livestock

Absence of domestic livestock such as cattle, buffaloes or goats in prey density estimates arises from a sampling artefact. Though all the permanent transects were widely distributed, they were laid well within the core zone (National Park - 292 km^2) of the Tiger Reserve subjected to maximum protection and patrolling. This in effect ensured the total absence of livestock from the prey assessment for the Tiger Reserve.

Prey Densities

Prey density estimates recorded in Pench are very high (215.2 animals km^{-2} or 149.4 ungulates km^{-2}) mainly due to chital and sambar. The corresponding prey density in Nagarahole was much lower at 91 animals km^{-2} (Karanth and Sunquist 1995). The relatively smaller coefficient of variation of chital and sambar density estimates (16% and 17% respectively) indicate the widespread spatio-temporal distribution of these two prey species through Pench TR.

Prey Demography

Populations of both the two major prey species, chital and sambar, were dominated numerically by adult females, showing a clear female-biased sex ratio. In the case of chital, adult females constitute nearly half of the population, whereas in sambar adult female form more than half the population. The adult sex ratios were higher in chital (50 males to 100 females) than sambar (22 males to 100 females).

The chital sex-ratio ratio is much higher than that recorded in Mudumalai (chital 38 males: 100 females (Venkataraman *et al.* 1995), or Nagarahole (chital 72 males: 100 females; sambar 42 males: 100 females) (Karanth and Sunquist 1992) but lower than that recorded in Bandipur (68 males to 100 females) (Johnsingh 1992). The sambar sex ratio is much lower than that recorded in Mudumalai (sambar 32 males: 100 females) (Venkataraman *et al.* 1995), Nagarahole (sambar 42 males: 100 females) (Karanth and Sunquist 1992), or Bandipur (42 males to 100 females) (Johnsingh 1992).

The fawn: female ratio (27 fawns to 100 females for chital; 30 fawns to 100 females for sambar) recorded in this study was much lower than that recorded in Nagarahole (57 fawns to 100 females for chital; 44 fawns to 100 females for sambar) (Karanth and Sunquist 1992). Fawn to female ratio in Bandipur (Johnsingh 1983) was 28-70 fawns to females for chital, and 11-44 fawns to females for sambar.

Prey Biomass

The amount of “edge” available in a wildlife habitat is extremely crucial as ungulates tend to reach maximum biomass levels, where open grassland or meadow patches and forested patches (fawning and escape cover) inter mingle (Eisenberg and Lockhart 1972). For precisely these reasons, Pench appears to provide ideal conditions for achieving such high ungulate biomass levels.

4.6. Summary

In order to collect basic information on the prey species of dholes, this study aimed to estimate the density, encounter rates, biomass, and the population structure and composition of the major prey species within the study area.

Eventually, this data would represent prey available to predators – in numbers, proportions, or sizes.

Systematic estimation of prey abundance was conducted on 19 permanently marked line transects and 10 un-marked GPS-based transects, averaging a length of 2.3 km each (1.2 - 3.5 km) for the dry seasons (Nov-June) from 2001 to 2003, using the Line Transect Method. Line transect sampling was carried out only within the approximate ranges of each radio-tagged pack, for the period November 2003 – June 2004. The transect lines covered an actual area of 85.2 km2, which was ca. 29 % of the National Park area, and 11 % of the Tiger Reserve. Over the study period, the total annual length of transects in the study area averaged 41.2 km (27.3 – 51.0 km). Sighting angles and distances were recorded accurately using a compass and a laser rangefinder respectively. The computer Program DISTANCE Version 4.1 Release 2 was used for analyses of line transect data, choosing the appropriate models with the lowest Akaike information criterion values, to yield density estimates of the different dhole prey species. The common langur data used was only from those individuals of a troop that were sighted on ground, to reflect what was available as prey to dholes. Data regarding the encounter rates (numbers of animals sighted per km travelled) and group composition (group sizes, age-sex structure, etc.) of dhole prey species were also recorded using vehicle-based road counts from a four-wheel drive vehicle. A total of 660 km was travelled for the period 2001-2004. Biomass densities of the different prey species were computed by multiplying the estimated mean numerical densities by the published average weights of the respective age/sex-classes of the species. From the population structure of the prey species obtained from the *ad libitum* counts, the biomass was corrected for the actual population structure.

The number of sightings from line transects was high for chital (n=449) and langur (n=261), medium for sambar (n=142), adequate for wild pig (n=70). Chital, followed by langurs on ground, were most encountered dhole prey species from both line transects and road counts.

Chital by far were the most numerous of the prey species in Pench. This species dominates the landscape in Pench in terms of both sheer numbers and biomass. Sambar, though, being the third-most numerous prey species in Pench, contribute the most in biomass next to chital. Their density in Pench is relatively on the high side, and this fact corroborates the great potential of Pench for large carnivores, as sambar is a keystone prey species.

Populations of both the two major prey species, chital and sambar, were dominated numerically by adult females, showing a clear female-biased sex ratio. In the case of chital, adult females constitute nearly half their population, whereas in sambar adult female form more than half the population. The adult sex ratios in the two prey species were: 50 males to 100 females in chital; 22 males to 100 females in sambar. The female: fawn ratio was 1: 0.27 for chital, and 1: 0.3 for sambar. Mean group size of chital was 22.58 (± 2.2 SE), while that of sambar was 3.15 (± 0.2 SE).

Plate 1. Dhole scat being collected from a latrine site (intersection of paths) used frequently by a dhole pack, in Pench T.R., Madhya Pradesh.

Plate 2. A dhole pack feeding on their kill of a chital stag.

Chapter 5. DHOLE PREDATION

5.1. Introduction

Predation has been defined as individuals of one species eating living individuals of another species (Taylor 1984). Mammalian carnivores, as keystone predators, have great ecological value, playing a relatively major role in shaping prey communities, especially in tropical forests (Terborgh 1988). The process by which they seek and kill has important implications for their impact upon prey. By their predation, they regulate herbivore numbers thereby reducing the amount of pressure the latter exert on the vegetation (Terborgh 1988).

Large mammalian carnivore assemblages are chiefly mediated by the structure of the available prey assemblage. Top carnivores, such as dholes, are therefore highly sensitive to changes in prey base and habitat quality, thus serving as indicator species. Consequently, understanding the role of predation upon a prey species in this situation would require an understanding of the context within which it occurs.

The feeding ecology of a carnivore determine to a great extent vital life history strategies such as their spatio-temporal distribution, movements, activity, behaviour and social organization (Bekoff *et al*. 1984; Sunquist and Sunquist, 1989).

Vertebrate predators would be selective energy maximizers (selective predation) in prey-rich habitats, but non-selective number maximizers where large prey is scarce (Griffiths 1975). In the case of mammalian carnivores, since they spend considerable time and energy in pursuing and handling prey, they would naturally be selective in their prey preference and would pursue only prey that would be profitable (Schoener 1971), especially large-sized prey (Griffiths 1975). Prey selectivity is defined as the killing of prey types in frequencies that are different from those expected based on their availability in the environment (Chesson 1978). 'Selection' would mean either preference (greater than expected under random killing of prey species) or avoidance (less than expected offtake) of certain types of prey (Alldredge and Ratti, 1986).

An assessment of the prey base and prey use by dholes is vital to predict their viability, survival, and persistence within their present range and to plan for their future. In addition, the temporal and spatial availability of prey also influences predator-prey relationships and prey selectivity.

The objective was to determine the relative proportions of different prey species in diet of dholes, in terms of frequency of occurrences, biomass, and numbers of individuals consumed. The aim was also to study predation by dholes in relation to prey availability and utilization within Pench Tiger Reserve, i.e. to see if dholes killed prey randomly or selected specific kinds of prey. If that was so, the ecological factors intrinsic to that prey which may influence prey selection were assessed. An attempt was also made to compare the findings from this study with those of previous long-term studies on dholes.

5.2. Methods

Various techniques are used by researchers to study predation and feeding ecology of mammalian carnivores, such as stomach content analyses, scat analyses, kill investigation, and by continuously following the carnivore under study to estimate kill rates and consumption rates.

A “hunt” was defined as an orientation and an approach towards a particular prey animal or prey group. While observing hunts by dhole packs, the position of the hunting pack and the time at the start and end of the hunt, the size and composition of prey group approached, the species, size and age-sex of prey chased, and the outcome of the chase, were all noted systematically, whenever possible.

The diet of dholes was estimated using two techniques. Firstly, analyses were conducted on dhole scats (faeces), since remains of prey species are very much evident in carnivore faeces. Besides determining the relative frequency of occurrence of prey remains in dhole diet, this method also gives information on the various species of prey consumed by dholes.

The second method was to estimate prey consumption from observations of dhole pack feeding at kills, and later determining the frequency of kills of particular prey species. This latter method helps in determining age and sex class of prey that is killed (Johnsingh 1983, Karanth & Sunquist, 1995). The health and body condition of prey, especially through bone marrow condition (Brooks *et al.* 1977), can also be assessed from kills.

From the data collected using these two approaches, prey selection by the dholes was arrived at following Karanth and Sunquist (1995). Since prey distribution and abundance varies seasonally, dhole diet for the wet and dry seasons was compared.

5.2.1. Scats

Scat analysis is an established technique for determining the diet of carnivores (Putman 1984), and has been effectively used to study dhole diet (Johnsingh 1983, Karanth & Sunquist, 1995, Venkataraman *et al.*, 1995). This method permits a regular and frequent assessment of food habits and degree of importance of different prey in the diet. Moreover, this is a cost- and time-effective process, especially with scats being readily available in field.

An inherent problem with carnivore scat analyses is that the more obvious characteristics of the prey are lost during mastication and digestion. Only the hard indigestible parts that are voided out in the scats can be used to identify prey remains, depending what part of the prey is consumed. Fortunately, large carnivores such as dholes often ingest sufficient hair, soft bones, hooves or teeth of prey to permit identification of the prey consumed.

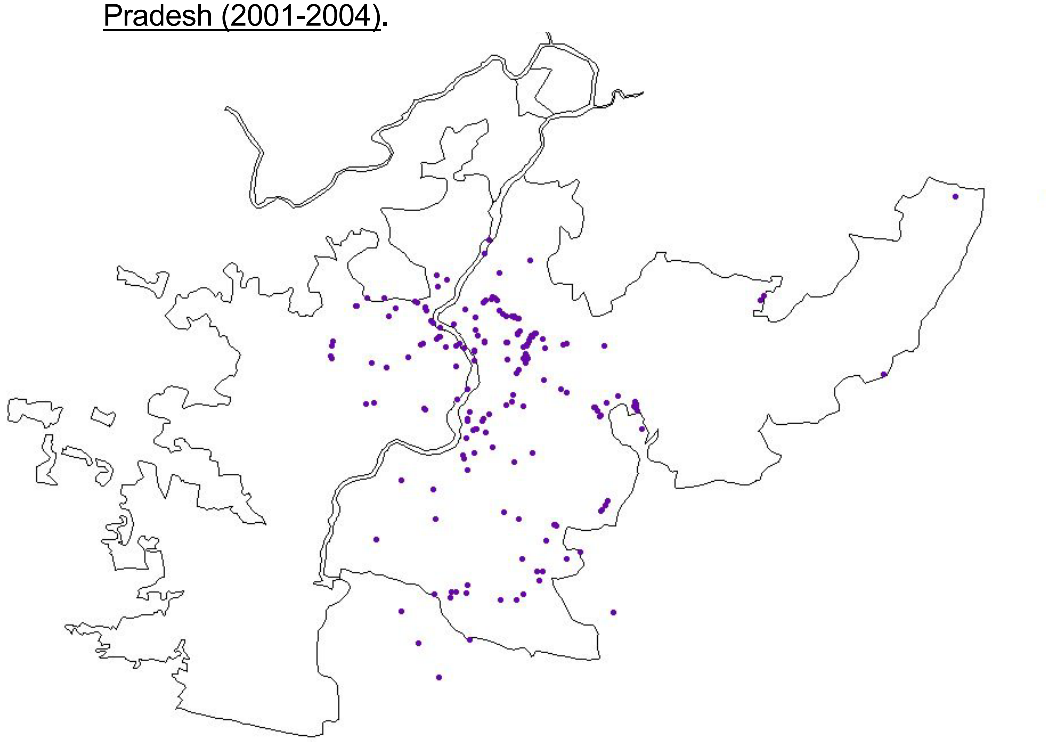
Scat Collection

Mammalian carnivores are known to move along and defecate on and along forest roads and trails. The same is true for large carnivores in India and an extensive network of forest roads in Pench TR facilitated the collection of representative samples of predator scats in this study. The scats of only the three main carnivores of Pench, i.e. dholes, tigers and leopards, were collected for this study.

Scats were collected either by actively searching for them on forest roads or paths, or as and when encountered during the course of fieldwork. When defecation was visually observed, details such as predator species, defecation date and time etc., were noted before the scat was collected. In case of defecations by dholes, the identity of the individual or pack (if known) was recorded. The chances of observing defecations, or locating and assigning scats to dhole known packs greatly increased with radio-collaring of individual dholes.

Scats not observed being deposited were assigned to predators based on size, appearance, and associated signs and tracks. Dhole scats were easily distinguishable from those of the tiger and leopard. Dhole scats are much smaller, with a characteristic odour, usually found in a bunch at cross-roads or intersections, and mostly deposited on bare or exposed soil. The felid scats were larger, stickier in consistency, and deposited on grass alongside tracks, foot paths or roads, or between the wheel tracks of motorable road, as observed by Johnsingh (1983) and Karanth (1993). Tiger and leopard scats were distinguished using the size and shape of the scats, or secondary evidences such as pugmarks and scrapes. When the identity of the predator was not established, the scat was recorded as that of an unknown predator.

Map 5. Locations from where scats of dholes were collected in Pench TR, Madhya Pradesh (2001-2004).



Whenever a scat was collected, the predator species, collection date and time, geographical location and locality, substrate, and secondary evidences such as tracks were recorded for each collected scat. Geographical locations i.e. latitude-longitude were recorded on a Global Positioning device (GPS Receiver - Garmin® GPS 12XL, Garmin International, Inc., Kansas, USA) (see map 5). Each individual collected scat was assigned to a unique identity code that reflected the predator species and the date of collection (e.g. LS020314b – second scat of leopard for that day on 14th March 2002).

For dhole scats, only one scat was collected per latrine site per pack per day. This was done to ensure scat samples were independent and represent individual kills, preventing the overestimation of prey items in the diet. Moreover, since dhole scats function as home range markers, removal of only one scat was deemed minimal disturbance of dhole latrine sites. Only fresh (< I day old) intact dhole scats were collected in field, assuming that these represented the previous kill or meal. Usually it was the largest scat piece from a latrine site that was collected for analyses.

Scat Processing

In field, entire scats of carnivores were collected in a polythene bag, and later transferred to plastic jars appropriately labeled with the identity code. Within the jars the scats were soaked for 2-3 days in water laced with a little detergent in order to facilitate the separation of prey remains in the scat from faecal matter.

After being soaked for adequate time in jars, the scats were washed in running water on to a 1-mm sieve and undigested prey remains such as hair, bones, teeth, hooves, etc., were retained while faecal matter was washed away. These washed remains were dried under direct sunlight for at least half a day, following which they were stored under moisture-free conditions in dry paper bags retaining the original labelling containing the specific identity of the individual scats, pending analyses.

Laboratory Procedures

Processed samples of scat remains were dried for a day before prey remains were carefully examined under a binocular microscope. The most prevalent prey remains were hair and skin. Intact hooves of very young ungulates were not uncommon in scat remains. Teeth and bone remains were usually absent or too fragmented to be of any use.

A subset of confirmed reference slides (of dhole prey species present in Pench) was made from the catalogue of reference slides of known hair samples in the laboratory of the Wildlife Institute of India, Dehradun. Prey hair found in each scat sample was compared with this reference collection, following the micro-histological methods as described in Reynolds and Aebischer (1991). A minimum of 20 hairs was taken from each scat (Mukherjee *et al.* 1994) and examined under the microscope. Macro- and microscopic study of hair specimens was carried out primarily using diagnostic features such as colour, length, thickness, patterns of the hair cuticle, and also using the internal structure of hair such as the configuration of hair medullae (Moore *et al.* 1974, Koppikar and Sabnis 1981, Rajaram and Menon, 1986).

5.2.2. Kills

Though the analysis of carnivore scats is an unbiased method for estimating the diet or prey species consumed by carnivores, it does not provide information such as the sex, age class, body size, physical condition and health of the killed prey animal. Therefore, locating the kills of carnivores and recording these pertinent information becomes extremely vital in understanding predation ecology (Schaller 1967, Sunquist 1981, Johnsingh 1992).

Locating Kills

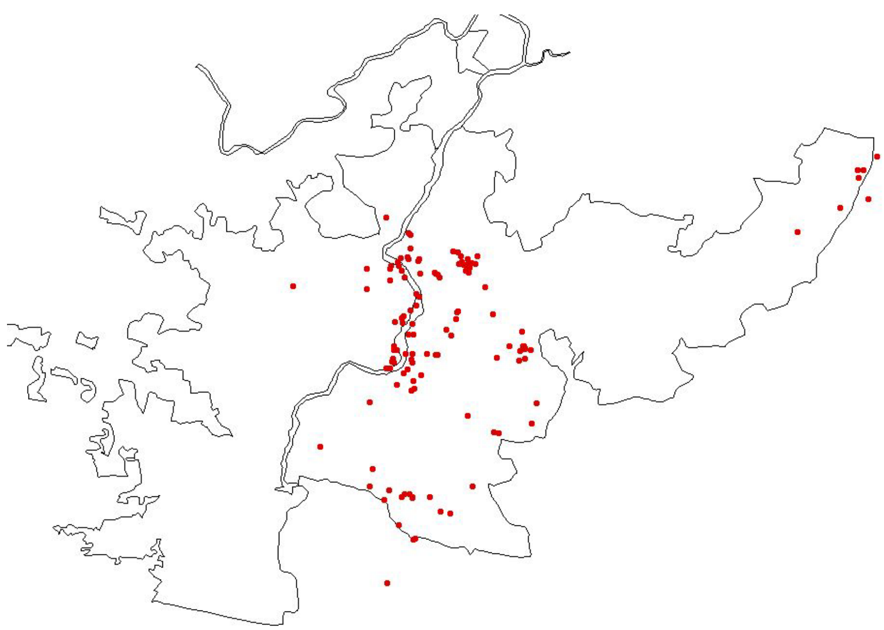
Throughout the study period, kills made by predator were located by actively searching the study area for the same, or on an *ad libitum* basis. Prime indicators of the presence of kills were the persistence of predators in the vicinity, alarm or distress calls of prey, sounds from the feeding predator, the calls of large-billed crows (*Corvus macrorhynchos*), or the sight of hovering or descending vultures (*Gyps bengalensis*). The location of the kills was usually pinpointed by the sighting of the feeding carnivores or scavengers, by the odour of the decomposing carcass, and occasionally, by the tell-tale signs indicating dragging of the carcass by the predator (drag line). In addition to this, constant monitoring of radio-collared dholes greatly helped in successfully locating kills made by them. Whenever dholes or other predators were observed spending an unusually long time (> 15 min) at one spot, these locations were later on searched for kills. On several occasions, information on kills was obtained from field staff of the Tiger Reserve or tourist guides. Non-predation deaths were also accounted for. Confounding elements in locating kills, especially during the rainy season, were the thick vegetation cover, heightened scavenger activity and rapid decomposition of carcasses.

Recording of Kills

Once the kills were located, a detailed investigation was carried out and the relevant information was recorded. Kills were given a unique identity code (e.g. DK020314a – first kill of dholes for that day on 14th March 2002). In the absence of conclusive evidences, the predator responsible for the kill and the mode the killing (e.g. neck bite, evisceration, etc.) was determined by scrutinizing the carcass and the surrounding site for tell-tale signs. After all this, if the identity of the predator responsible for the kill could not be deduced, the kill was recorded as that made by an unknown predator.

If predators were present on the kill, the carcass was inspected always after the predators had left the kill site, not only to ensure the accurate recording of consumption by the predators but also to avoid any disturbance to the natural process of feeding.

Map 6. Locations from where kills of dholes were recorded in Pench TR, Madhya Pradesh (2001-2004).



Information recorded at each kill included parameters of the prey animal such as age, sex, body weight (estimated), amount of meat eaten (estimated), physical health condition, colour and texture of marrow fat of the femur bone (Brooks 1977, Riney 1982), physical disabilities and evidences of disease. The relative age of killed prey was determined based on eruption and wear of premolar and molar teeth on the mandible, when available. Sex of the prey was determined by gender-specific characteristics such as antlers, horns, or external genitalia. Size and condition (velvet or hard) of antlers were also recorded for cervid males. Weight of remains, both in parts and in entirety, was recorded using appropriate weighing balances. Geographical location (latitude-longitude) (map 6), locality, date-time, and general characteristics of the kill site such as vegetation type, cover, terrain, etc, were also recorded for each kill. Prey was also categorized as small (< 25 kg), medium (26-50 kg), large (51-100 kg), and very large size prey (> 100 kg) following Johnsingh (1992).

5.3. Analyses

The number of hunts recorded from start to finish were limited, since hunting dhole packs could be followed and observed only from vehicle on forest roads, and never pursued off road. Therefore, the observed kills constituted only those on which dholes were present (feeding or otherwise) and the prey identifiable carcass. Therefore, for a better understanding and quantification of dhole diet, indirect estimates of dhole food habits were mainly relied on.

Prey encounter rates obtained from line transects and road counts were used as indices of prey encounter by dholes. From the kill data, Pearson's correlation analysis was carried out to check for any significant correlation between dhole pack size and the body weight of prey killed. The statistical package SPSS Version 8.0 (SPSS 2001) was used for this analysis.

5.3.1. Scats

Some scats contained little or no hair, nor bones, but dark digested meat, occasional strips of partly digested muscle or tendon, or just grass.

Standardized analyses of prey remains were performed the independent samples of dhole scats. This sample was further split into seasons: winter, summer and monsoon. Since scat samples were independent, it was assumed that 'identifiable' prey remains in each scat represented one prey individual, following Floyd *et al.* (1978).

In order to evaluate if the requisite and representative number of scats had been obtained for each of the three main seasons of sampling, sample size adequacy analyses were conducted following Mukherjee *et al*. (1994). Random batches of five scats each were selected successively until all scats within a season were analysed for prey presence. For each season, the cumulative number of different prey species identified was plotted against the cumulative number of scats analysed. The point (no. of scats) at which the curve reaches an asymptote (i.e. no further addition of prey species), decided the minimum sample size required to deem the analyses adequate and representative of that season.

Percentage occurrences of different prey species in dhole scats were calculated by enumerating the number of scats with remains of a particular species out of the total number of scats with prey remains, depicted in the form of a percentage figure (Reynolds and Aebischer 1991). Frequency of occurrence of a prey species was calculated as the number of occurrences of that prey species divided by the total number of scats analysed (Ackerman *et al.* 1984). This frequency was also expressed as a percentage. While frequency of occurrence indicates how often a prey species occur in dhole diet, percentage occurrence provides an idea of prey intake.

According to Ackerman *et al.* (1984), percentage occurrence provides a better indication of the relative frequency with which each prey is consumed because it accounts for scats containing the remains of more than one species. However, they also point out that if more than one prey species regularly occur in scats, frequency of occurrence provides a better index of predator diet (*Ibid* 1984, Putman 1984).

For a clearer understanding of dhole predation, the relative numbers and biomass of different prey consumed by dholes also needs to be estimated (Putman 1984, Ackerman *et al.* 1984). This computation however requires a correction factor to avoid overestimation of smaller prey species in dhole diet. This overestimation is because smaller prey consumed, because of their higher surface to volume ratio or hair to biomass ratio compared to larger prey, results in more scats being produced per unit body weight (Mech 1970), therefore greater is their frequency in scats. To correct for the phenomenon where number of collectible scats is inversely related to prey size, Floyd *et al.* (1978) developed a correction equation for wolf scats that rectifies the overestimation of small prey. In the absence of such an equation developed specifically for dholes, the same equation was used for dholes in Pench, assuming wolf (ca. 40 kg) digestion is not very dissimilar to that of dholes (15-17 kg). The correction equation is calculated as:

$$Y(i) = 0.035 + 0.020\,X(i),$$

where:

$Y(i)$ = weight of prey species i consumed per field collectible dhole scat

$X(i)$ = average weight of an individual of species i.

The average weight $X(i)$ of individuals of different dhole prey species taken for this calculation is given in table 5. This prey weight consumed per scat (Yi) yields the relative weight of each prey species when multiplied by the proportion of scats of species i among all scats. From this the relative biomass contribution of different prey species to the dhole diet was estimated. The average number of collectable scats produced by dholes from an individual of prey species i was also calculated as:

$$\lambda_i = Xi \; / \; Yi$$

Further, using these values, the estimated number of individuals of species i killed and relative biomass contribution of species i to dhole diet were computed, following Ackerman *et al.* (1984)

To ascertain whether dholes in Pench were killing prey randomly or selectively, proportions of each prey species from scat analyses (observed) were compared with the proportions of the same species obtained from the transect data (expected). The expected proportion of scats (π_i) from a kill of prey species i, according to the prediction of a null hypothesis of no prey selection (Manly *et al.* 1972), was computed following Link & Karanth (1994) using a multinomial likelihood estimator as:

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

where:
d_i = population density of species *i*
λ_i = number of scats produced from a single dhole kill of species *i*

The value of λ_i, as explained earlier, was derived using the equation developed for wolves by Floyd *et al.* 1978). The software program SCATMAN (Hines 2002) was used to compute bootstrapped estimates of expected number of scats and frequencies of each dhole prey species in scats, using the individual density estimates of prey species (groups) obtained from line-transect sampling, based on an assumption of non-selective predation. If there were remains of two prey species within one scat sample, each prey species was counted as 0.5.

To test the null hypothesis that dholes killed prey in proportion to their availability, the observed proportions of prey species in scats to the expected proportions from Program SCATMAN were compared using a χ^2 goodness-of-fit test (Zar 1984), in conjugation with Bonferroni's simultaneous confidence intervals (see Neu *et al.* 1974). The χ^2 goodness-of-fit test indicates whether there is significant presence of prey selectivity, and the Bonferroni intervals help to test which of the prey species are preferred or not.

For depicting prey selectivity figuratively, the Jacobs' index (Jacobs 1974) was used. This index D_i computed as:

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}$$

where:

r_i is the fraction of scat of prey species *i* deemed as observed predation or "used" and,

p_i is the fraction of prey species *i* in the population deemed as expected predation or "available".

The value of the index D_i ranges from a maximum of +1 to a minimum of –1. Positive and negative values indicate preferences and avoidance respectively.

To compare prey selectivity, both used and available proportions of prey species is required. However, for one of the prey species, cattle, there was no sightings on transects, a sampling artefact arising out of transects located only inside the highly protected Core Zone. Therefore, this prey species was kept out of the prey selectivity analysis.

Since prey distribution and abundance varies seasonally, wet and dry season diets were compared between these seasons using the χ^2 goodness-of-fit test (Zar 1976), using frequency of occurrence.

Using a feeding rate of 1.86 kg per day for a dhole (Johnsingh 1983), the biomass consumed by dholes was calculated and the number of prey species required was determined.

5.3.2. Kills

The age-sex class distribution of each major prey species in the kill data was compared with the corresponding population age-sex distribution recorded from road counts and *ad libitum* counts, to check if dholes were selecting for a particular age-sex class of each prey. The statistical comparison was carried out using a χ^2 goodness-of-fit test (Zar 1984), in conjugation with Bonferroni's simultaneous confidence intervals (Neu *et al.* 1974). The χ^2 goodness-of-fit test indicates whether there is significant selectivity of age-sex class, and the Bonferroni intervals help to identify the age-sex class(es) are preferred and those that are not.

For depicting class selectivity figuratively, the Ivlev's Preference Index (PI) (Ivlev 1961) was used:

$$PI = \frac{(U - A)}{(U + A)}$$

where U = proportion used, A = proportion available.

The proportions (U) of each age-sex used was obtained from the kill data while the proportion available (A) was obtained from the population data from road counts and *ad libitum* counts.

In this same way, to check if dholes killed prey according to weight classes (irrespective of species) in proportion to their availability, the observed proportions of prey weight classes in dhole kills was compared to the expected proportions of prey weight classes in the population, using the χ^2 goodness-of-fit test (Zar 1984), in conjugation with Bonferroni's simultaneous confidence intervals.

5.4. Results

Analysis of 725 scats and 137 kills indicated that dholes consumed a minimum of seven prey types (tables 14 and 21), ranging in size from a full-grown sambar stag to a squirrel.

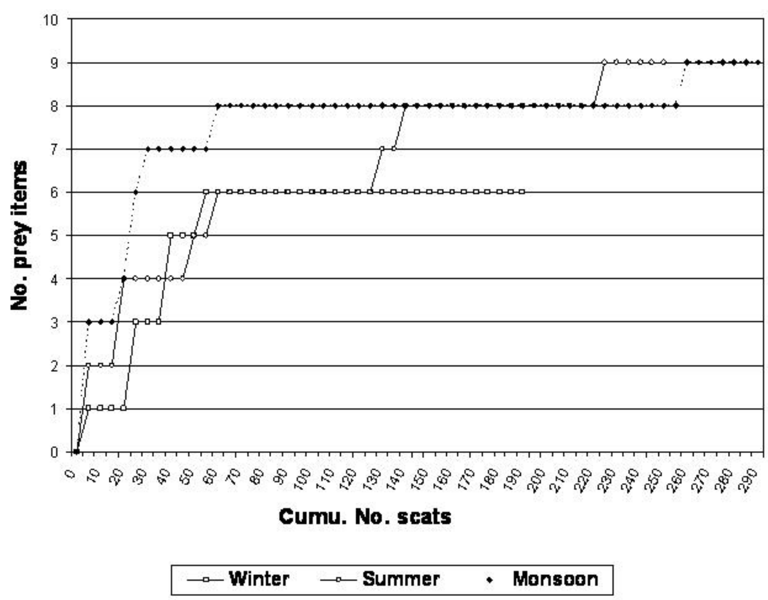
5.4.1. Scats

A total of 883 predator scats were collected from field. Of these 778 were dhole scats, 96 were tiger scats, and 9 were leopard scats.

Of the 778 dhole scats, 725 scats contained prey remains suitable for analyses. Standardized analyses of prey remains were performed on these 725 independent samples of dhole scats. This sample was further split into seasons: winter (n = 187 scats); summer (n = 249 scats); and monsoon (n = 289).

Sample size calculations indicated that the minimum sample size of dhole scats required to consider the analyses adequate and representative of dhole predation of major prey for a season was around 65 scats (figure 5).

Figure 5. Calculation of sample adequacy for analyses of dhole scats collected in Pench T.R., Madhya Pradesh, 2001-2004 (n = 3 seasons)

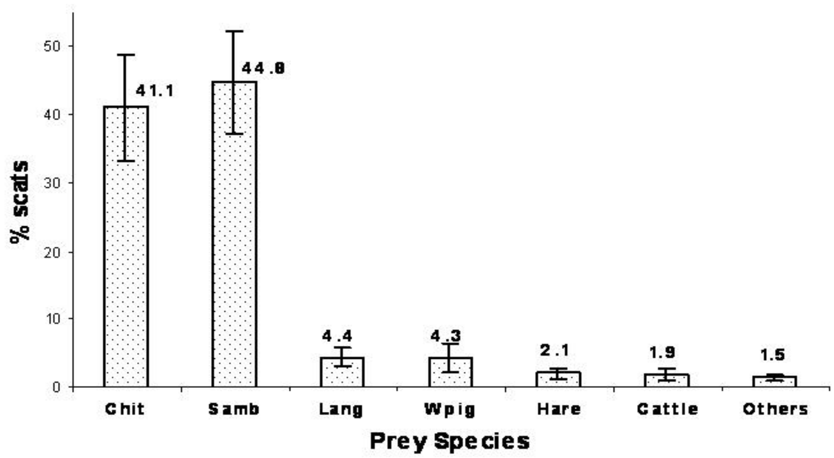


Of the 725 dhole scats analysed, sambar remains were the most frequent prey item in dhole scats (nearly 50 %), followed by that of chital (38%) (see table 14 and figure 6). Significantly, 31 scats contained remains of langur. Around 6 % scats contained remain of more than one prey species.

Table 14. Details of prey items recorded from dhole scats collected in Pench T.R., M.P. 2001-2004 (n = 725).

Prey species	No. of scats with presence	% of scats with presence	No. of times present	% of times present
Sambar	377	49.0	366	50.5
Chital	298	38.7	294	40.6
Langur	31	4.0	19	2.6
Hare	20	2.6	14	1.9
Wild pig	19	2.5	14	1.9
Cattle	14	1.8	12	1.7
Rodent	7	0.8	3	0.3
Gaur	1	0.1	1	0.1
Buffalo	1	0.1	1	0.1
Mongoose	1	0.1	1	0.1
Bird	1	0.1	1	0.1

Figure 6. Frequency of occurrence of remains of major prey species (> 1%) in dhole scats collected in Pench T.R., Madhya Pradesh, averaged over 13 seasons covered in 2001-2004 (n = 725). (Error bars represent standard error on mean %)



Tables 15 and 16 give a break-up of the frequency of occurrences of remains of prey species in dhole scats.

Table 15. Annual frequency of occurrence of remains of major prey species in dhole scats collected in Pench T.R., Madhya Pradesh, 2001-2004 (n = 725 scats).

Prey species	Years								Overall (n=4)	
	2002		2003		2004		2005			
	N	%	n	%	n	%	n	%	N	%
Chital	109	68.6	88	42.3	84	26.5	17	18.3	298	41.1
Sambar	24	15.1	95	45.7	196	61.8	62	66.7	377	44.8
Wild pig	11	6.9	8	3.8	8	2.5	4	4.3	19	2.1
Langur	10	6.3	4	1.9	4	1.3	1	1.1	31	4.4
Hare	1	0.6	4	1.9	11	3.5	4	4.3	20	4.3
Cattle	1	0.6	4	1.9	11	3.5	4	4.3	14	1.9
Others	3	1.9	5	2.4	3	0.9	1	1.1	12	1.5
Total	159	100	208	100	317	100	93	100	770	100

N.B.: Year-end = June 15th = onset of monsoon; Year 2002 = May 5th 2001 – June 15th 2002

Table 16. Seasonal frequency of occurrence of remains of major prey species in dhole scats collected in Pench T.R., Madhya Pradesh, 2001-2004 (n = 725 scats).

Prey species	Seasons						Overall (n=13)	
	Winter (n = 4)		Summer (n = 5)		Monsoon (n = 4)			
	n	%	n	%	n	%	n	%
Chital	89	45.9	105	39.0	104	33.8	298	41.1
Sambar	83	42.8	135	50.2	159	51.6	377	44.8
Langur	13	6.7	7	2.6	11	3.6	31	4.4
Wild pig	1	0.5	6	2.2	12	3.9	19	2.1
Hare	5	2.6	7	2.6	8	2.6	20	4.3
Cattle	0	0.0	6	2.2	8	2.6	14	1.9
Others	3	1.5	3	1.1	6	1.9	12	1.5
Total	194	100	269	100	308	100	770	100

The estimates of how much prey weight is represented by one dhole scat for the major prey species is listed in table 17. For chital the figure was 1.48 kg per scat, and 1.78 kg per scat of sambar.

Table 17. Estimates of prey weight consumed per dhole scat (Y_i) for major (> 1%) prey species in Pench TR, Madhya Pradesh.

Prey species	Prey weight (kg) *	Prey weight / scat Y_i (kg)
Sambar	70	1.78
Chital	55	1.48
Langur	8	0.54
Hare	3	0.44
Wild pig	31	1.0
Cattle	350	7.38

* average weight for each species used

The estimates of average number of field-collectable scats produced by dholes from one kill of each major prey consumed is listed in table 18. For chital the figure was ca. 37 scats per kill, and ca. 39 scats per kill of sambar.

Table 18. Estimates of average number of field-collectable scats produced (λ_i) by dholes from one kill of major (> 1%) prey species consumed in Pench TR, Madhya Pradesh.

Prey species	No. of scats/kill (λ_i)	No. of kills/scat ($1/\lambda_i$)
Sambar	39.33	0.025
Chital	37.16	0.027
Langur	14.81	0.068
Hare	6.82	0.147
Wild pig	31.0	0.032
Cattle	47.43	0.021

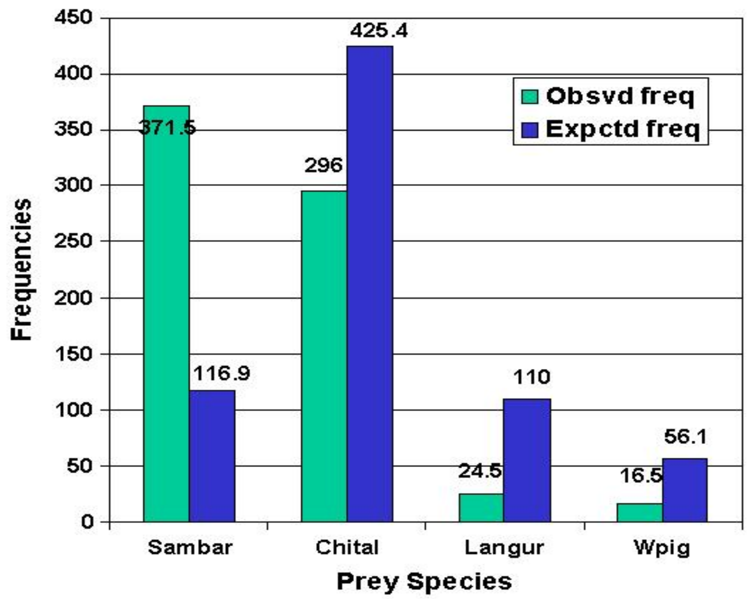
Sambar (52 %) and chital (34 %) alone contributed the bulk (ca 87 %) of the biomass consumed by dholes in Pench (Table 19). The 8% contribution that came from cattle was essentially a result of occasional scavenging on discarded carcasses on the fringes of villages of the buffer zone.

Table 19. Estimates of relative percent contribution of major (> 1%) prey species to dhole diet in Pench TR, Madhya Pradesh, from 725 dhole scats.

Prey species	% of scats with presence	% kills Contribution	% biomass Contribution
Sambar	49	40.2	52.58
Chital	38.7	34.4	34.56
Langur	4.0	9.0	1.31
Hare	2.6	12.6	0.69
Wild pig	2.5	2.6	1.49
Cattle	1.8	1.3	8.1

The comparison of the observed proportions of major prey species in dhole scats to that expected (Table 20), using the χ^2 goodness-of-fit test, resulted in the rejection of the null hypothesis that dholes killed prey in proportion to their availability (χ^2 =94.4, df = 3, P < 0.001). Therefore, the data clearly confirms that dholes are selective in taking particular prey species.

Figure 7. Comparison of observed and expected frequencies of prey consumption by dholes of the four major prey species, generated by Program SCATMAN from 725 dhole scats in Pench T.R., Madhya Pradesh, 2001-2004.



When Bonferroni's simultaneous confidence intervals were constructed on the above results, it was found that sambar was the only prey species that was taken significantly more than availability (preferred), while chital, langur and wild pig were all taken significantly much lesser than their availability (not preferred) in the study area (tables 20 and 21; figures 7 and 8).

Table 20. Prey selectivity by dholes of the four major prey species, using Bonferroni's Confidence Intervals (Neu *et al.* 1974), from 725 dhole scats in Pench T.R., Madhya Pradesh, 2001-2004, based on expected frequencies generated from transect data using Program SCATMAN.

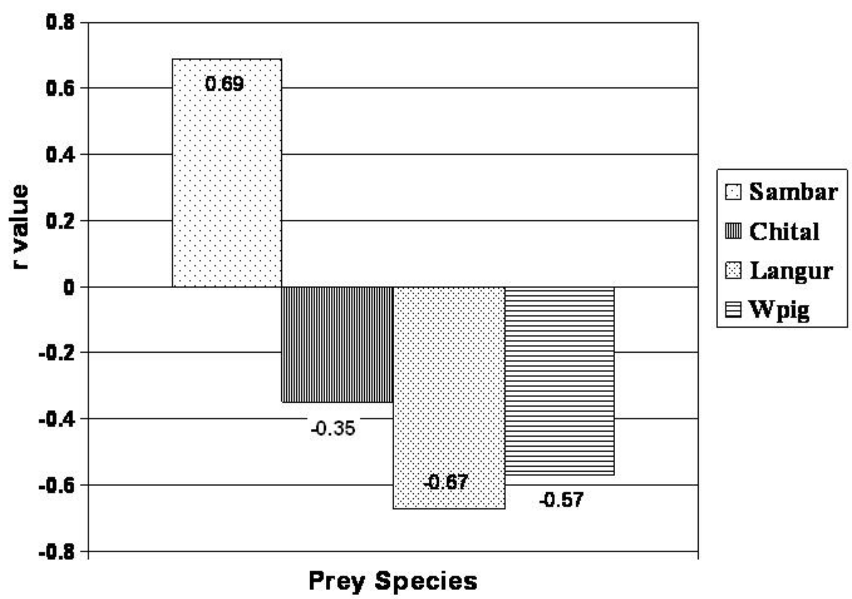
Prey species	Observed fraction of scats P_O	Expected fraction of scats P_E	Bonferroni intervals for P_E
Sambar	0.524	0.165	$0.477 \le p \le 0.571$
Chital	0.418	0.601	$0.371 \le p \le 0.464$
Langur	0.035	0.155	$0.017 \le p \le 0.052$
Wild pig	0.023	0.079	$0.009 \le p \le 0.037$

$Z\alpha/2k = 2.495$; all significantly different at $\alpha = 0.05$

Table 21. Prey selectivity by dholes of the four major prey species, using Jacob's (1974) index, from 725 dhole scats in Pench T.R., Madhya Pradesh, 2001-2004, based on expected frequencies generated from transect data using Program SCATMAN.

Prey species	Observed freq. of scats	Observed fraction of scats	Expected freq. of scats	Expected fraction of scats	Jacobs' D
Sambar	371.5	0.524	116.9	0.165	+0.696
Chital	296	0.418	425.4	0.601	-0.354
Langur	24.5	0.035	110	0.155	-0.674
Wild pig	16.5	0.023	56.1	0.079	-0.566

Figure 8. Prey selectivity using Jacob's (1974) index, from analyses of dhole scats, Pench T.R., Madhya Pradesh, 2001-2004.



Wet and dry season diets of dholes did not show any significant difference (χ^2 =1.59, df = 6, P > 0.05) in terms of frequency of occurrence of prey species.

5.4.2. Kills

In total 198 kills of the three major predators of Pench were recorded, out of which 137 kills were identified as made by dholes, 17 by leopards, and 12 by tigers. 32 kills could not be assigned to any predator. 54% of the dhole kills recorded were made in the forenoon, whereas 32% were kills made after noon. In particular, 53% of the kills were made in the morning, 27% in the evenings and 6.5% were kills around mid-day. Only one kill was recorded to have been made in the night. Of the 20 kills for which body condition was assessed from the bone marrow, 31.6% were in 'good' body condition, 36.8% in 'fair' condition and 31.6% in 'poor' body condition. The 137 dhole kills were assessed with respect to prey species, their age-sex class, and identity of dhole pack. More than 80 % of these kills were that of chital, and around 13 % that of sambar (see table 21 and figure 9). There was no significant correlation between dhole pack size and the prey weight (Pearson's correlation coefficient $r = 0.096$, $p > 0.05$). Average meat available for consumption per dhole per kill amounted to 7.54 kg.

Figure 9. Major prey species killed by dholes in Pench T.R., Madhya Pradesh (n = 137), 2001-2004.

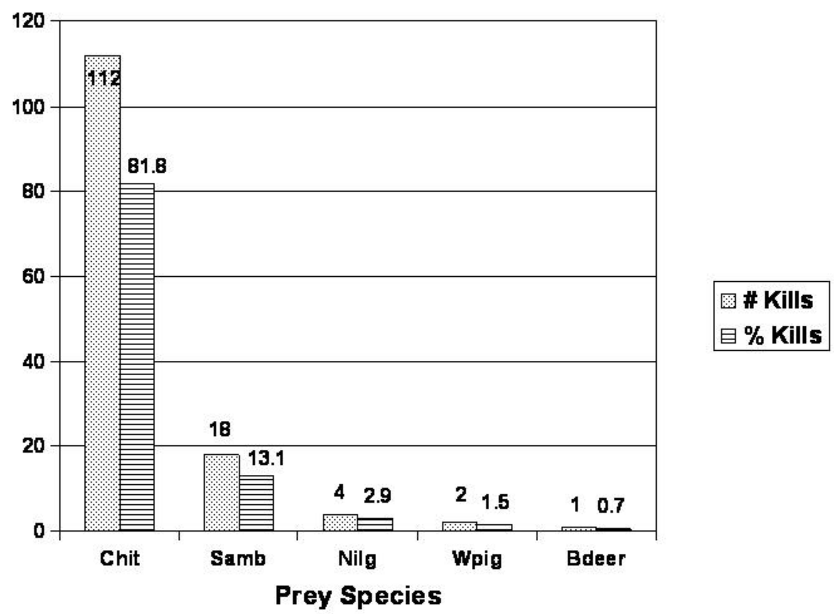


Table 21. Major prey species killed by dholes in Pench T.R., Madhya Pradesh (n = 137), 2001-2004.

Prey species	No. of kills	% of kills	♂	♀	Juv	Unk
Chital	113	81.8	43	18	49	3
Sambar	19	13.1	3	2	13	1
Nilgai	4	2.9	2	0	2	0
Wild pig	2	1.5	0	0	2	0
Barking deer	1	0.7	1	0	0	0

Prey weight selectivity

The average weight of the major prey killed by dholes was 55.3 kg (± 3.12 SE). 33.3 % of the kills were of prey that belonged to the medium (26-50 kg) size class, and 35.5 % of the kills were of large (51-100 kg) size. While 26.8 % kills were that of small (< 25 kg) prey, only 4.3 % kills were of very large (> 100 kg) size prey. In effect, 68.8 % of the kills were of the intermediate (26-100 kg) size class. The χ^2 goodness-of-fit test indicated that dholes showed significant selection of weight classes of prey (χ^2 =56.3, df = 3, P < 0.001). Bonferroni's simultaneous confidence intervals showed that only the large size (51-100 kg) prey class were taken significantly more than their availability in the population, whereas the small size (< 25 kg) prey class and the medium (26-50 kg) size class were taken significantly less than their availability in the population. There was no significant selection for very large (> 100 kg) size prey by dholes.

Prey age-sex selectivity

The juvenile age class (sub-adults and fawns) accounted for nearly half the chital kills by dholes, followed by adult males (43%) (figure 10). The χ^2 goodness-of-fit test indicated that dholes did show significant selection of age-sex classes of chital (χ^2 =23.8, df = 3, P < 0.001). Bonferroni's simultaneous confidence intervals showed that adult chital stags and fawns were taken significantly more than their availability in the population, whereas adult chital does were taken significantly less than their availability in the population (figure 11 and table 22). There was no significant selection for sub-adult chital by dholes. Ivlev's preference index used on the chital kill data showed that even though the adult male class constituted most kills by number, it is the juvenile age class that was preferred or used by dholes more than that availability (see figures 11 and 12). For those chital stags killed by dholes for which antler status could be determined (n= 40 kills), 65% stags had antlers in the velvet stage, whereas 35 % were in hard antler.

Figure 10. Composition of chital (n = 113) and sambar (n = 19) killed by dholes in Pench T.R., Madhya Pradesh, 2001-2004

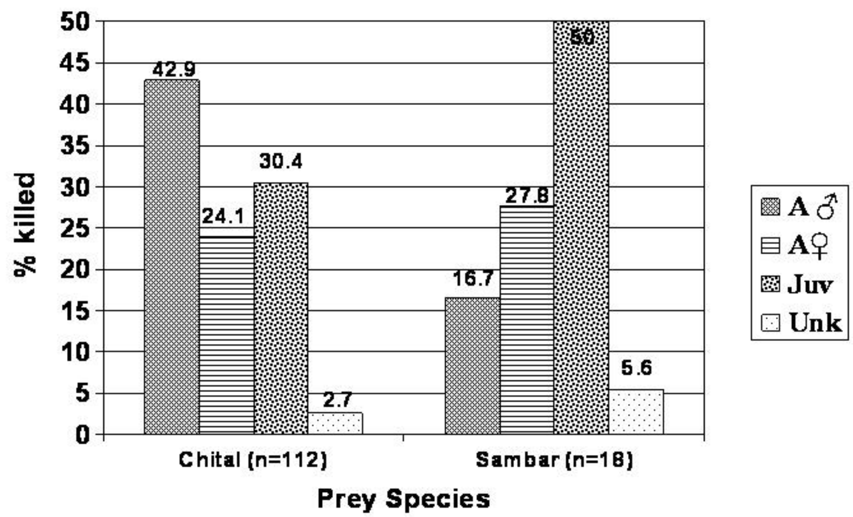


Figure 11. Comparison of availability of different age/sex classes of chital in the wild and their use (from 113 kills) by dholes in Pench T.R., Madhya Pradesh, 2001-2004

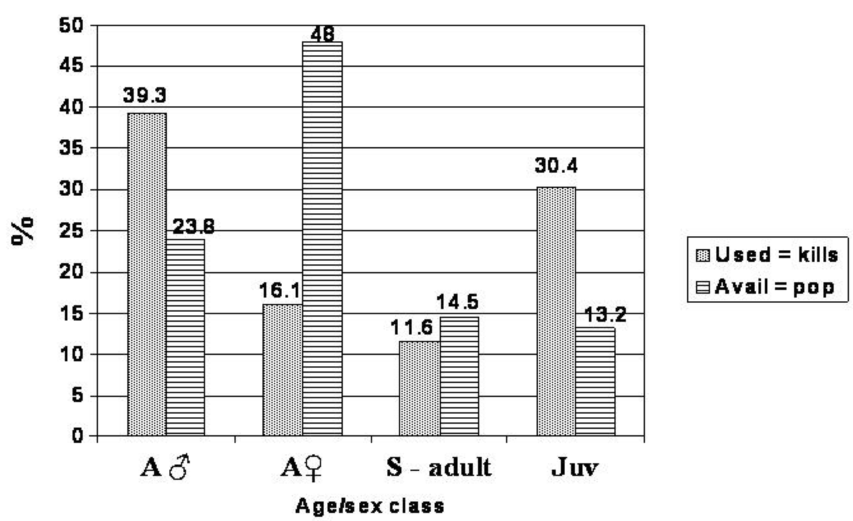
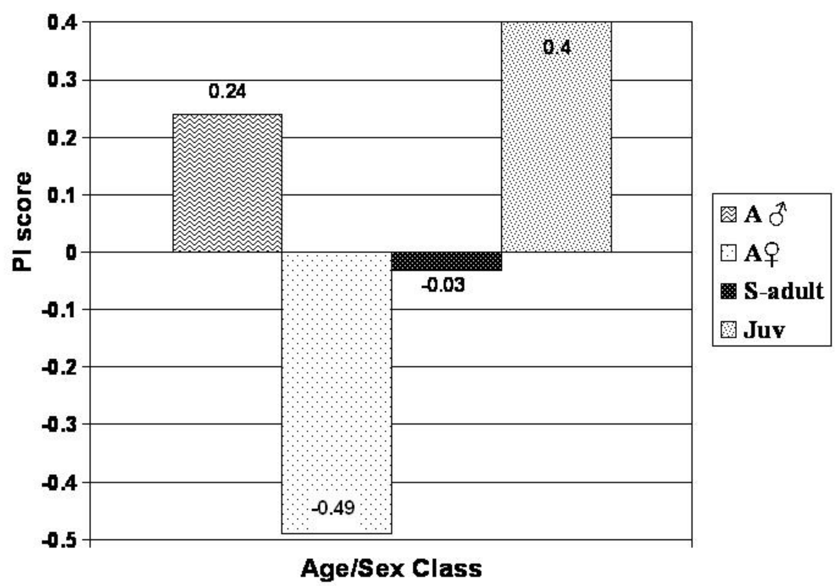


Table 22. Selectivity of chital age-sex classes by dholes from 113 dhole kills of chital in Pench T.R., Madhya Pradesh, 2001-2004, using Bonferroni's Confidence Intervals (Neu *et al.* 1974).

Age-sex class	Observed fraction of kills P_O	Expected fraction of kills P_E	Bonferroni intervals for P_E
Adult ♂	0.391	0.240	0.477 ≤ p ≤ 0.571*
Adult ♀	0.164	0.482	0.371 ≤ p ≤ 0.464*
Sub-adult	0.137	0.145	0.017 ≤ p ≤ 0.052
Fawn	0.309	0.133	0.009 ≤ p ≤ 0.037*

$Z\alpha/2k = 2.495$; * significantly different at $\alpha = 0.05$

Figure 12. Ivlev's index of preference/avoidance of different age/sex class of chital by dholes from 113 kills in Pench TR, Madhya Pradesh, 2001-2004.



PI = (U-A)/(U+A) (Ivlev 1961); where U = proportion used, A = proportion available

From the pack-wise kill data, it appears that all dhole packs seemed to be taking a lot more chital compared to other prey species (see table 22).

Table 23. Pack-wise prey off-take for four main dhole packs (2001-2004) in Pench T.R., Madhya Pradesh.

Pack Name	Pack size	Kills	Prey species				
			Chital	Sambar	Nilgai	Wpig	Bdeer
TIKARI	6-14	43	35	5	2	1	0
BANDAPACK	11-31	23	17	4	1	0	1
77PAIR	2	15	13	1	0	1	0
BCPACK	9	8	8	0	0	0	0

In the case of sambar, the juvenile age class (sub-adults and fawns) accounted for more than three-quarter (78%) of sambar killed by dholes, of which fawns alone formed half the number of kills (figure 10). The χ^2 goodness-of-fit test indicated that dholes showed significant selection of age-sex classes of sambar too (χ^2 =20.2, df = 3, P < 0.001). Bonferroni's simultaneous confidence intervals showed that sub-adult sambar and fawns were taken significantly more than their availability in the population, whereas adult sambar does were taken significantly less than their availability in the population. There was no significant selection for adult sambar stags by dholes, despite the fact that around 16% of dhole kills of sambar were that of adult stags.

There was no significant correlation between dhole pack size and the prey weight (Pearson's correlation coefficient = 0.096, p > 0.05). Average meat available for consumption per dhole per kill amounted to 7.54 kg.

5.5. Discussion

Major Prey

Even though dholes prey on a wide variety of prey species in Pench, they concentrate their predation on a small select number of species. Sambar and chital constitute by far the main prey of dholes, with just these two species making up about 95 % of all kills and scats recorded in this study. It seems logical that the dholes would prey mainly on these large and abundant herbivores, because of the formers' body size (approximate weight of a dhole pack = 120 kg), the habit of travelling in packs, and their ability to consume and digest great quantities of food in short periods (Fox 1984), much like wolves (Mech 1970). Larger vertebrate predators, as energy maximizers, tend to forage optimally on large-bodied prey (Griffiths 1975). Therefore, dholes would be expected to take the largest prey that could safely be killed (Sunquist and Sunquist 1989). The body conditions of killed prey were evenly distributed from ‘good’ to ‘poor’ conditions. No conclusions about selectivity by dholes for prey body condition can be arrived at since the actual proportions of these different body conditions of prey in the population was not known. The average weight of killed dhole prey recorded in this study (55.3 kg) was much higher than that recorded in Nagarahole (43.4 kg - Karanth and Sunquist 1995). The 68.8% proportion of the dhole kills in the intermediate (26-100 kg) prey size class is more than the 56.6% recorded in Bandipur (Johnsingh 1992) for the same size group, and the 56% kills that fell in the 30-175 kg class of the Nagarahole study (Karanth and Sunquist 1995).

Scat Data

From the scat analyses, it is evident that sambar is the most favoured prey of dholes in Pench, considering that nearly 50% of dhole scats contained sambar remains, while nearly 39 % scats contained chital remains. This is fraction is very different from earlier studies, all of which recorded higher number of dhole scats with chital remains than those of sambar - Bandipur (14% sambar; 52 % chital) (Johnsingh 1992), Mudumalai (22.6% sambar; chital) and Nagarahole (10.2% sambar; 49.7% chital) (Karanth and Sunquist 1995). Sambar would be energetically the most profitable prey species for dholes in Pench, if the ratio of energy gain to handling time for predator were to be considered (Scheel 1993). Sambar spend more time in the dense vegetation, live in smaller groups and do not frequent in open areas (Johnsingh 1983), making them very profitable, vulnerable and convenient prey for predators. Sambar are capable of escaping from dhole predation by baying in shallow pools of water. There were very few such pools available in the study area. All this, combined with the comparatively much higher abundance of sambar in Pench, could be the reason why sambar figure more prominently than chital in dhole scats from Pench, as compared to other dhole sites.

Kill data

Unlike in the scat data, kills of chital were in much greater numbers (81%) in the dhole kill data than those of sambar (13%). This could occur just from a greater visibility of the remains of the former. Chital kills are more easily spotted or conspicuous for a variety of reasons. Open habitats and forest roads are more frequently used by dholes for foraging and locating prey, as compared to closed forest habitat. Chital tend to aggregate in open habitats to forage and to avoid predators (Johnsingh 1983), and are very often spotted alongside forest roads that serve as long open grassy strips of land, ideal for grazing chital. If they were not chased far from their original location when hunted, one would expect to locate their carcasses in these open patches or roadsides with higher probability. Sambar on the other hand favour dense cover and frequent the interior forest areas, not frequented much by human. Most kills of sambar recorded by this study were found while either tracking or following dholes much into the interior. A similar situation could have occurred with dhole kills of very small prey that are not successively located. Therefore, the kill data of sambar could be a gross underestimation of the off-take of sambar by dholes. For this reason, the scat data was preferred for estimating prey species in dhole diet, and kill data for prey age/sex composition in dhole diet.

Future predation studies could greatly benefit from employing GPS-telemetry whereby the chances of locating sambar kills of dholes deep in the forests, even if delayed, is enhanced manifold by inspecting clustered hourly locations generated from telemetry, as with wolves (Sand *et al.* 2005).

The fact that fawns of both chital and sambar were preferentially selected could still be a gross underestimation as it is highly likely that most kills of fawns go undetected. With this in mind, there is strong possibility of dholes actually favouring chital and sambar fawns much more than depicted here. The young prey animals are naturally much less likely to escape the attacks of predators than adults (Mech 1970, Curio 1976). This could be reason why both chital and sambar fawns were favoured by dholes in Pench.

Chital

With chital, there appears to be a significant sex-bias in dhole predation. Dholes made significantly more kills of adult male chital (40% of kills) compared to their availability in the population, while adult females were taken much less than their availability. This is similar to that observed in the Bandipur study (Johnsingh 1992) and Nagarahole (Karanth and Sunquist 1995). However, in the Mudumalai study (Venkataraman *et al.* 1995), there did not appear to be a significant sex-bias in chital kills by dholes (17 stags: 16 does). Male chital tended to range more widely during the rut, and are often solitary, increasing their chances of encountering predators. This fact and their weakened condition after the rut (Hornocker 1970) could increase their vulnerability to dhole predation. To a lesser degree, chital fawns were also favoured (30% of kills), more than their availability in the population.

Sambar

Sambar fawns (along with sub-adults) were the preferred age-class for dholes preying on sambar. However, this proportion (50%) of fawn kills was much lesser than that recorded in Mudumalai (75 % of kills) (Venkataraman *et al.* 1995) or Bandipur (82 % of kills) (Johnsingh 1983). There was no significant sex-biased selection for adult sambar stags by dholes as with the Mudumalai study (Venkataraman *et al.* 1995), but the Bandipur study (Johnsingh 1992) showed that dholes killed more sambar stags than expected. However, all these studies, including this one, suffer from very low sample sizes of kills, so a definite conclusion cannot be made about dhole predation on sambar. This aspect requires prioritized investigation.

Wild pigs

Wild pigs, being aggressive prey, naturally do not appear to figure prominently in dhole diet (2.5 % scats; 2 kills). As observed by us on three occasions (two of which were failed hunts), this could not only be due to the strength in numbers of wild pig sounders, but also the ferocity of the counter-attacks of the wild boars and their lethal sharp tushes (Eisenberg and Lockhart 1972). Both the dhole kills of wild pig recorded by us were that of piglets. However, some of the scats with wild pig remains did suggest that adult pigs too are taken occasionally. The Bandipur study (Johnsingh 1992) had recorded only one kill of a wild pig that had bayed itself in a large depression, before being killed by dholes.

Langurs

Oddly, despite the presence of langur remains in 31 dhole scats, there were no records direct evidences of dhole kills of langurs throughout the study period, as was the case with the Bandipur study (six scats with langur remains) (Johnsingh 1983), and in Nagarahole (Karanth and Sunquist 1995), where only 1% of dhole scats contained langur remains. Occasional reports by tourists (twice) or Reserve staff (once) could not be corroborated with actual sighting of dholes hunting or feeding on langurs. Besides, there is always a possibility that the dholes may have often scavenged on langur remains, possibly killed by a leopard. Other than the obvious reason that dholes do not climb trees, their hunting style of coursing conspicuously in packs could mean that langurs can detect them easier and earlier than they would the ambush predators, tiger or leopard, and thus can take evasive action. With unconfirmed but reliable reports of langurs killed by dholes in Pench, and the nearly 5% presence of langur remains in dhole scats collected in this study, langurs still have to be considered as prey of dholes, though not a significant one.

Nilgai

The converse was true in the case of nilgai. Four kills of nilgai by dholes were located, but no remains of nilgai were found in any of the dhole scats collected in this study. Resulting scats from these four kills were not obtained since all four kills were made by non-radiotracked dhole packs that could not be successfully followed subsequent to their leaving these kills after feeding. Nevertheless, despite not having matching presence of nilgai in dhole scats, this study would serve as a landmark account of nilgai as a prey of dholes, with very few other dhole strongholds inhabited by nilgai too (e.g. Kanha TR).

Gaur

Another potential prey species of dholes are gaur (only one scat had gaur remains). This study had three observations of dholes interacting with gaur. On two of these occasions, the dholes were making unsuccessful attempts to attack the heavily guarded gaur calves. On the third occasion, the dholes did not appear to be carrying out a serious attack. Rather, the engagement appeared to be just a sport for the dholes. The absence of definite evidences of dhole predation on gaur in this study in no way reduces the possibility of gaur (especially juveniles) being potential prey of dholes.

Livestock

There was no direct evidence of doles preying on cattle, buffaloes or goats in Pench, although on two occasions dholes were directly observed feeding on the carcasses of dead cattle outside the Tiger Reserve limits. No reports of dholes killing livestock were received by the Reserve staff from surrounding villages, within the duration of this study**.** Even the Bandipur study (Johnsingh 1983) recorded only 2.75% presence of cattle in scats, and three cattle calves killed.

The negligible cattle remains seen in dhole scats (1.8 % scats) or the fewer incidents of dholes seen feeding on cattle, were definitely from their rare tendency to scavenge (especially in the outer fringes of the Tiger Reserve with low wild prey numbers). Moreover, livestock that graze in the buffer zone forests are invariably accompanied by people, and invariably dholes flee on sighting these men.

The above facts not only indicate a welcome absence of dhole-human conflict, but also demonstrate the ample availability and widespread distribution of the dholes' natural prey within the Tiger Reserve.

Sympatric predators

Despite the absence of adequate data from this study on predation by tigers and leopards, one can surmise that selective predation probably contributes to the coexistence of the three main predators in Pench (tigers, leopards and dholes), primarily by the more than adequate availability of diverse prey in a variety of size classes. There may be some form of niche separation between the three predators because of differences in their activity periods, relative to those of the prey species (Johnsingh 1983; Johnsingh 1992). However, there may be no spatial exclusion among the predators, which may arise from habitat specificity or social dominance behaviour (Karanth and Sunquist 2000).

Considering the presence of another canid, the wolf (*Canis lupus pallipes*) in the sparsely forested and non-forested areas around the Reserve, and dholes being essentially species of dense forests avoiding very open habitats, there seems to be a clear cut spatial separation between these two canids in the region.

5.6. Summary

The objective of this study was to determine the relative proportions of different prey species in diet of dholes, in terms of frequency of occurrences, biomass, and numbers of individuals consumed. The aim was also to study predation by dholes in relation to prey availability and utilization within Pench Tiger Reserve, i.e. to see if dholes killed prey randomly or selected specific kinds of prey. If that was so, the ecological factors intrinsic to that prey which may influence prey selection were assessed.

Dhole scats (n= 725) and kills (n=137) were recorded whenever encountered, for dietary analyses to yield information on the prey species consumed, their age and sex class, and further on, biomass consumed. Only one scat was collected per site/pack per day to ensure scat samples were independent. Kills made by dholes were located by actively searching the study area for the same, or on an *ad libitum* basis. The diet of dholes was estimated using standardised faecal analysis to determine the relative frequency of occurrence of prey species remains in scats, and also by recording the frequency of kills of particular prey species to determining age and sex class of prey killed. From these, prey selection by the dhole was arrived at. Prey encounter rates obtained from line transects and road counts were used as indices of prey encounter by dholes. Percentage frequencies of different prey species in dhole scats was calculated by enumerating the number of scats with remains of a particular species out of the total number of scats with prey remains, depicted in the form of a percentage figure. Frequency of occurrence of a prey species was calculated as the number of occurrences of that prey species divided by the total number of scats analysed, also expressed as a percentage. Further, the relative numbers and biomass of different prey consumed by dholes and the relative biomass contribution of different prey species to the dhole diet was estimated.

Analysis of dhole scats and kills indicated that dholes consumed a minimum of seven prey types. Of the 725 dhole scats analysed, sambar remains were the most frequent prey item in dhole scats (nearly 50 %), followed by that of chital (38%). Significantly, 31 scats contained remains of langur. Around 6 % scats contained remain of more than one prey species. Analyses indicated that sambar was the only prey species preferred by dholes i.e. consumed more than their availability in the study area, while chital, langur and wild pigs were consumed less than their availability. Wet and dry season diets of dholes did not show any significant difference.

In total 137 dhole kills were assessed with respect to prey species, its age-sex class, and identity of dhole pack (if known). 53% of the dhole kills recorded were made in the morning, 27% in the evenings and 6.5% were kills around mid-day. Only one kill was recorded to have been made in the night. 31.6% of the prey killed by dholes were in ‘good’ body condition, 36.8% in ‘fair’ condition and 31.6% in ‘poor’ body condition. The age-sex class distribution of each major prey species in the kills data was compared with the corresponding population age-sex distribution recorded from road counts and *ad libitum* counts, to check if dholes were selecting for a particular age-sex class of their prey. More than 80 % of the 137 dhole kills recorded for this period were that of chital, and around 13 % that of sambar.

There appears to be a significant sex-bias in dhole kills of chital, with more kills of adult stags compared to those of does. Adult chital stags and fawns were taken significantly more than their availability in the population, whereas adult chital does were taken significantly less than their availability. There was no significant selection for sub-adult chital by dholes. Among chital stags killed by dholes, 65% were in ‘velvet’, and 35 % in ‘hard’ antler. In the case of sambar, the juvenile age class (sub-adults and fawns) accounted for more than three-quarter (78%) of sambar killed by dholes, of which fawns alone formed half the number of kills. Dholes showed selection for age-sex classes of sambar too. Sub-adult sambar and fawns were taken significantly more than their availability in the population, whereas adult sambar does were taken significantly less than their availability. There was no significant selection for adult sambar stags by dholes.

In all, sambar and chital constituted by far the main prey of dholes, with just these two species making up about 95 % of all kills and scats recorded in this study.

The average weight of the major prey killed by dholes was 55.3 kg. Nearly 70% of the kills were that of the 26-100 kg size class, with the large (51-100 kg) prey size being the preferred weight class by dholes. There was no significant correlation between dhole pack size and the prey weight. Average meat available for consumption per dhole per kill amounted to 7.54 kg.

Plate 3. Attachment of radio-collar on to immobilized dhole in Pench Tiger Reserve, Madhya Pradesh.

Plate 4. Tracking of radio-collared dhole with the help of a VHF receiver and Yagi antenna from a vantage point in Pench Tiger Reserve, Madhya Pradesh.

Chapter 6. DHOLE SPATIAL ECOLOGY

6.1. Introduction

The term habitat refers to an area that meets an animal's basic life requisites such as food, water, cover and space (Giles 1978). A number of interdependent variables play a role in the formation of a particular habitat. An animal occupies or utilizes a habitat based on the spatio-temporal variation of such interdependent habitat variables (Norman *et al.* 1975).

An area with a certain productivity that meets the energy requirements of an individual or group of animals that occupies it forms a home range (Jewell 1996). An animal's home range was defined by Burt (1943:351) as "that area traversed by the animal in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, shouldn't be considered part of the home range". Such a home range would include areas used in a variety of ways, for a variety of activities. Even within this home range, not all parts or regions might be equally important or used evenly.

The size of this home range would depend on the body mass and energy requirements of that species. The kind of food utilized would also influence home range size (McNab 1963). Carnivores would need larger areas for food acquisition than herbivores. Carnivore home range sizes are usually determined by important aspects such as habitat, prey distribution and abundance (Gittleman and Harvey 1982).

Most wild animals are secretive, cryptic, and not easy to observe and study over extended periods of time. In solving this problem, wildlife radio-telemetry has become an indispensable tool to study these animals and their lives. Wildlife radio-telemetry or radio-tracking is the transmission of information from a radio-transmitter on a free-ranging wild animal to a radio-receiver. Using this technique, a researcher can monitor an animal by remotely tracking a radio signal emitted from a transmitter (i.e., radio-collar) attached to the animal. By tuning a radio-receiver to the transmitter's specific frequency and scanning the surroundings with a directional antenna, the researcher can track the signal, and hence, the collared animal's location. The closer one is to the transmitter, the stronger the signal reception. By radio-collaring study animals, researchers can identify individuals, locate and follow them at any time of the day. In terms of wildlife telemetry, the home range would refer to a mapped area produced from telemetry location fixes of the tracked animal, in the form a numeric estimate of the area used by the animal, usually with km^2 as units.

The objective of this study was to collect information on the spatial ecology of dholes with special reference to home range sizes, core areas, and movement patterns of radio-collared dholes. This study has the distinction of being the first long-term radio-telemetry study of dholes in South Asia.

6.2. Methods

6.2.1. Dhole Capture, Immobilization and Radio-collaring

In order to collect information on the ranging and movement and patterns of dholes, three individuals from different packs were captured, immobilized, fitted with radio-collars and subsequently tracked for five to 12 months in this study. Since the objective was to determine the spatial ecology of an animal that lives in social groups (packs), it was deemed adequate to radio-collar only one individual of a pack in order to document the movements of an entire pack.

For the radio-collaring operations, dholes were required to be chemically restrained. Three individual full-grown adult dholes (> 1.5 years old) dholes (one male and two female) were captured, immobilized and radio-collared within the duration of this study. On locating the targeted dhole pack, the individual to be captured was selected, and later darted (remotely injected) from vehicle at a distance of around 15 metres using a Vario 11 mm 3 ml lightweight syringe dart, equipped with a 1.5 x 20 mm non-collared needle, fired from a Telinject Vario air-rifle.

On induction of the injected drug, the dhole was first weighed and fitted with the radio-collar. It was then placed in lateral recumbency for monitoring and sample collection purposes. Each immobilized dhole was sexed and aged based on dentition (tooth eruption and wear) with an underlying assumption of a January 1st birth-date. Morphometric measurements and relevant biological samples were collected from the immobilized animal before it recovered conscience.

The radio-collars used in this study, manufactured by Telonics Inc, Inc., Arizona, USA, contained a VHF radio-transmitter (MoD-335) of frequency range within 151 MHz with an activity sensor (MS9) that is activated by the collared animal's head movements. To differentiate between radio-collared dholes, each one was given an identity reflecting it's sex and transmitter frequency (e.g., M 77 for male with transmitter frequency 151.77 MHz).

One adult female dhole ♀82 (from a pack of three dholes) was captured, immobilized and radio-collared on July 20th 2002, near Karmajhiri. The movements of this female dhole and her pack (VadruJodi pack) was already being monitored since March 2002 in the regions south-east and north-west of Karmajhiri Forest Village. She was a healthy full-grown adult, around 3½ years old as indicated by her dentition. After being weighed (ca. 16 kg), she was fitted with a radio-collar. Telazol® (tiletamine HCl + zolazepam HCl – 120 mg at 8 mg kg^{-1} body weight), a safe, fast-acting anaesthetic drug was used to immobilize her. Of the active components tiletamine HCl is a dissociative anesthetic, while zolazepam HCl is a sedative muscle relaxant. The drug combination has previously been used to capture and immobilize several species of wild mammals, especially canids e.g. Ballard *et al.* (1991), Vila and Castroviejo (1994), and Sillero-Zubiri (1996). The intended dosage of 8 mg kg^{-1} was similar to that used for grey wolves (Ballard *et al.* 1991) and Ethiopian wolves *Canis simensis* (Sillero-Zubiri 1996). The reported advantages of this combination are short induction time, low dosage quantity, high safety margins, reliable immobilization time, and smooth recovery. Next, a solitary male dhole (M 77) was captured and radio-collared on 25th August 2003, near Alikatta, in a similar fashion.

The third dhole (an adult female), belonging to a pack of 14 dholes (pack: 5 ♀: 3 ♂: 5 s.a.: 1 pup), was captured and radio-collared on 16th March 2004 near Karmajhiri, using a combination of Ketamine HCl (a dissociative anaesthetic) and Xylazine HCl (a sedative muscle relaxant), at an intended dosage of 5 mg kg^{-1} body weight for ketamine and 2 mg kg^{-1} for xylazine.

6.2.2. Radio-tracking

Radio-transmitters are usually made up of a transmitting device that produces radio signals, a source of power, such as a battery, that powers the transmitter, and a built-in antenna that broadcasts the signal to the outside. By the process of radio-tracking, this transmitted signal is picked up by an antenna and conveyed to receiver device, which amplifies the signal and makes it audible to the person tracking the signal.

The dholes radio-collared in this study were monitored and tracked mainly using a hand-held three-element Yagi antenna and a TR2 radio-receiver (Telonics Inc, Arizona, USA). Sometimes an H-type antenna (RA-2AK -Telonics Inc, Arizona, USA) was also used. Tracking was initially carried out from a four-wheel drive vehicle. Whenever radio-signals were not discernable, higher vantage points such as hill-tops, rock outcrops and watchtowers were made use of. Signals were first detected usually between 0.5 and 3 km, depending on the activity and location of radio-collared dhole. When the increasing strength of the signal indicated the radio-tagged dhole was close by, the tracking team proceeded on foot in the direction of strongest signals, until the dhole or its pack was sighted by "homing in". This is a simple and effective non-triangulation technique for obtaining the exact location of a radio-collared animal without any error. Other advantages of "homing in" include sampling of a better and accurate proportion of habitat use by dholes, getting to observe the actual activity of the dhole and it's pack, increase in chances of locating dhole kills, and in general, a much greater quality of data. The disadvantages are the time-intensive efforts required to "home in" on such a fast-moving animal, and the risk of disturbing its normal movements and behaviour.

Care was taken to visually locate the dhole or its pack without disturbing them. The radio-collared individual or the pack was watched from a distance of around 100 m; closer approach was avoided for fear of influencing the behaviour or movement of the study pack, especially near a den or resting site. Nevertheless, because the study packs were accustomed to the tracking team over long periods, this presence, at a distance (> 100 m), was tolerated by the dholes without any noticeable change in behaviour except for their keeping a watchful eye. Invariably, in such situations, the tracking team did not linger for long at the spot, and would leave unobtrusively after recording location and other details, while constantly monitoring the radio-signals to ensure there is no significant change in the dholes' activity during this exercise. Needless to say, it was not necessary to approaching the dholes on foot when they were visible from the vehicle.

Geographic locations of the radio–collared dhole (and pack) were recorded by using the Global Positioning System (GPS) receiver. This was done remotely by first storing the location of the tracking team, and then feeding into the receiver the distance (measured using a laser rangefinder) and bearing/angle (measured using a compass) to the dholes, to yield the actual location of the dholes by projection (for details see Garmin 1997:20). When visibility, line of sight, bad satellite reception etc., prevented recording locations in this fashion, the locations were recorded from the very spot the dholes were in, but at a later time, in their absence. The position averaging function in the GPS receiver was used to increase the accuracy of the locations. Locations were recorded as latitude-longitude coordinates on the rectangular Universal Transverse Mercator (UTM) meter system. Stored locations were transferred from the GPS receiver to a PC using the software GPS TrackMaker® Version 10.0 (Junior 2004). Locations of radio-collared dholes were recorded evenly throughout a 24-hour period with a minimum of one radio-location per dhole per day being the target.

Besides the dholes' locations, data was also collected on the habitat they were sighted in, pack members present, signs of feeding, behaviour and activity. For each location, dhole activity was recorded either as "sedentary" or as "active", based on pulse rates of the transmitter's signals.

Female 82

She was tracked until December 5th 2002, when she succumbed to infection of wounds on her body, near Rayyarau, Rukhad Range, Pench TR. This dhole was successfully located on 72 days of the 139 days she was with the collar.

Male 77

He was single at the time of his capture in August 2003. Subsequently he joined a pair (presumed breeding), quit that pair to be solitary again, and finally paired with a female to the south of his earlier beat. The last location of this male dhole was recorded on July 31st 2004 in the proximity of Saddle Dam, Pench Tiger Reserve, Maharashtra, around 10 km from his capture spot. No subsequent signal was received from this radio-collared animal. This dhole was located on 158 days of the 324 days he was with the collar.

Female 44

She was from a pack of 14 dholes (pack: 5 ♀ : 3 ♂: 5 s.a. : 1 pup) and was radio-collared on 16th March 2004 near Karmajhiri. The last radio-telemetry location of this female dhole was recorded on October 6th 2004 in Jamtara area of the Tiger Reserve, when the radio-collar fell off. Of the 201 days the collar was on her, she was successfully located by us on 106 days. Subsequently this female and her pack were indeed located, but infrequently, without the aid of radio-telemetry. Map 8 depicts all recorded radio-locations of dholes superimposed on the study area map.

6.3. Analyses

In all, 414 independent radio-locations were obtained on the three radio-collared dholes (♀82, ♂77 and ♀44) (see table 25).

Table 25. Season-wise break-up of independent radiolocations recorded for the three radio-collared dholes (♀82, ♂77 and ♀44) during the study period, within Pench TR, Madhya Pradesh (2002-2004).

Dhole ID	Period	No. locations	Dhole Seasons		
			Pre-denning	Denning	Post-denning
♀82	Jul'02 - Dec'02	104	91	13	0
♂77	Aug'03 - Jul'04	225	74	84	67
♀44	Mar'04 - Oct'04	169	53	0	116

Even though radio-locations should be a random sample of the animal's spacing behaviour, sampled (tracking) was carried out at all times possible when the study animal was within the range of radio-reception. This was because of the fact that receiving signals and locating the dholes was by itself an arduous task in field. However, only independent locations (locations separated by > 5 hours) and only three such locations per 24-hour period were taken for analysis to avoid autocorrelation of dhole locations. It was assumed a five hour period would be adequate time to allow the dholes to traverse their home ranges, the criterion suggested by Swihart and Slade (1985) to minimize autocorrelation of successive locations. Locations of the first day from collaring were also omitted from these analyses to ensure that data represents behaviour of dholes fully acclimatized to collars.

Program CALHOME 1.0 (Kie *et al.* 1996) was used for analyses of the location data to yield home range estimates. Program CALHOME generated specific estimates through three specific estimation methods: the Minimum Convex Polygon method (henceforth MCP) (Mohr 1947) – for demarcating home range boundaries; the Adaptive Kernel method (Worton 1989) (ADK) – for identifying areas of high use; and, the Harmonic Mean method (Dixon and Chapman 1980) (HMM) – for mapping centres of activity. While the polygon method gives the extent of the animal's range, the other two methods address intensity of use. Obvious far-reaching exploratory excursions by the radio-collared dholes were excluded from the calculation of range size within Program CALHOME, by using only 95% of the radio-locations.

6.3.1. Home Range Size

The minimum convex polygon is the smallest polygon enclosing all the recorded locations and the area of this polygon is the estimated home range size. In effect the method uses a polygon area estimation from peripheral points or points furthest apart. The MCP method remains the most commonly used home range estimator as it is most appropriate for a quick approximate estimate of home range size. Despite widespread documentation of this method's weaknesses (Worton 1989**,** Harris *et al.* 1990, White and Garrott 1990), this method was used for comparison of range sizes with those of earlier studies elsewhere that used this method, and its ease of calculation. The monthly range sizes of the three radio-collared dholes were also calculated as 100% MCPs.

6.3.2. Core Areas

Kernel method identifies areas of high use or 'core areas' of the home range. Kernel methods produce a density estimate that can be interpreted as utilization distributions (van Winkle 1975) that include a 3rd dimension of time spent in a given area of the home range. The location data was analysed using kernel analysis following Worton (1989) and Boulanger and White (1990), using least-squares cross-validation (LSCV) to select the level of smoothing, following Seaman *et al.* (1999).

6.3.3. Activity centres

The Harmonic Mean Method identifies single or multiple centres of activity of the radio-collared animal within the home ranges. This method estimates centres of activity by assuming a parametric form for the utilization distribution function, and fitting of this form to the location data. The term ‘centre of activity’ is defined as the geographical location within the home range of the point of greatest activity (Dixon and Chapman 1980).

6.3.4. Movements

Travel speeds or movement rates of dhole packs were determined by recording successive locations (at ± 10 min intervals) of dhole packs on the move (movement < 50 m), from vehicle by following them at an appropriate distance (usually 50 m) - adequate not to disturb their natural movement patterns, at the same time ensuring accuracy of location recording. Each sequence of movement location was stored as individual routes on the GPS receiver and later downloaded into the PC for analyses. Travel speed of a session (route) was calculated by dividing the total straight-line distances between successive locations in that session by the total time interval of that session.

Daily movement distances (distance moved from one day to the next) of radio-collared dhole packs were determined by measuring the straight-line distances between consecutive daily locations, whenever recorded. For uniformity, only the first recorded location of each day of the sequence was taken for this analysis.

Distances between locations were measured using Traverse XL, a Microsoft® Excel-based computer software (Fredericks and Wing 2006).

6.4. Results

6.4.1. Home Range Estimates

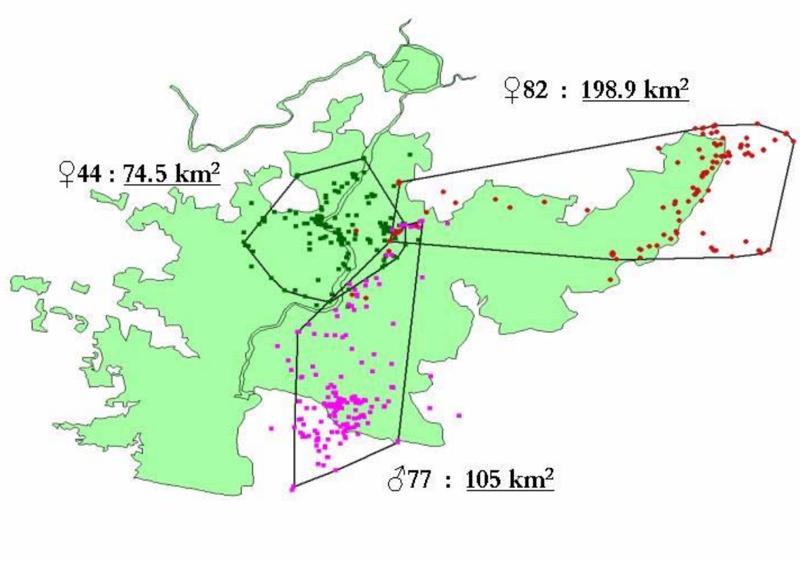
Home range sizes of radio-collared dholes in Pench covered 66.4 km² to 202.8 km² (95% MCP). Seasonal home range size averaged 77.58 (± 26.6 SE) km² (95% MCP). Table 26 depicts the results of the home range analyses of tracking locations of the three radio-collared dholes obtained from Program CALHOME.

Table 26. Home range estimates for three radio-tracked dhole packs in Pench.T.R., M.P., 2002-2004

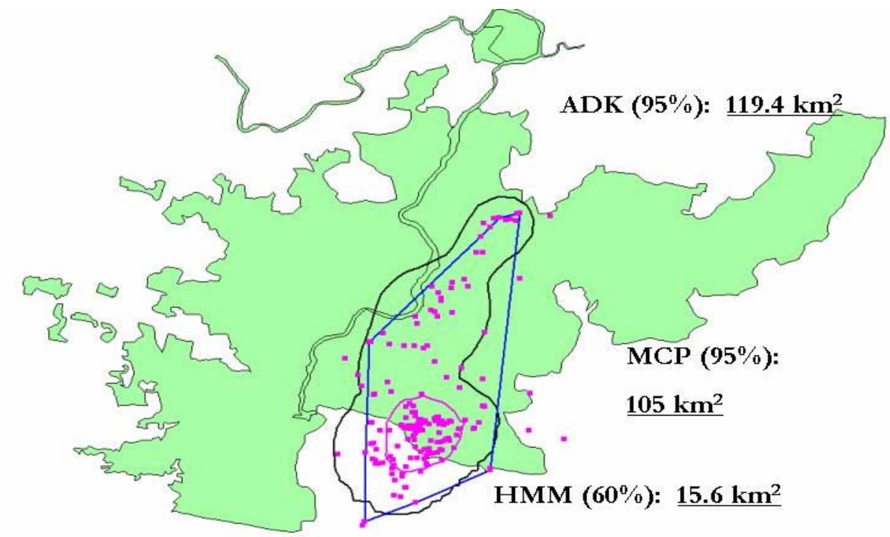
Dhole ID	Pack size	Season	No. of locs. (Indep.)	Home Range Estimates (% locs.) (km^2)		
				ADK (80 %)	HMM (85 %)	MCP (95 %)
♀ 82	3-12	Pre-denning	104	139.7	86.8	202.8
♂ 77	1-3	Pre-denning	74	78.0	26.7	79.9
	2	Denning	84	15.6	15.7	25.5
	2	Post-denning	67	19.9	14.1	26.1
	1-3	Overall	241	60.7	53.4	105.0
♀ 44	14	Post-denning	116	41.7	32.1	66.4
	11	Pre-denning	53	50.3	28.4	64.8

ADK - Adaptive Kernel Method - areas of high use
HMM - Harmonic Mean Method - activity centres
MCP - Minimum Convex Polygon Method - home range boundaries

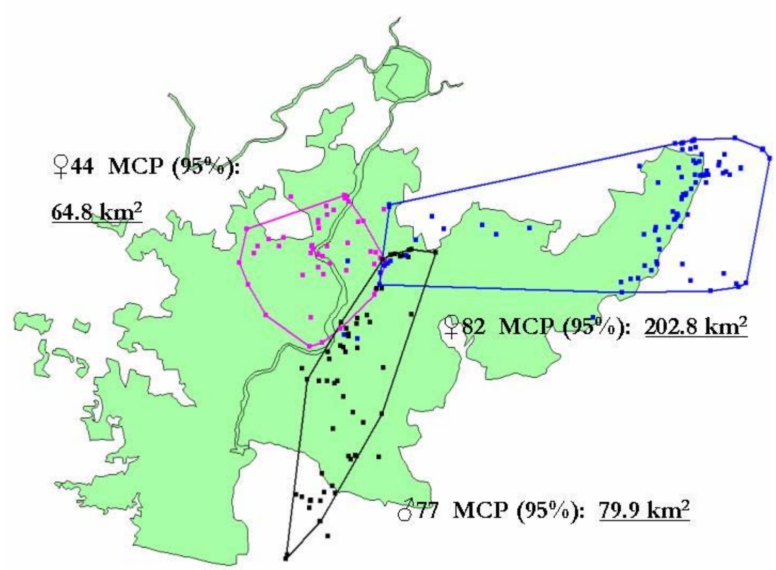
Map 8. Home range boundaries (MCP 95 % locations) and radio-tracking locations for three radio-tracked dhole packs in Pench.T.R., Madhya Pradesh, 2002-2004.



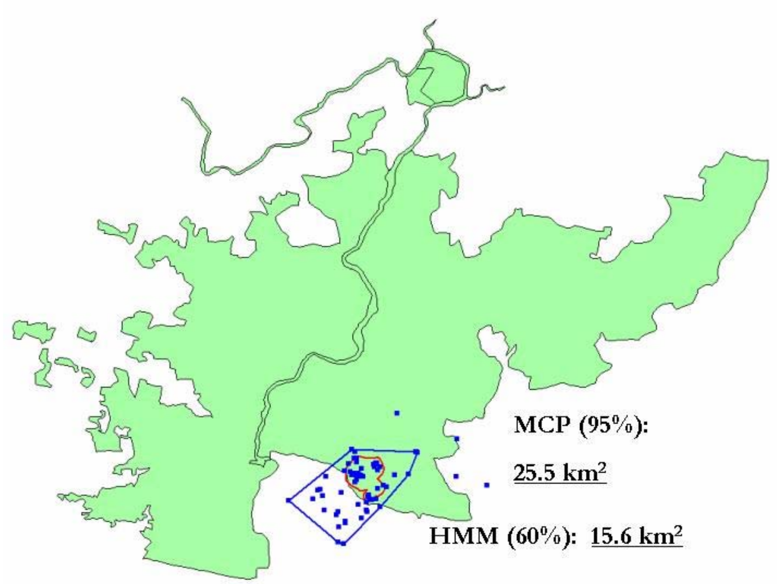
Map 9. Annual home range boundaries (MCP), areas of high use (ADK), and activity centres (HMM) of one radio-collared adult male dhole M 77, 2003-2004, in Pench Tiger Reserve, Madhya Pradesh.



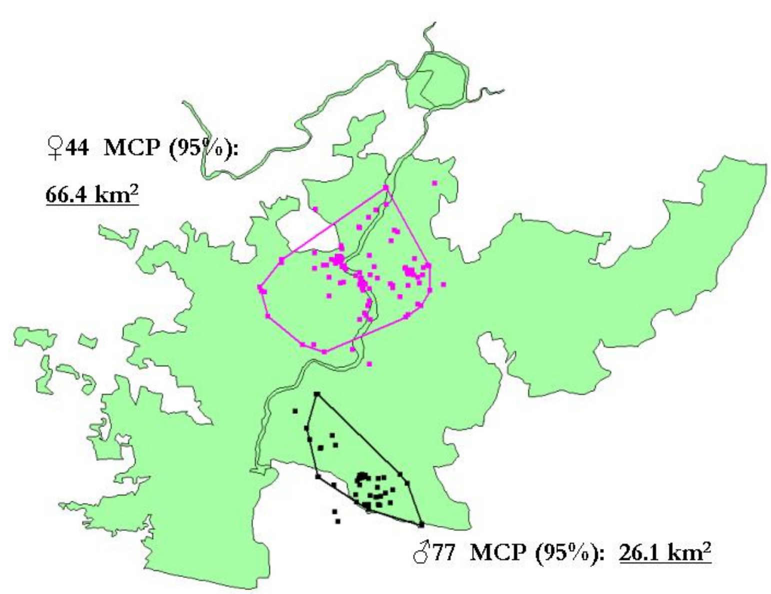
Map 10. Home range boundaries (MCP) of three radio-collared dholes, 2002-2004, for the pre-denning season, in Pench Tiger Reserve, Madhya Pradesh.



Map 11. Home range boundaries (MCP), and activity centres (HMM) of one radio-collared adult male dhole M 77, for the denning season 2003, in Pench Tiger Reserve, Madhya Pradesh.



Map 12. Home range boundaries (MCP) of two radio-collared dholes, for the post-denning season 2004, in Pench Tiger Reserve, Madhya Pradesh.



Monthly range sizes of the radio-collared dholes ranged from a minimum of 1.5 km^2 (♂ 77: pack size 2, January) to a maximum of 92.6 km^2 (♂ 77: pack size 1-2, October). On an average, monthly ranges covered around 38 km^2 (Table 27).

Table 27. Monthly range sizes (100% MCP) of three radio-tracked dhole packs in Pench.T.R., M.P., 2002-2004

Dhole ID	Pack Size	No. months	Mean Range size (km^2)	± SE	Min-Max (km^2)
♀ 82	3-12	5	56.0	10.0	21.7 - 80.4
♂ 77	1-3	11	23.8	8.0	1.5 – 92.6
♀ 44	14	7	47.7	6.6	13.2 - 63.8
All	**-**	**23**	**38.1**	**5.5**	**1.5 – 92.6**

Female 82

This female dhole was collared at a time corresponding with the dhole dispersal season or the end of the post-denning phase. Therefore, it was no surprise that she would range over large areas during and after this period until the approach of the denning season. Pre-denning home range area of this female dhole and her pack (Aug – Nov 2002, 91 independent locations) encompassed 202.8 km² (95% MCP) (see Table 21).

Male 77

Overall, the period from the time this male was collared till the last location recorded (Aug 2003 – July 2004, 241 independent locations) spanned close to one year, and constituted this male's annual home range (see Map 9) whose boundaries encompassed 105 km² (95% MCP).

The period from the time this male was collared till the denning period, constituted the dispersal, breeding, and pre-denning season. Solitary at the beginning of this period, this male subsequently joined a pair of dholes, quit that pair to be solitary again, and finally paired with a female. For this period (Aug – Nov 2003, 63 independent locations) this male's home range boundaries encompassed 79.9 km² (95% MCP), i.e. ca. 76% of annual home range area.

During the denning season (December 2003 – February 2004), home range of one dhole pack (a pair – 95 independent locations) shrunk to an area of 25.5 km² (95% MCP). The home range and movements of this male and partner during this denning period were centred on a den among boulders, and covered ca. 24 % of the annual home range size. This reduced home range size persisted despite the fact that the pair failed to successfully raise a litter of pups in this period. This trend continued for the same pair, during the post-denning season (March 2004 – July 2004, 67 independent locations), when boundaries of home range increased marginally to 26.1 km² (95% MCP) which formed ca. 25 % of their annual home range size.

Female 44

For the third pack (14 dholes), during the post-denning season (March 2004 – June 2004, 116 independent locations), boundaries of home range covered 66.4 km² (95% MCP). Thereafter, for the pre-denning season (July – Oct 2004, 53 independent locations) the boundaries covered 64.8 km² (95 % MCP).

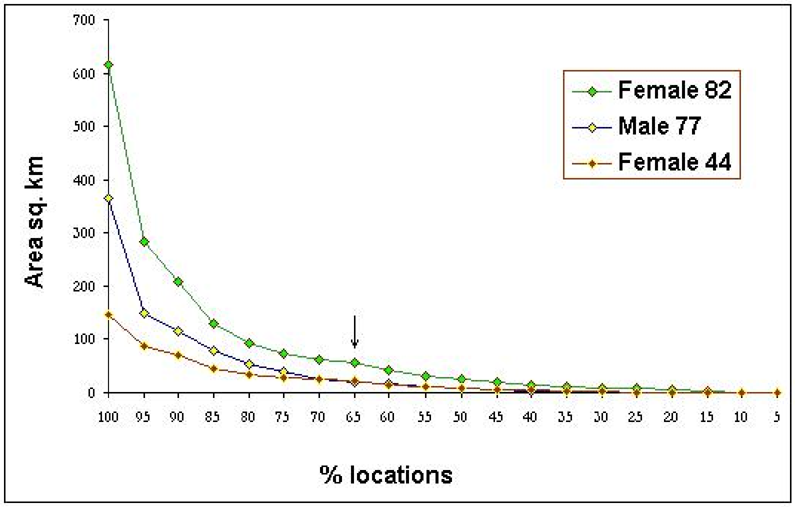
6.4.2. Core Areas

Areas of high use or core areas of home ranges (80% ADK) encompassed 151.4 km² for dhole ♀82, 60.7 km² for ♂77, and 48.4 km² for ♀44 (table 26). Seasonal core areas of dhole packs averaged 57.5 (± 18.8 SE) km² (80% ADK).

6.4.3. Activity centres

For each of the three dholes, the different harmonic mean area estimates were plotted against their corresponding percentage of locations (figure 12). It was noticed that the point of inflection corresponded almost invariably with the 65% isopleth. Therefore, it was concluded that the estimate corresponding to the 65% isopleth represents the area of the dholes activity centres. The activity centres for the three dholes would ♀82 – 56.95 km^2, ♂77 – 18.44 km^2, and ♀44 – 21.2 km^2 respectively. Considering ♀82's locations showed a huge dispersal shift, while those of ♂77 and ♀44 were relatively stable, it can be seen that the activity centre for dholes hover around 20 km^2 (18–21 km^2).

Figure 12. Plot of harmonic mean estimates of three radio-collared dholes in Pench TR, M.P., for different % locations to obtain isopleth.



6.4.4. Movements

In all, 204 sequences of consecutive days of locating the three radio-collared dholes were analyzed. Mean daily distance (inter-day distance) moved by dholes in Pench spanned 2.96 km (± 0.16 SE). Details of daily movement distances for individual radio-tracked dholes (and their packs) are given in table 28.

Table 28. Daily movement distances for three radio-tracked dhole packs in Pench.T.R., M.P., 2002-2004

Dhole ID	Pack Size	No. of seqs.	Mean Distance (km)	± SE	Range (km)
♀ 82	3-12	48	3.59	0.34	0.17 - 8.9
M 77	1-3	90	2.28	0.20	0.01 - 9.22
♀ 44	14	66	3.44	0.29	0.03 - 10.84
All	**-**	**204**	**2.96**	**0.16**	**0.01 - 10.84**

From 51 sessions (routes) of continuous locations of dholes on the move, the mean travel speed of dholes packs was 2.54 km h^{-1} (± 0.36 SE), with a maximum travel speed of 16.1 km h^{-1} in one session.

6.4.5. Dhole Density

Based on this constant and extensive monitoring in this study, the population of dholes in the Pench Tiger Reserve (750 km^2), M. P. and its immediate surroundings was estimated as 6-10 packs of dholes (80-200 individuals) at a density of 0.1-0.3 dholes km^{-2}. Dhole numbers (from known packs) within the National Park fluctuated from 36 in 2001, to 28 in 2002, and finally 64 in August 2004. The reasons for these fluctuations were not known, as the packs were not continuously followed throughout the year. Therefore, key information regarding the births and mortality were not available.

For a more accurate estimate of dhole density, the monthly range sizes and corresponding pack sizes of the three dhole packs were used. An average of 23 monthly density figures indicated that density of dholes in Pench was 0.29 (± 0.08 SE) dholes km^{-2}, or 2.9 dholes per 10 km^2. This density ranged from a minimum of 0.02 to a maximum of 1.34 dholes km^{-2}. If one of the study packs, the Tikari pack (♀44 + 13 dholes), with a home range of 60-70 km^2 were to be considered as the ideal dhole pack, then the density would be 0.2-0.23 dholes km^{-2} or 1.43-1.66 packs per 100 km^2.

6.5. Discussion

This radio-telemetry study revealed that the dhole packs restricted themselves to a small area (15-20 km^2) during the denning and nursing season (winter: Nov-Feb). Ranges increased (30-60 km^2) gradually during post-denning (pup-rearing) season (spring-summer: Mar-June). A great increase in home range sizes occurred during the dispersal and pre-denning season (monsoon: July-October). Based on intensive tracking of an optimal pack of 14 dholes, it can be concluded that 60-70 km^2 would constitute the ideal home range area required for a dhole pack, with a smaller activity centre of ca. 20 km^2. Consequently, the entire Pench Tiger Reserve can easily support 10-12 dhole packs.

This estimate of the ideal home range (60-70 km^2) and the average seasonal home range (77 km^2) compares favourably with the estimates from Mudumalai (Venkataraman *et al.* 1995), where home ranges encompassed 54.2 km^2 and 83.3 km^2 respectively for two different packs. In the adjacent Bandipur, the study dhole pack ranged over area of around 40 km^2 with a 20 km^2 activity core (Johnsingh 1982b). Another study in Nagarahole (Karanth and Sunquist 2000) estimated a dhole pack's home range size to 23.4 km^2 (MCP 95%), with 27.5 km^2 area of high use (ADK 95%), and activity centre (HMM 95%) of 27.4 km^2. However, it has to be kept in mind that the Mudumalai, Bandipur, and Nagarahole home ranges constitute minimum home range estimates, based on re-sightings of identified packs and not monitoring through radiotelemetry.

The relatively large portion of home range occupied and the distances travelled during pre-denning period reflected a dhole pack's need for adequate resources during the imminent breeding and gestation periods, and also involve social behaviour such as territorial marking and den searching.

The 69% reduction of total occupied home range during the denning period indicated that activity was limited to the dens site areas. The Bandipur study (Johnsingh 1983) also showed a shrink in home range size during the denning season, from 40 km^2 to 11 km^2, as observed in the current study in Pench (79.9 km^2 to 25.5 km^2). The Mudumalai study (Venkataraman *et al.* 1995) too observed reduction in home range sizes coinciding with the denning season. Increased movement and extension of occupied areas was evident again during the post-denning period following the abandonment of dens in February-March, and the months thereafter were used for explorations and pup rearing and training. This increased area of occupancy provides adequate resources for self-maintenance and development of the young. In particular, the monsoon months and the concurrent increase in vegetation cover make the search for prey all the more difficult, necessitating the increased foraging space and time. The reduction in home range size in the dhole pair (♂77) in winter despite not having pups, and just a marginal increase during the post-denning period echoes a similar occurrence in the Mudumalai study (Venkataraman *et al.* 1995). Therefore, denning and pup-guarding may not be the sole factor for this reduced home range size, with issues such as water availability emerging as a vital factor in this dry period. This indeed could have been the case with this dhole pair, since their main source of water was an artificial water-trough regularly supplied with pumped water that served more or less as a perennial source of water with easy reach (< 500 m) of the den.

In this study, it was observed that average daily distances (distance between consecutive days) were less than 3 km (maximum < 11 km), showing a great degree of site fidelity by dhole packs to their resting sites or favourite spots. Moreover, the high density and availability of prey meant that dholes did not require travelling long distances in search of prey.

This study could not definitely confirm that these home ranges were actual pack territories, as none of the dhole packs in the immediate surroundings the study packs were radio-collared. Even during the period from March 2004 to July 2004, when two radio-tagged dhole packs were being simultaneously tracked, their locations were too far apart. As a consequent, home range overlaps with neighbouring dhole packs could have existed, but were not determined.

It is recommended that future studies of dholes ideally record more than 50 independent locations per animal (minimum 30 locations). Collecting more frequent locations may result in increased autocorrelation between locations. However, several authors (Reynolds and Laundré 1990, Swihart and Slade 1997, Otis and White 1999) have argued that adequate sampling is more important than independence between locations, for biological relevance. Spatial autocorrelation would be difficult to avoid completely as dholes show a certain degree of site fidelity, with maximum inter-day displacement less than 11 km. Moreover, difficulty in tracking and locating radio-collared dholes made recording more frequent locations obligatory. Therefore, this study attempted to strike a balance between adequate sampling and avoiding location auto-correlation by using a maximum three locations per 24-hour period separated by > five hours for home range analyses. Future studies would do well to maximize the number of radio-locations using fixed time interval (ideally five hours) to increase the accuracy and precision of their home range estimates. Besides this five-hour separation of locations for home range analyses, continuous recording of locations every 15 minutes within activity period when the radio-collared animals are in sight, for studying movement and activity patterns, is also recommended.

Dhole ♀82, along with a male and pup, was initially using the National Park, Reserve Forests, and village land, in and around Karmajhiri. This pack was even located resting for the night within cornfields. Then the trio migrated eastwards from there into the Mowgli Pench Wildlife Sanctuary (118.30 km^2), and ultimately to the Rukhad and Kurai Reserved Forests (South Seoni Territorial Forest Division – ca. 150 km^2) beyond the Sanctuary, joining up with another dhole pack there. The National Highway No. 7 (NH 7), part of the busy North-

South Highway Corridor, and forming the eastern boundary of the Tiger Reserve, proved to be no barrier for the dholes that appeared to cross the same (width ca. 12 m) many times in the course of a day, especially under a bridge north of Rukhad Forest Checkpost.

The other radio-collared dhole, a male ♂77, who was oscillating north and south of the centrally-located Alikatta, paired up with a female dhole south of Kalapahaad and moved across the Tiger Reserve and State boundary into Pench Tiger Reserve, Maharashtra (257.26 km^2), and eventually settled down just near this boundary using both sides of this boundary with equal ease.

These two radio-collared dhole packs have proved this beyond doubt by dispersing or migrating beyond the limits of the intensive study area envisaged for the study. Other than the obvious, the reasons for this are many. None of these various administrative units (Pench MP, Pench MH and Rukhar RF) are fenced off or demarcated in anyway for wildlife to perceive any difference. The vegetation and habitat are not very different, rather mostly contiguous, to an extent of about 1164 km^2 of forested landscape. Even though administered by different agencies, these three units are managed similarly, with their buffer areas also sizable to accommodate minor use by wildlife, providing source-sink conditions for wildlife.

This telemetry study has clearly demonstrated the larger context of the Pench landscape for wildlife, in this case, dholes. The requisites of food (prey), cover and water are available even within small subsets of the Reserve and dhole density is therefore correspondingly high. Dholes are very shy of humans and human activity is a limiting factor for dholes in many ways in this region too. The core zone (National Park) of the Tiger Reserve therefore affords the dholes relatively human-free environment for the sustenance of propagation of their population. In addition to this area, the surrounding patches of unprotected commercial forests are home to packs of dholes too, since these forests also have vital resources for dholes e.g. water, den sites, and prey.

6.6. Summary

The objective of this study was to collect information on the spatial ecology of dholes with special reference to home range sizes, core areas, and movement patterns of radio-collared dholes. To collect this information, three individual dholes from different packs were captured, immobilized, fitted with radio-collars and subsequently tracked for five to 12 months in this study.

The radio-telemetry study revealed that home range sizes of radio-collared dholes in Pench covered 66.4 km^2 to 202.8 km^2 (95% MCP). Seasonal home range size averaged 77.58 (± 26.6 SE) km^2, while core areas of dhole packs averaged 57.5 (± 18.8 SE) km^2 (80% ADK). Dhole packs restricted themselves to a small area (15-20 km^2) during the denning and nursing season (winter: Nov-Feb). Ranges increased (30-60 km^2) gradually during post-denning (pup-rearing) season (spring-summer: Mar-June). A great increase in home range sizes (< 100 km^2) occured during the dispersal & pre-denning season (monsoon: July-Oct). Based on intensive tracking of an optimal pack of 14 dholes, it was concluded that 60-70 km^2 would constitute the ideal home range area required for a dhole pack, with a smaller activity centre of ca. 20 km^2. Thus, the dhole density in Pench would be 0.2-0.23 dholes km^{-2} or 1.43-1.66 packs per 100 km^2.

Mean daily distance (inter-day distance) moved by dholes in Pench spanned 2.96 km (± 0.16 SE) whereas mean travel speed of dholes packs was 2.54 km h^{-1} (± 0.36 SE), with a maximum travel speed of 16.13 km h^{-1} in one session.

Based on the monthly range sizes and corresponding pack sizes of the three dhole packs, it was found that mean density of dholes in Pench was 0.29 (± 0.08 SE) dholes km^{-2}, or 2.9 dholes per 10 km^2. This density ranged from a minimum of 0.02 to a maximum of 1.34 dholes km^{-2}. If one of the study packs, ♀44 + 13 dholes, with a home range of 60-70 km^2 were to be considered as the ideal dhole pack, then the density would be 0.2-0.23 dholes km^{-2} or 1.43-1.66 packs per 100 km^2.

REFERENCES

Ables, E. D., (ed). 1974. Kleberg Studies in Natural Resources: The Axis Deer in Texas. The Caesar Kleberg Research program in Wildlife Ecology & Department of Wildlife and Fisheries Sciences, Texas Agricultural Experiment Station, The Texas A & M University System.

Acharya, B. B. 1997. Habitat Occupancy by Wild Ungulates In Pench Tiger Reserve, Madhya Pradesh. M.Sc. Thesis. Saurashtra University, Rajkot.

Ackerman, B. B., F. G. Lindzey, and T. P. Hemker. 1984. Cougar food habits in southern Utah. Journal of Wildlife Management 48:147-155.

Alldredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50:157-165.

Anderson, D. R., J. L. Laake, B. R. Crain, and K. P. Burnham. 1979. Guidelines for for transect sampling of biological populations. Journal of Wildlife Management 43:71-79.

Arjo, W. M., and D. H. Pletscher. 2004. Coyote and wolf habitat use in Northwestern Montana. Northwest Science 78:24-32.

Balakrishnan, M., and P. S. Easa. 1986. Habitat preferences of the larger mammals in the Parambikulam Wildlife Sanctuary, Kerala, India. Biological Conservation 37:191-200.

Ballard, W. B., L. A. Ayres, K. E. Roney, and T. H. Spraker. 1991. Immobilization of gray wolves with a combination of tiletamine hydrochloride and zolazepam hydrochloride. Journal of Wildlife Management 55:71-74.

Bekoff, M., T. J. Daniels, and J. L. Gittleman. 1984. Life history patterns and the comparative social ecology of carnivores. Annual Review of Ecology and Systematics 15:191-232.

Bertram, B. C. R. 1982. Leopard ecology as studied by radio tracking. Symposia of the Zoological Society of London 49:341-352.

Berwick, S. H. 1974. The community of wild ruminants in the Gir forest ecosystem, India. Ph.D thesis Thesis. Yale University, New Haven.

Biswas, S., and K. Sankar. 2002. Prey abundance and food habit of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India. Journal of Zoology 256:411-420.

Boulanger, J. G., and G. C. White. 1990. A comparison of home range estimators using Monte Carlo simulation. Journal of Wildlife Management 54:310-315.

Brander, A. A. D. 1923. Wild animals in Central India. Edward Arnold and Co, London.

Brockelman, W. Y. and Ali, R. 1987. Methods of surveying and sampling forest primate populations. *In*: Primate Conservation in the Tropical Forest, C. W. Marsh and R. A. Mittermeier (eds.), pp. 23-62. Alan R. Liss, New York.

Brooks, P. M., J. Hanks, and J. V. Ludbrook. 1977. Bone marrow as an index of condition in African ungulates. South African Journal of Wildlife Research 7:61-66.

Buckland, S. T., D. R. Anderson, and K. P. Burnham. 1993. Distance Sampling: Estimating abundance of Biological Populations. Chapman and Hall, London.

Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monographs 72:1-202.

Burt, W. H. 1943. Territoriality and home range concepts on applies to mammals. Journal of Mammalogy 24:346-352.

Burton, R. W. 1899. Jungle notes. Journal of the Bombay Natural History Society 12:587-589.

Burton, R. W. 1925. Panther and wild dogs. Journal of the Bombay Natural History Society 30:910-911.

Burton, R. W. 1940. The Indian wild dog. Journal of the Bombay Natural History Society 41:691-715.

Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. Science 295:2273-2276.

Champion, H. G., and S. K. Seth. 1968. A Revised Survey of the Forest Types of India. Manager of Publications, Government of India, New Delhi.

Chesson, J. 1978. Measuring preference in selective predation. Ecology 59:211-215.

Clutton-Brock, J., G. B. Corbet, and M. Hills. 1976. A review of the family Canidae with a classification by numerical methods. Bulletin of the British Museum (Natural History) Zoology 29:119-199.

Cohen, J. A. 1977. A review of the biology of the dhole or Asiatic wild dog (*Cuon alpinus* Pallas). Animal Regulation Studies 1:141-158.

Cohen, J. A. 1977. Species identification and age classification of the jaws of some common Indian ungulates near Mudumalai Wildlife Sanctuary. Journal of the Bombay Natural History Society 74:246-248.

Cohen, J. A. 1978. Cuon alpinus. Mammalian Species 100:1-3.

Cohen, J. A., M. W. Fox, A. J. T. Johnsingh, and B. D. Barnett. 1978. Food habits of the dhole in south India. Journal of Wildlife Management 42:933-936.

Connell, W. 1944. Wild dogs attacking a tiger. Journal of the Bombay Natural History Society 44:468-470.

Corbet, G. B., and J. E. Hill. 1992. The Mammals of the Indomalayan Region: A systematic Review. Natural History Museum Publications, Oxford University Press, New York.

Corbett, L. K. 1989. Assessing the diet of dingoes from feces: A comparision of three methods. Journal of Wildlife Management 53:343-346.

Curio, E. 1976. Ethology of Predation. Springer-Verlag, Berlin.

Daniel, J. C. 1991. Ungulate conservation in India - problems and prospects. Applied Animal Behaviour Science 29:349-359.

Davidar, E.R.C., 1968. The Nilgiri Wild life Association and the status of wild life in the Nilgiris. Journal of the Bombay Natural History Society 65:431-443

Davidar, E. R. C. 1974. Observation at the dens of the dhole or Indian wild dog (*Cuon alpinus*). Journal of the Bombay Natural History Society 71:183-187.

Dinerstein, E. 1979. An ecological survey of the Royal Karnali Bardia Wildlife Preserve, Nepal. Part II. Habitat/animal interaction. Biological Conservation 16:265-300.

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Eisenberg, J. F., and M. Lockhart. 1972. An ecological reconnaisance of Wilpattu National Park, Ceylon. Smithsonian Contributions to Zoology 101:1-118.

Eisenberg, J. F., and J. Seidensticker. 1976. Ungulates in Southern Asia: A consideration of biomass estimates for selected habitats. Biological Conservation 10:293-308.

Ellerman, J. R., and T. C. S. Morrison-Scott. 1966. Checklist of Palaearctic and Indian mammals, 1758 to 1946, 2nd Edition. British Museum (Natural History), London.

ESRI. 1999. ArcView GIS version 3.2. Environmental Systems Research Institute. Redlands, CA, USA.

Estes, R. D., and J. Goddard. 1967. Prey selection and hunting behavior of the African wild dog. Journal of Wildlife Management 31:52-70.

Floyd, T. J., L. D. Mech, and P. A. Jordan. 1978. Relating wolf scat content to prey consumed. Journal of Wildlife Management 42:528-532.

Forsyth, J. 1919. The Highlands of Central India: Notes on the Forests and Wild Tribes, Natural History and Sports. Chapman and Hall, London, (First published 1871).

Fox, M., and A. J. T. Johnsingh. 1975. Hunting and feeding in wild dogs. Journal of the Bombay Natural History Society 72:321-326.

Fox, M. W. 1971. Behaviour of wolves, dogs and related canids. Krieger Publishing Company, Malabar, Florida.

Fox, M. W. 1984. The Whistling Hunters: Field Studies of the Asiatic Wild dog (*Cuon alpinus*). State University of New York Press, Albany.

Frame, L. H., and G. W. Frame. 1976. Female African wild dogs emigrate. Nature 263:227-229.

Fredericks, B., and M. G. Wing. 2006. Traverse XL: An EXCEL-based program for entering, displaying, and analyzing spatial measurement data. Surveying and Land Information Science 66:65-72.

Fuller, T. K., and P. W. Kat. 1990. Movement, activity, and prey relationships of African wild dogs (*Lycaon pictus*) near Aitong, southwestern Kenya. African Journal of Ecology 28:330-350.

Garmin. 1997. GPS12XL Owner's Manual. Software Version 2.00-3.62), Rev. A. (http://www.garmin.com/products/gps12xl/)

Giles, R. H., Jr. 1978. Wildlife Management. W. H. Freeman and Company, San Fransisco.

Ginsberg, J. R., and D. W. Macdonald. 1990. Foxes, wolves, jackals and dogs: an action plan for the conservation of canids. Gland, Switzerland. IUCN.

Girman, D. J., P. W. Kat, M. G. Mills, J. R. Ginsberg, M. Borner, V. Wilson, J. H. Fanshawe, C. Fitzgibbon, L. M. Lau, and R. K. Wayne. 1993. Molecular genetic and morphological analyses of the African wild dog (*Lycaon pictus*). Journal of Heredity 84:450-459.

Gittleman, J. L., and P. H. Harvey. 1982. Carnivore Home-Range Size, Metabolic Needs and Ecology. Behavioral Ecology and Sociobiology 10:57-63.

Gottelli, D., C. Sillero-Zubiri, G. D. Applebaum, M. S. Roy, D. J. Girman, J. Garcia-Moreno, E. A. Ostrander, and R. K. Wayne. 1994. Molecular genetics of the most endangered canid: the Ethiopian wolf *Canis simensis*. Molecular Ecology 3:301-312.

Graf, W., and L. Nichols Jr. 1966. The Axis deer in Hawaii. Journal of the Bombay Natural History Society 63:629-734.

Green, M. J. B. 1981. A checklist and some notes concerning the mammals of the Langtang National Park. Journal of the Bombay Natural History Society 78:77-87.

Green, M. J. B. 1985. Aspects of the ecology of the Himalayan musk deer. Ph. D. Thesis. Cambridge University.

Green, M. J. B. 1987. Ecological separation in Himalayan ungulates. Journal of zoology. Series B 1:693-719.

Griffiths, D. 1975. Prey availability and the food of predators. Ecology 56:1209-1214.

Haibin, W., and T. K. Fuller. 1996. Food habits of large canids in southeast China. Journal of Wildlife Research 1:155-157.

Haque, N. 1990. Study on the ecology of wild ungulates of Keoladeo National Park, Bharatpur. Ph.D. Thesis. Centre for Wildlife and Ornithology, Aligarh Muslim University, Aligarh.

Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight - a reevaluation. Ecology 60:389-402.

Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20:97-123.

Hines, J. E. 2002. SCATMAN. Version 2.0. USGS-PWRC.http://www.mbr-pwrc.usgs.gov/software/.

Hirst, S. M. 1969. Road-strip census techniques for wild ungulates in African woodlands. Journal of Wildlife Management 33:40-48.

Hood, R. 1895. Wild dogs. Journal of the Bombay Natural History Society 10:127-132.

Hornocker, M. 1970. An analysis of mountain lion predation upon mule deer and elk in Idaho primitive area. Wildlife Monographs 21.

Israel, S., and T. Sinclair, editors. 1987. Indian Wildlife. APA Productions, Singapore.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University, Connecticut, New Haven.

Jacobs, J. 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413-417.

Jayapal, R. 1997. A Study On Bird Communities-Habitat Structure Relationships In Pench National Park, M.P. M.Sc. Thesis. Saurashtra University, Rajkot.

Jerdon, T. C. 1874. The Mammals of India. John Wheldon, London.

Jewell, P. A. 1966. The concept of home range in mammals. Symposia of the Zoological Society of London No. 18:85-109.

Johnsingh, A. J. T. 1982a. Reproductive and social behaviour of dholes. Journal of Zoology 198:443-463.

Johnsingh, A. J. T. 1982b. Ecology and Behaviour of dhole or Indian wild dog (*Cuon alpinus* Pallas 1811) with special reference to predator-prey relations at Bandipur. Ph.D. Thesis. Madurai Kamaraj University, Madurai.

Johnsingh, A. J. T. 1983. Large mammalian prey-predators in Bandipur. Journal of the Bombay Natural History Society 80:1-57.

Johnsingh, A. J. T. 1985. Distribution and status of dhole *Cuon alpinus* Pallas, 1811 in South Asia. Mammalia 49:203-208.

Johnsingh, A. J. T. 1986. Diversity and conservation of carnivorous mammals in India. Proc. Indian. Acad. Sci. (Anim. Sci.) Suppl:73-89.

Johnsingh, A. J. T. 1992. Prey selection in three large sympatric carnivores in Bandipur. Mammalia 56:517-526.

Junior, O. F. 2004. GPS TrackMaker® Software Version 10.0. (http://www.gpstm.com).

Karanth, K. U., and M. E. Sunquist. 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. Journal of Tropical Ecology 8:21-35.

Karanth, K. U., and M. E. Sunquist. 1995. Prey selection by tiger, leopard and dhole in tropical forests. Journal of Animal Ecology 64:439-450.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852-2862.

Karanth, K. U., and M. E. Sunquist. 2000. Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. Journal of Zoology 250:255-265.

Keller, R. 1973. Einige Beobactungenzum Verhalten des Dekkan-Rothundes (*Cuon alpinus dukhunensis* Sykes) in Kanha National Park.

Vierteljahresschrift der Naturforschenden Gesellschaft in Zurich 118:129-135.

Khajuria, H. 1963. The wild dog *Cuon alpinus* (Pallas) and the tiger *Panthera tigris* (Linn). Journal of the Bombay Natural History Society 60:448-449.

Khan, J. A. 1993. Ungulate-habitat relationships in Gir forest ecosystem and its management implications. Ph.D. Thesis. Aligarh Muslim University, India.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1996. CALHOME: a program for estimating animal home ranges. Wildlife Society Bulletin 24:342-344.

Kleiman, D. G. 1967. Some aspects of social behavior in the Canidae. American Zoologist 7:365-372.

Koppikar, B. R., and J. H. Sabnis. 1981. Aids to the identification of Artiodactylian hairs with general comments on hair structure. Journal of the Bombay Natural History Society 78:299-303.

Kotwal, P. C. 1981. Tranquilisation of Indian wild dog (*Cuon alpinus* Pallas). Cheetal 23:34-35.

Krishnan, M. 1972. An ecological survey of the larger mammals of peninsular India. Part II. Journal of the Bombay Natural History Society 69:26-54.

Krüger, S. C., M. J. Lawes, and A. H. Maddock. 1999. Diet choice and capture success of wild dog (*Lycaon pictus*) in Hluhluwe-Umfolozi Park, South Africa. Journal of Zoology 248:543-551.

Kumar, S. 1989. Management Plan of Pench Tiger Reserve, Madhya Pradesh (1990-1995). Unpublished. Madhya Pradesh Forest Department.

Leopold, A. 1961. Game management, 2nd Edition. Charles Scribner's Sons, New York.

Leopold, B. D., and P. R. Krausman. 1986. Diet of three predators in Big Bend National Park, Texas. Journal of Wildlife Management 50:290-295.

Link, W. A., and K. U. Karanth. 1994. Correction for overdispersion in tests of prey selectivity. Ecology 75:2456-2459.

Malcolm, J. R. 1989. Social organization and communal rearing in African hunting dogs. Ph.D. Dissertation. Harvard University.

Malcolm, J. R., and K. Marten. 1982. Natural selection and the communal rearing of pups in African wild dogs *Lycaon pictus*. Behavioral Ecology and Sociobiology 10:1-13.

Manly, B. F. J., P. Miller, and L. M. Cook. 1972. Analysis of a selective predation experiment. The American Naturalist 106:719-736.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. The American Naturalist 47:133-140.

Mech, L. D. 1967. Telemetry as a technique in the study of predation. Journal of Wildlife Management 31:492-496.

Mech, L. D. 1970. The Wolf: The Ecology and Behavior of an Endangered Species. University of Minnesota Press, Minneapolis.

Mech, L. D., and S. M. Barber. 2002. A critique of wildlife radio-tracking and its use in national parks: a report to the U.S. National Park Service. U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, N.D. Jamestown, ND: Northern Prairie Wildlife Research Center Online.

Middleton, A. 1951. The Indian wild dog. Journal of the Bombay Natural History Society 50:162-163.

Mishra, H. R. 1982. The ecology and behaviour of chital (*Axis axis*) in Royal Chitwan National Park, Nepal. Ph.D. Thesis. University of Edinburgh, Edinburgh, U.K.

Mivart, St. G. J. 1890. Dogs, Jackals, Wolves and Foxes, Monograph of the Canid‘. R. H. Porter, London.

Mohr, C. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37: 223-249.

Moore, T. D., L. E. Spence, and C. E. Dugnolle. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game & Fish Department, Wyoming. Bull. No. 14.

Morris, R. C. 1933a. Wild dogs driving a panther from its kill. Journal of the Bombay Natural History Society 36:744-745.

Morris, R. C. 1933b. Wild dogs killing a panther. Journal of the Bombay Natural History Society 36:744.

Mukherjee, S., S. P. Goyal, and R. Chellam. 1994. Standardisation of scat analysis techniques for leopard (*Panthera pardus*) in Gir National Park, Western India. Mammalia 58:139-143.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541-545.

Newton, P. N. 1984. The Ecology and Social Organisation of Hanuman Langurs (*Presbytis entellus* Dufresne 1797) in Kanha Tiger Reserve, Central Indian Highlands. Ph.D. Thesis. University of Oxford, Oxford.

Ngampongsai, C. 1987. Habitat use by sambar (*Cervus unicolor*) in Thailand. Pages 289-298 *In*: C. M. Wemmer, editor. Biology and management of the Cervidae. Smithsonian Institution Press, Washington, D.C., Research Symposia of the National Zoological Park.

Norman, H. S., R. J. Hudson, V. C. Brink, and W. D. Kitts. 1975. Determinants of spatial distribution of Rocky Mountain bighorn sheep. Journal of Wildlife Management 39:387-401.

Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analyses of radiotracking data. Journal of Wildlife Management 63:1039-1043.

Pasha, M. K. S., R. Jayapal, G. Areendran, Q. Qureshi, and K. Sankar. 2004. Birds of Pench Tiger Reserve, Madhya Pradesh, central India. Newsletter for Ornithologists 1:2-3.

Patel, A. H. 1992. Are chital stags more vulnerable to dhole predation than does? Journal of the Bombay Natural History Society 89:153-155.

Paulraj, S., N. Sundararajan, A. Manimozhi, and S. Walker. 1992. Reproduction of the Indian wild dog (*Cuon alpinus*) in captivity. Zoo Biology 11:235-241.

Phythian-Adams, E. G. 1927. Wild dogs in Mysore. Journal of the Bombay Natural History Society 31:1028-1029.

Phythian-Adams, E. G. 1939. The Nilgiri Game Association - 1879 - 1939. Journal of the Bombay Natural History Society 41:384-396.

Phythian-Adams, E. G. 1949. Jungle memories. Part IV - Wild dogs and wolves, etc. Journal of the Bombay Natural History Society 48:645-655.

Pocock, R. I. 1936. The Asiatic Wild Dog or Dhole (*Cuon javanicus*). Proceedings of the Royal Society of London 1936:33-65.

Prater, S. H. 1980. The Book of Indian Animals. Bombay Natural History Society, Oxford University Press, Bombay.

Putman, R. J. 1984. Facts from faeces. Mammal Review 14:79-97.

Rajaram, A., and R. K. Menon. 1986. A scanning electron microscope study on the hair keratins of some animals of the Indian subcontinent - a preliminary report. Journal of the Bombay Natural History Society 83:427-428.

Raman, T. R. S., R. K. G. Menon, and R. Sukumar. 1996. Ecology and management of chital and blackbuck in Guindy National Park, Madras. Journal of the Bombay Natural History Society 93:178-192.

Ramanathan, S. 1982. A sighting of a large dhole pack in Kanyakumari district, Tamil Nadu. Journal of the Bombay Natural History Society 79:665-666.

Reynolds, T. D., and J. W. Laundré. 1990. Time intervals for estimating pronghorn and coyote home ranges and daily movements. Journal of Wildlife Management 54:316-322.

Reynolds, J. C., and N. J. Aebischer. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpus*. Mammal Review 21:97-122.

Richardson II, W. A. 1972. A natural history survey of sambar deer (*Cervus unicolor*) on the Powderhorn Ranch, Calhoun Country, Texas. M.S. Thesis. A & M Univ., Texas.

Riney, T. 1982. Study and management of large mammals. John Wiley & Sons, Chichester.

Rodgers, W. A. 1988. The wild grazing ungulates of India: an ecological review. Pages 404-419 *In:* P. Singh and P. S. Pathak, editors. Rangelands - resource and management. Proceedings of the National Rangeland Symposium, IGFRI, Jhansi, November 9-12, 1987. IGFRI, Jhansi.

Rodgers, W. A. 1991. Techniques for Wildlife Census in India: A Field Manual. Techniques for Wildlife Census in India: A Field Manual, Wildlife Institute of India, DehraDun.

Rodgers, W. A., and H. S. Panwar. 1988. Planning a wildlife protected area network in India, Vol II, State summaries. A report prepared for the Department of Environment, Forests and Wildlife, Government of India at Wildlife Institute of India, pp.217-230.

Sand, H., B. Zimmerman, P. Wabakken, H. Andren, and H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf ungulate ecosystems. Wildlife Society Bulletin 33:914-925.

Sankar, K. 1994. The ecology of three large sympatric herbivores (Chital, Sambar and Nilgai) with special reference for reserve management in Sariska Tiger Reserve, Rajasthan. Ph.D. Thesis. University of Rajasthan, Jaipur.

Sankar, K., Q Qureshi, M.K.S. Pasha, and G. Areendran, G. 2000a. Ecology of gaur *Bos gaurus* in Pench Tiger Reserve, Madhya Pradesh. Final Report. Wildlife Institute of India, Dehra Dun.

Sankar, K., Q. Quresh, V.B. Mathur, S.K. Mukherjee, G. Areendran, M.K.S. Pasha, R. Thapa and P. Lal. 2000b. Mapping of the Protected Area (PA) and surrounding areas in Pench Tiger Reserve, Madhya Pradesh. Wildlife Institute of India, Dehradun

Schaller, G. B. 1967. The Deer and the Tiger. University of Chicago Press, Chicago.

Scheel, D. 1993. Profitability, encounter rates, and prey choice of African lions. Behavioral Ecology 4:90-97.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369-404.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

Shea, S. M., L. B. Flynn, R. L. Marchinton, and J. C. Lewis. 1990. Part 2. Social behavior, movement ecology, and food habits. Pages 13-62 In: Ecology of sambar deer on St. Vincent National Wildlife Refuge, Florida. Bull. No. 25. Tall Timbers Research Station, Tallahassee, Florida.

Sheffield, W. J., B. A. Fall, and B. A. Brown. 1983. The nilgai antelope in Texas. Kleberg studies in Natural Resources. Texas A. & M. University, 100 pp.

Shukla,R. 1990. An ecological study of interactions between wild animals and vegetation in Pench Wildlife Sanctuary and its environs. Ph.D. Thesis, Dr. Harisingh Gour Vishwavidyalaya, Sagar. 249 p.

Sillero-Zubiri, C. 1996. Field immobilization of Ethiopian wolves. Journal of Wildlife Diseases {B32}:147-151

Sosnovskii, I. P. 1967. Breeding the Red dog or dhole *Cuon alpinus* at Moscow Zoo. International Zoo Yearbook 7:120-122.

Soulé, M. E., and D. Simberloff. 1986. What do genetics and ecology tell us about the design of nature reserves? Biological Conservation 35:19-40.

SPSS. 2001. SPSS 8.0 for Windows. SPSS Inc, Chicago, Illinois, USA.

Sterndale, R. A. 1887. Seonee, or Camp Life on the Satpura Range. Thacker, Spink and Co., Calcutta and Simla.

Stewart, P. 1993. Mapping the Dhole. Canid News 1:18-21.

Sunquist, M. E. 1981. The social organization of tigers (*Panthera tigris*) in Royal Chitawan National Park, Nepal. Smithsonian Contributions to Zoology No. 336.

Sunquist, M. E., and F. C. Sunquist. 1989. Ecological constraints on predation by large felids. Pages 283-301 *In:* J. L. Gittleman, editor. Carnivore Behavior, Ecology and Evolution. Volume 1. Chapman and Hall, London.

Swihart, R. K., and N. A. Slade. 1997. On testing for independence of animal movements. Journal of Agricultural, Biological, and Environmental Statistics 2:1-16.

Tamang, K. M. 1982. The status of the tiger (*Panthera tigris tigris*) and its impact on principal prey populations in the Royal Chitawan National Park, Nepal. Ph.D. Thesis. Michigan State University.

Taylor, R. J. 1984. Predation. Chapman and Hall, New York.

Terborgh, J. W. 1988. The big things that run the world - a sequel to E.O Wilson. Conservation Biology 3:350-361.

Thenius, E. 1954. On the origins of the dhole. Osterreichischer Zoologischer Zeitschrift 5:377-388.

Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, and J. R. B. Bishop. 2004. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, U.K. http://www.ruwpa.st-and.ac.uk/distance/

Van Heerden, J., G. E. Swan, J. Dauth, R. E. J. Burroughs, and J. Dreyer. 1991. Sedation and immobilization of wild dogs *Lycaon pictus* using a medetomidine-ketamine hydrochloride combination. South African Journal of Wildlife Research 21:88-93.

van Winkle, W. 1975. Comparison of several probabilistic home-range models. Journal of Wildlife Management 39:118-123.

Varman, K. S., and R. Sukumar. 1995. The line transect method for estimating densities of large mammals in a tropical deciduous forest: An evaluation of models and field experiments. Journal of Biosciences 20:273-287.

Venkataraman, A. B. 1995. Do dholes (*Cuon alpinus*) live in packs in response to competition with or predation by large cats? Current Science 69:934-936.

Venkataraman, A. B. 1998. Male-biased adult sex ratios and their significance for cooperative breeding in dhole *Cuon alpinus* packs. Ethology 104:671-684.

Venkataraman, A. B., R. Arumugam, and R. Sukumar. 1995. The foraging ecology of dhole (*Cuon alpinus*) in Mudumalai Sanctuary, southern India. Journal of Zoology 237:543-561.

Vila, C., and J. Castroviejo. 1994. Use of tiletamine and zolazepam to immobilize captive Iberian wolves (*Canis lupus*). Journal of Wildlife Diseases 30:119-122.

Wayne, R. K., E. Geffen, D. J. Girman, K. P. Koepfli, L. M. Lau, and C. R. Marshall. 1997. Molecular systematics of the Canidae. Systematic Biology 46:622-653.

Wesley, D.G. 1977. Census of wild animals in Bandipur Tiger Reserve. My Forest 13: 15-19.

White, G. C., and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, New York.

Wikramanayake, E. D., E. Dinerstein, J. G. Robinson, U. Karanth, A. Rabinowitz, D. Olson, T. Mathew, P. Hedao, M. Conner, G. Hemley, and D. Bolze. 1998. An Ecology-Based Method for Defining Priorities for Large Mammal Conservation: The Tiger as Case Study. Conservation Biology 12:865-878.

Witt, D. O. 1907. Note on effect of strychnine poison on wild dogs. Journal of the Bombay Natural History Society 18:211-213.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126-2128.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Wright, F. 1890. Panthers tree'd by wild dogs. Journal of the Bombay Natural History Society 5:191-192.

Zar, J. H. 1984. Biostatistical Analysis, 2nd Edition. Prentice-Hall, Englewood Cliffs, New Jersey.

APPENDICES

Appendix 1. Details of the 19 permanent line transects laid within Pench T.R., Madhya Pradesh, for the enumeration of dhole prey species.

Sl. No.	Range name	Transect name	Starting Point	Ending point	Length (km)
1	Karmajhiri	Singungarh	N 21 49' 32" E 79 18' 55"	N 21 49' 35" E 79 17' 44"	2.0
2	Karmajhiri	Jamun Nala	N 21 50' 01" E 79 17' 27"	N 21 50' 02" E 79 18' 24"	1.6
3	Karmajhiri	Khairbanmatta	N 21 48' 13" E 79 18' 57"	N 21 48' 11" E 79 17' 43"	2.3
4	Karmajhiri	Badjodi	N 21 47' 58" E 79 17' 34"	N 21 47' 58" E 79 18' 54"	2.3
5	Karmajhiri	Kasai	N 21 47' 35" E 79 18' 46"	N 21 47' 29" E 79 17' 25"	2.3
6	Karmajhiri	Mannutalab	N 21 47' 33" E 79 18' 57"	N 21 48' 27" E 79 19' 24"	1.7
7	Karmajhiri	GurluTek	N 21 47' 09" E 79 19' 33"	N 21 47' 07" E 79 17' 58"	2.3
8	Karmajhiri	Bison Camp	N 21 46' 50" E 79 17' 55"	N 21 46' 55" E 79 20' 11"	3.6
9	Karmajhiri	Pivarthari	N 21 45' 16" E 79 17' 29"	N 21 44' 26" E 79 18' 17"	2.5
10	Karmajhiri	Joda Munhara	N 21 46' 24" E 79 18' 18"	N 21 45' 01" E 79 18' 14"	2.7
11	Karmajhiri	25 Number	N 21 44' 41" E 79 18' 45"	N 21 46' 06" E 79 18' 42"	2.5
12	Karmajhiri	Seewan Nala	N 21 44' 33" E 79 19' 19"	N 21 45' 55" E 79 19' 18"	2.4
13	Karmajhiri	Kala Pahad	N 21 44' 30" E 79 16' 40"	N 21 45' 18" E 79 16' 39"	1.2
14	Karmajhiri	Baara Mod	N 21 47' 44" E 79 20' 22"	N 21 47' 36" E 79 19' 36"	1.3
15	Karmajhiri	Jandi Pahad	N 21 47' 31" E 79 20' 28"	N 21 47' 29" E 79 19' 07"	2.3
16	Gumatra	Rohni	N 21 49' 15" E 79 14' 14"	N 21 49' 14" E 79 16' 06"	3.1
17	Gumatra	Gumtara	N 21 48' 50" E 79 14' 55"	N 21 48' 44" E 79 13' 42"	2.0
18	Gumatra	Chita Pahad	N 21 48' 34" E 79 16' 36"	N 21 48' 29" E 79 15' 16"	2.3
19	Gumatra	Naagdev	N 21 49' 35" E 79 14' 03"	N 21 49' 43" E 79 15' 31"	2.5

Appendix 2. Details of the 14 vehicle-based road transects used within Pench T.R., Madhya Pradesh and Maharashtra, for the enumeration of dhole prey species

Route No.	Starting Point	Ending Point	Total Length (km)
1	Gorsal Ghat	Alikatta	6.1
2	Kalapahad T	Turia Gate	5.6
3	Gorsal Ghat	BaaraMod	3.7
4	TikariGate	MahuaMod	7.9
5	Kamreet T	Turia Gate	5.9
6	ChhindiMatta	Dhaudikund	7.7
7	JamunJodi	JodaMunharaCamp	5.3
8	ChitaGhat	MahadevGhat	2.3
9	Gumtra T	Chendia T	5.5
10	Jamtra T	Chendia T	4.0
11	Kalachopun	Chiklakaari	5.0
12	StateBorder	SaddleDam 7	4.6
13	SaddleDam7	BhimSenTower	4.4
14	SaddleDam7	ChiklakaariMH	4.7

Appendix 3. Frequency of occurrence of remains of major prey species in tiger (n=65) and leopard (n=6) scats collected in Pench T.R., M.P. 2001-2004.

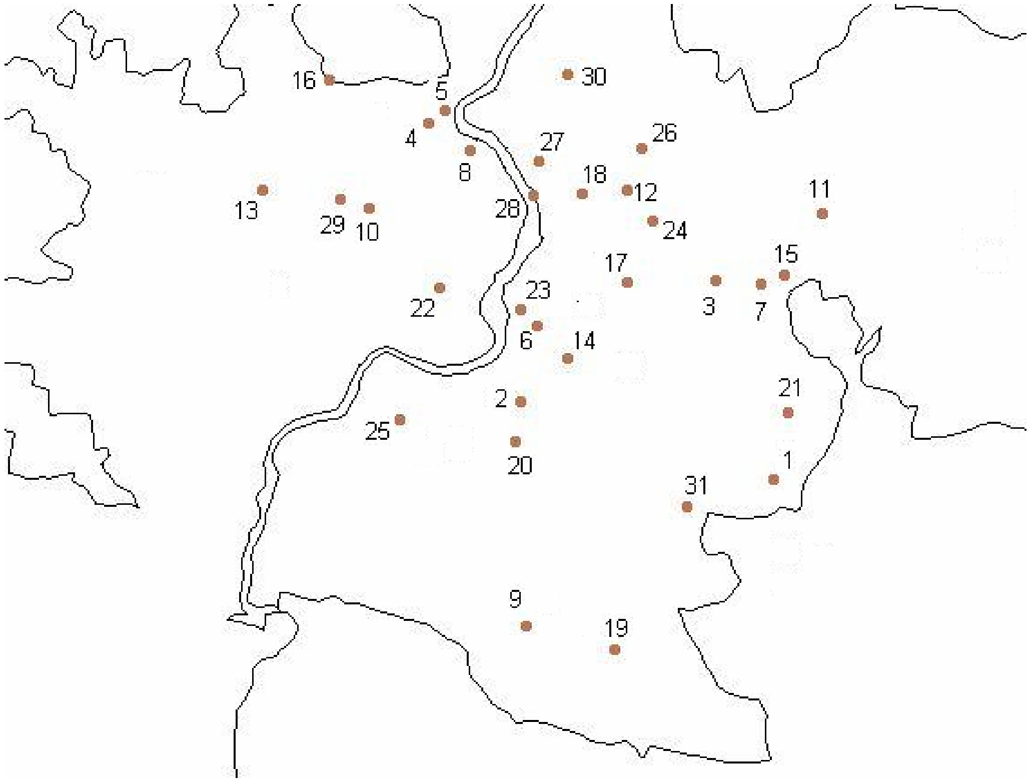
Prey species	Tiger scats		Leopard scats	
	No.	%	No.	%
Sambar	21	31.3	-	-
Chital	35	52.2	2	33.3
Langur	3	4.5	3	50.0
Wild pig	3	4.5	1	16.6
Buffalo	2	3.0	-	-
Cattle	2	3.0	-	-
Gaur	1	1.5	-	-

No. = No. of scats with presence
% = % of scats with presence

Appendix 4. Major prey species killed by tigers (n = 12) and leopards (n = 17) in Pench T.R., Madhya Pradesh, 2001-2004.

	Prey species	No. of kills	% of kills	♂	♀	Juv	Unk
Tiger	Chital	9	75	4	4	1	0
	Sambar	1	8.3	1	0	0	0
	Wild pig	1	8.3	0	1	0	0
	Gaur	1	8.3	1	0	0	0
Leopard	Chital	14	82.3	4	10	1	0
	Wild pig	2	11.7	0	2	0	0
	Nilgai	1	5.8	0	1	0	0

Appendix 5. Locations of known and frequently used latrine sites of dholes in Pench TR, Madhya Pradesh (2001-2005)



No.	Location	No.	Location	No.	Location
1 -	38 # Camp	12 -	Gorsal Ghat	22 -	Mahadev-Gumtra
2 -	Alikatta	13 -	Gumtra	23 -	MahuaMod
3 -	BaaraMod	14 -	Jodamunhara	24 -	Manutalab T
4 -	BadjodiTalab	15 -	Jhirpa	25 -	Sapat
5 -	BakodiKhassa	16 -	Jamtra	26 -	Signboard
6 -	Bison Camp	17 -	Jhandipahad	27 -	Sukurpaen
7 -	BodaNala-Bagdev	18 -	KhairbanMatta	28 -	Thumri Er
8 -	ChendiaMaidaan	19 -	Kalachopun-MarkaKhassa	29 -	TigerSaucer
9 -	Chiklakaari	20 -	Kalapahaad	30 -	TikariBarrier
10 -	ChitaPahad	21 -	Kamreet	31 -	TuriaGate
11 -	Dhakipaen				