K., Yoganand, 2005, *"Behavioural Ecology of Sloth Bear (Melursus ursinus) In Panna National Park, Central India",* thesis PhD, Saurashtra University

BEHAVIOURAL ECOLOGY OF SLOTH BEAR (*Melursus ursinus*) IN PANNA NATIONAL PARK, CENTRAL INDIA

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

K. YOGANAND

Wildlife Institute of India
Dehradun

October 2005

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

7 October 2005

CERTIFICATE

I certify that the thesis titled "**Behavioural Ecology of Sloth Bear (*Melursus Ursinus*) in Panna National Park, Central India**", 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 **K. Yoganand,** under my supervision. No part of this thesis has been submitted in part or full to any other University/Institution for the award of any other degree, and it fulfills all the requirements laid down by Saurashtra University.

Dr. A. J. T. Johnsingh
Dean, Faculty of Wildlife Sciences
Wildlife Institute of India

Forwarded

Director
Wildlife Institute of India
Dehradun

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

Post Box No. 18, Chandrabani, Dehra Dun - 248001. India
EPBAX : +91-135-2640111 to 2640115, 2640990 **FAX** : 2640117 **GRAM :** WILDLIFE
E-Mail : wii@wii.gov.in

ACKNOWLEDGEMENTS

Many institutions and people have contributed to this study in various ways. I am grateful to them for their valuable support and am motivated by their goodwill. I would like to express my appreciation for them, and also apologize to those who I may have inadvertently missed out in this hurriedly written section.

This study was carried out as a part of a collaborative project between Wildlife Institute of India and United States Fish and Wildlife Service, and was supported by the US-India Fund. The project was provided additional funding support by The National Geographic Society, Chicago Zoological Society, Bevins Foundation of the International Association for Bear Research and Management. Wildlife Institute of India (WII) provided me institutional facilities during the writing stages of this dissertation. I would like to thank the present and former Directors of WII for this much-needed support. Smithsonian Institution's National Zoological Park (NZP) and Friends of the National Zoo (FONZ) supported me with a pre-doctoral fellowship during data analysis and writing stages. National Zoo's Conservation & Research Center hosted me at its Front Royal campus when I did some of the work on this dissertation. I am extremely grateful to NZP and FONZ for their greatly encouraging support, which has immensely helped me in improving the quality of this dissertation.

I thank the Madhya Pradesh State Forest Department and the Ministry and Environment and Forests, Government of India, for giving us the necessary permission to conduct the study. Panna National Park provided tremendous logistics support for the study. I would like to especially thank Mr. P. K. Chawdhry, former Field Director of the Park, for his interest in the study and for his excellent support during the field work. Park Range Officer, Mr. M. P. Tamrakar was of great help during the course of the field study. I am grateful to them both. Other Park Range Officers, Forest Guards, Watchers and other Park staff provided a lot of support to this study at various times.

This study would have been much less successful without the able and untiring assistance provided by the Project Assistants Utham, Ramjan, Mahadev, Jahar, and Kishori. They were a great asset to the Project and I am extremely grateful to them.

Dr. A. J. T. Johnsingh provided overall supervision to this study and has been a great source of inspiration. Dr. Cliff Rice gave all possible inputs at every stage of this study, besides having had 'husbanded' the Project for many years before we could start fieldwork for this Project. Drs. Johnsingh and Rice also reviewed many sections of this dissertation. Dr. John Seidensticker has been a mentor and gave excellent insights on sloth bear behaviour, and particularly

provided valuable moral support during the writing stages of this study. I am extremely grateful to all of them.

I would like to thank Dr. William Cochran and USACERL for lending us the Activity Recorder Units, providing software improvements and fixing the units every time they failed. Dr. Gary Koehler took part in the fieldwork in Panna and hosted me at his American black bear study site in Washington State. His inputs on trap design helped me improve the efficiency of trapping bears in Panna. Dr. John Mugaas provided me insights on animal physiology and helped me design the thermal measurements part of the study. He also reviewed the chapter on activity. I thank Drs. Chris Wemmer and William McShea of NZP/CRC for their support while I was there. Dr. H. S. Pabla helped us select the study site and start the study in Panna. I thank them for their valuable contributions to this study. I also would like to thank Dave Garshelis for the many discussions we had on sloth bears over email.

G. Areendran helped me a lot with image analysis and in preparing the habitat map of the study area. Anup Joshi clarified my doubts on scat analysis method. K. V. R. Priyadarshini helped me zealously in counting the numerous termite heads in bear scats and in other lab analysis. She also read through many sections of this dissertation at various times, and has almost single-handedly done the formatting and printing of it. Ashish David carefully read through most of this dissertation and suggested valuable improvements. Bhaskar Acharya did a final proof reading of some sections. I appreciate their help.

Mr. Fred Bagley and Mr. Dave Ferguson of the USFWS Office of International Conservation, and Mr. B. C. Choudhury and the staff of WII-USFWS Projects office at WII have provided excellent support to me during the Project. I am grateful to the library, computer section, GIS, laboratory and herbarium staff at WII for their help in various work related to the study. I thank Neel Gogate and Dr. Raghu Chundawat and their Project staff for their support in field work in Panna.

I have been fortunate to have many friends at WII and elsewhere for the various discussions we have had, which helped me shape my ideas and methods related to this study. I would especially like to thank Christy Williams, Bivash Pandav, Ramesh, Jayapal, Bhaskar, Rajapandian, Vijayakumar, Sivakumar, Suresh Kumar, Anupama and Dr. S. P. Goyal for their encouragement and support for long. I would like to thank Mr. Mohamed Ali, for being a friend and a philosopher. My parents, brother and other family members were very supportive of my various endeavours all along and I am indebted to them. Lastly, I would like to thank my wife for having supported me during the tiring and anxious stages of the study when I needed her help the most.

TABLE OF CONTENTS

Page No.

Chapter 5 **Sloth bear activity patterns and underlying ecological influences**

Chapter 6 **Sloth bear space use and habitat selection**

Chapter 7 **Ecology of sloth bear feeding behaviour**

Chapter 8 **Sloth bear conflict with humans**

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

ABSTRACT

A study on the behavioural ecology of sloth bear was carried out in Panna National Park, central India, from 1996 to 2000. The objectives of this study were to examine the key behavioural aspects of sloth bear and assess the ecological factors that influence them. The main aspects that I studied include daily and seasonal activity, space use and habitat selection, food habits and foraging behaviour. Lastly, I studied bear conflict with humans and identified the behavioural and ecological factors that lead to conflicts.

I recorded activity states by monitoring radio-collared bears, and by deploying automated receiver-recording units. Daily and seasonal changes in thermal conditions of microhabitats used by bears were measured using loggers. Tiger and human activities were monitored to assess the influence of these on bear activity patterns. Bears were found to be essentially nocturnal and crepuscular in activity, and they rested during midday. Overall, bears were active for 48% to 54% of the whole day, in all seasons. Escarpment habitat was most frequently used (50% to 85%) for day-resting, followed by *Lantana* shrub thickets (15% to 50%). The use of escarpment was predominant during dry season months and decreased during monsoon and post-monsoon months, with a converse increase in the use of *Lantana* habitat. In the forest-open habitat, temperatures were the highest and temperature ranges were the largest in the dry season. Among the different microhabitats, temperature variability was the lowest in dens.

Diel activity patterns of bears and tigers were largely similar. Human activity too overlapped with bear activity during early morning and evening hours. Tiger or human activity did not seem to influence bear activity patterns. Bears seem to be cueing to both sunset and sunrise times and heat conditions to start and end their diel activity. Bear activity in day time seemed to have an inverse relationship with temperature in forest-open habitat. It was minimal during the period of high temperature. At night, when bear activity was high, temperatures were commonly <25 ^{o}C. However, even at low temperatures such as 10 ^{o}C or at relatively high temperatures such as 30 ^{o}C, if the period was crepuscular, bear activity nevertheless peaked. High heat

stress conditions have probably influenced the bears to rest during the daytime and in the sites where they could reduce heat gain and increase heat loss. Dens provided the best shelter from heat conditions. The differences among individual bears in the usage of habitats for day-resting were related to the availability of different habitats within home ranges. Bear activity timings, rather than responding to concurrent environmental stimuli, seem to have been synchronised with time of day, probably founded on an endogenous circadian rhythm.

I studied sloth bear space use and habitat selection by monitoring nine radio collared bears (5 females and 4 males). Habitat map of the study area classified using satellite imageries was used to assess habitat selection by bears. Habitat quality for sloth bears was assessed by measuring characteristics such as food plant densities, and prey insect colony densities. 95% fixed kernel estimates of total home ranges ranged from 12.4 km^2 for a female to 85 km^2 for a male. Annual, total, and seasonal home range sizes of male bears were, on an average, larger than those of females. The range sizes were not much different among seasons for females, while they were considerably different for males. There was a high overlap in home ranges between sexes and among males. Seasonal shifts in location of core ranges and changes in habitat use were observed. The bears that had substantial dense forest (and associated escarpment) habitat within their home ranges used that habitat frequently in dry season. Some bears shifted to more open habitats in wet and cold seasons. Home ranges in day, crepuscular, and night periods varied in size, location and habitat composition. Day ranges were smaller and were composed largely of resting spaces and habitats (dense forest and dense shrub), and night ranges were much larger and composed of foraging spaces and habitats. Bears used open forest and open shrub habitats more often at night than during the day.

The annual home ranges of radio-collared bears had varied habitat composition. Some were randomly placed within the study area, while others showed selection for or against particular habitat types. Overall, dense shrub habitat was preferred, and short-grassland / open-savannah and degraded scrubland habitats were avoided in placement of home ranges. When habitat composition of actual locations of use was compared with habitat composition

of space considered available for each bear, dense forest and dense shrub habitats were preferred and open forest and short-grassland / open-savannah habitats were avoided by bears. Density of trees and key food plants of sloth bears was highest in dense forest habitat, followed by open forest, dense shrub and other habitats. Degraded scrubland habitat was the poorest in terms of diversity and densities of food plants and other trees. Dense forest habitat had the highest colony densities of important prey taxa of ants and termites, followed by open forest habitat. It appears that the bear home range sizes may be related to abundance of resources within home ranges. Sloth bears seem to have avoided habitats degraded by humans, which were lower in quality for bears. Food plant, total tree, and insect colony densities were higher in the preferred habitats as compared to avoided habitats.

I studied the food habits and foraging behaviour of sloth bears, by direct observations and estimating diet composition from faecal remains. I examined if seasonal changes in diet followed seasonal changes in food productivity. I further assessed if the bears selected for certain taxa, and specific traits in the fruits and insects they fed on, and whether they showed any preference. Sloth bears foraged frequently on two or more food-groups (fruit, ant, termite) or three or more food taxa in a day. This suggests that they were omnivorous within a day, less so when fruits were abundant and more so when insects were the main food. Fruits contributed 56%, ants 29%, and termites 10% to the annual diet, in terms of ingested biomass. The relative contribution in terms of energy was similar to ingested biomass. Among fruits, *D. melanoxylon* was the highest contributor, followed by *Z. mauritiana,* and among insects, *Camponotus* spp. ants made the greatest contribution to diet, followed by *D. labiatus* ant. Termites contributed a smaller, but consistent portion (about 10% to 25%) to the diet during most months. Fruits and ants complemented each other and constituted 70% to 95% of the diet.

No relationship between relative biomass contribution of various fruit species to annual diet and their relative productivity was found. This indicated selection by bears among the fruits. *D. melanoxylon*, *Z. mauritiana* and *C. fistula* fruits were selected, as they were consumed in a higher proportion to their productivity. *Z. mauritiana* was the most preferred species, followed by

D. melanoxylon, and *C. fistula*. The bears fed on insects in proportion to their abundance. Plant abundance, dispersion, fruiting length, fruit bite-size, fruit presentation, and ripe fruit taste were the plant traits, and colony abundance, colony size, and colony biomass size were the insect traits selected by bears. These traits suggest that the bears made an optimal food choice. The bears fed preferentially on fruits when they were available, and on insects when they were abundant or when fruits were not available. However, they consistently fed on insects even when fruits were abundant. Foraging behaviour and food habits of sloth bears in Panna suggest that they are omnivores with adaptations for myrmecophagy. Sloth bear is the only bear species that seems to almost entirely dependent on social insects for its protein requirements and thus, in this respect, is unique among bears.

Lastly, I investigated the ecological and behavioural conditions that led to attacks on humans by sloth bears, and identified measures that could reduce the frequency of attacks. I surveyed villages and interviewed people who had close encounters with sloth bears and who use forest areas intensively, and gathered information on various parameters associated with attack incidents and encounters. I used the data on other aspects of behavioural ecology of sloth bears to identify the possible factors underlying the attacks. 30 villages had reports of bear attacks, totalling 80 incidents. All attacks were defensive in nature and none appeared to be deliberate. Humans and sloth bears in Panna NP avoided direct encounters and only a small proportion of encounters resulted in attacks. The majority of the attacks took place in escarpment or other dense vegetation cover habitats, in the crepuscular period of wet and cold seasons. The period of overlap in human and bear activity was longer in the wet and cold seasons, and in the evenings than mornings in all seasons. Most attacks happened during these periods of high overlap in habitat use or activity, and in those habitats of greater simultaneous use. Bears attacked primarily when the encounter was sudden, and this was probably a defensive response. It appears that the habitat conditions often made the encounters sudden and the behavioural response of bears during such encounters caused the attacks. The circumstances that lead to sudden encounters can be avoided and thereby the frequency of attacks can be reduced.

CHAPTER 1. INTRODUCTION TO THE STUDY

The sloth bear (*Melursus ursinus*) is a widely distributed large carnivore endemic to the Indian subcontinent. Out of the eight species of mostly omnivorous bears of the world, along with Giant Panda, sloth bear is remarkably specialized in its food habits. It has several morphological and physiological adaptations to a myrmecophagous (feeding on ants & termites) niche. It also appears to show a variety of behavioural adaptations to varying resource and environmental conditions across its distributional range. It lives largely as a solitary animal, occurs in low densities and has a low reproductive rate, perhaps due to the energetic constraints imposed by its habits. These characteristics may make the sloth bear vulnerable to various stochastic events, and to the large-scale human impact on its habitat. Its large size, wide distribution, peculiar habits, remarkable physical and behavioural adaptations and its likely vulnerability make it an interesting study subject for behavioural ecology research.

Sloth bear is found in India, Nepal, Bhutan, Sri Lanka, and possibly Bangladesh. In the past, it was found in most non-arid, low-altitude forest areas of the subcontinent, including Bangladesh. In India, about 90% of sloth bear population is probably found in the deciduous (moist and dry) forests (Yoganand *et al.* in press). Dry deciduous forest alone, which comprises only 30% of the remaining forest cover in India, probably holds about 50% of the bear population. Human disturbance is also greater in this type of forest. Conserving the dry deciduous forest is important for the long-term conservation of the species. However, for planning efficient conservation measures, information on the ecology and behaviour of sloth bear in this habitat type becomes essential.

Starting with the natural history observations of British sportsmen (Fletcher 1911, Dunbar-Brander 1923, Phythian-Adams 1950, Prater 1965) in the early part of last century, field observations and short-term studies have been made on sloth bear in various parts of its range. Schaller (1967) reported the feeding habits of sloth bear in the moist deciduous forests of Kanha National Park in central India. Eisenberg and Lockhart (1972) observed its behaviour in Wilpattu National Park in Sri Lanka. Johnsingh (1981) studied its food habits in the deciduous forests of Bandipur National Park in southern India. Gopal (1991) reported observations on its behaviour in Kanha National Park. Sloth bear food habits were studied by Baskaran *et al.* (1997) in the dry deciduous forests of Mudumalai Wildlife Sanctuary and by Gokula *et al.* (1995) in Mundanthurai Wildlife Sanctuary, both in southern India. Laurie and Seidensticker (1977) made detailed observations on sloth bears in Royal Chitwan National Park in Nepal, and in their classic paper speculated on the functional significance of various behavioural traits they observed. Sunquist (1982) was the first researcher to radio-tag a sloth bear and he studied its movement patterns for a year, again in Chitwan.

The first intensive study that was focused on this species was conducted in the highly productive terai grassland - moist deciduous forest habitat of Chitwan, Nepal (Joshi 1996). Chitwan holds a high density of sloth bears and has also been relatively free of human disturbance for the past several years. In contrast, much of forest area in the sloth bear range has been degraded by human use. For conserving sloth bears in these human-impacted habitats that hold a major proportion of sloth bear population, it is essential to gather information on the ecology and behaviour of sloth bears in these habitats. A study in a human impacted area might also lead to an objective assessment of how the various human activities affect bear behaviour.

In this background, Panna National Park, a partly human-degraded, dry deciduous forest area in central India was chosen to carry out this intensive study on the behavioural ecology of sloth bear. Field work for this study was conducted for five years, from February 1996 until November 2000. The results of this study are presented and discussed in this dissertation.

In general, the objectives of this study were:

- To study the key behavioural aspects of sloth bear: their daily and seasonal activity patterns, space use and habitat selection, foraging behaviour and food habits, and examine the ecological factors that influence these behaviours.
- To assess the habitat requirements of sloth bear.
- To assess the impact of degradation of habitat by humans on sloth bear space and habitat use.
- To study the conflicts between bears and humans and identify the behavioural and ecological factors that lead to such conflicts.

This dissertation is organised into 8 chapters. Chapter 2 gives a brief account of biology and conservation of the sloth bear. It summarises various aspects such as the evolutionary history of the sloth bear, physical adaptations, distribution and status in India, and issues facing its conservation. Chapter 3 presents a description of the physical features, vegetation types, plant phenology cycle, animal diversity, conservation history and threats to the study area, Panna National Park. Chapter 4 describes the methods that are common to many chapters of this dissertation and the ones not described in other chapters.

The Chapters 5 to 8 are the main sections of this dissertation and they deal with the key behavioural aspects of sloth bears in Panna NP. In Chapter 5, I describe the daily activity patterns of sloth bears and present an assessment of the ecological influences that underlie the patterns. Detailed accounts of bear activity, thermal characteristics of various microhabitats used by bears, and a comprehensive assessment of the relationships bear activity had with influencing factors are presented. Chapter 6 deals with space use and habitat selection by radio-collared bears. Estimates of home range sizes, maps of range locations, and the changes in habitat use by the bears are presented in that chapter. Further, I present an evaluation of habitat quality for the bears and the impact of degradation of habitat by humans on habitat quality. Sloth bear food habits and foraging behaviour are described in Chapter 7. In Chapter 8, I describe the study on sloth bear conflict with humans and the assessment of the behavioural and ecological factors that lead to conflict.

CHAPTER 2. A BRIEF DESCRIPTION OF BIOLOGY AND CONSERVATION OF THE SLOTH BEAR

The sloth bear is entirely tropical and sub-tropical in distribution, endemic to the Indian subcontinent, perhaps evolved within its limits, and possesses several morphological, physiological and behavioural adaptations to the tropical habitat and the myrmecophagus (feeding on ants and termites) niche it relies on (Plate 1). It is widely distributed in India, where large patches of tropical forests still exist. However, its range has shrunk in recent times and the populations have become fragmented, threatening its overall survival. Active management of the existing populations and their degrading habitat is necessary for the long-term conservation of this species.

Taxonomy and Evolutionary History

The first description of the sloth bear was given by Shaw (Shaw and Nodder 1791) who named it *Bradypus ursinus* or a bear-like sloth. This species was initially assumed to be a sloth because of the shared characteristics with sloths – long claws and the absence of upper middle incisors (Erdbrink 1953). Meyer (1793, cited in Erdbrink 1953) was the first to recognise this animal as a bear and not a sloth, and gave it an appropriate name *Melursus lybius*. De Blainville (1817) gave it the name *Ursus labiatus*, identifying the animal as belonging to the genus *Ursus*.

Waits *et al.* (1999) examined the phylogenetic relationships of the bears using mitochondrial DNA analyses and attempted to resolve outstanding ambiguities. They concurred with earlier studies (Zhang and Ryder 1993, Talbot and Shields 1996) that the sloth bear is a basal ursine bear and a sister taxon to the later five species of bears (excluding the giant panda and the Andean (spectacled) bear that diverged much earlier). The genetic and morphological differentiation of the sloth bear therefore supports the separate placement in the genus *Melursus* (Wozencraft 1989, Corbet and Hill 1991, Waits *et al.* 1999). Pocock (1933) distinguished two races: *Melursus ursinus ursinus,* occurring in continental India and, *Melursus ursinus* *inornatus*, found only in Sri Lanka. The Sri Lankan race appears less shaggy and is smaller in general dimensions (Erdbrink 1953).

The sloth bear probably existed in its present form from the beginning of the Pleistocene Epoch (Erdbrink 1953), a period when the bears speciated and dispersed (Kurten 1968, Talbot and Shields 1996). It probably radiated from the ancestral stalk of Ursids during the mid-Pliocene (Erdbrink 1953, Kurten 1968, Goldman *et al.* 1989, Talbot and Shields 1996), and evolved within the subtropical region, developing several morphological characteristics suited to its habitat and feeding niche. Talbot and Shields (1996) inferred that the greater morphological divergence of sloth bear was likely to be due to recent adaptive change and not accompanied by molecular evolution.

Physical Description and Adaptations

Sloth bears are typically black, with a V- or U-shaped, whitish or buff coloured breast patch, although lacking in rare cases (Pocock 1933). The long, pale muzzle is sparsely covered with thin, short, greyish white hair. The forehead region and sides of the head are covered with short black hair and the neck region possesses dense, long hair. The rest of the body is covered with long coarse hair, perhaps variable in colour, texture and length according to season (Pocock 1933), and it lacks underfur. They stand 65-85 cm at shoulder and are 140-170 cm from nose to tail. Adult males weigh between 80 and 150 kg, are larger than adult females, which weigh between 60 and 100 kg (Prater 1965, Garshelis *et al.* 1999, this study).

Sloth bears exhibit several adaptations to their sub-tropical and tropical habitat and to their diet. To suit the tropics, it has no underfur; however, it has a long coat that perhaps helps in defending it from insect bites and also perhaps to exaggerate its size to predators (such as tiger and leopard) or conspecifics. Compared to other bear species, the lips and tongue are exceptionally protrusible, which helps in feeding on social insects like ants and termites. Sloth bears possess the same number of teeth as other bears. However, they lose the first two upper incisors at an early stage, which is a characteristic feature of this species (Erdbrink 1953). The front claws of sloth bears are long (up to 7 cm) and curved, an adaptation for digging. The claws on the hind leg are much shorter. The short hind legs of the sloth bear are suggestive of an adaptation for digging (Harris and Steudel 1997). The soles on the feet are naked. The sloth bear's low metabolic rate and high thermal conductance (McNab 1992) may be advantageous in the hot climates where it lives, in that they reduce heat production and facilitate heat loss. Although the sloth bear has diverged towards a diet comprising a lot of social insects, it has retained the ability to use a variety of foods, in conformation with its omnivorous ancestry.

Behaviour and Ecology

Sloth bears are solitary, but territoriality has not been observed (Laurie and Seidensticker 1977, Joshi *et al.* 1999, this study). They have stable home ranges and their home range sizes vary among populations, probably influenced by variability in resource abundance among habitats (Joshi *et al.* 1995, this study). The diet of sloth bears consists mostly of social insects and fruits. Mating generally takes place between May and July and the cubs are born between November and January (Jacobi 1975, Laurie and Seidensticker 1977, Joshi *et al.* 1999, this study). Cubs are born in secure dens (either natural caves or dens dug by the mother bears). A litter size of two is most common (Laurie and Seidensticker 1977, Joshi *et al.* 1999, this study). Cubs are frequently carried on their mothers' backs from the time they leave the den until they are about six months of age (Laurie and Seidensticker 1977, Joshi *et al.* 1999). Carrying cubs by the mother seems to be a defence against attacks by predators or other bears. Cubs stay with their mothers for 1.5 to 2.5 years, becoming independent just before the breeding season (Joshi *et al*. 1999). Thus, females breed at either two- or three-year intervals. Predation has been surmised to be responsible for several behavioural traits of the sloth bear. Tigers attack and kill sloth bears occasionally (Joshi *et al.* 1999, *personal observations*), however encounters between them are fairly common (unpublished data). Leopards, dholes, and even jackals could be threats to sloth bear cubs. Sloth bears do not climb trees as a means of escape or in response to disturbance. Sloth bears probably perceive humans similar to predators. At close quarters they reacted to human presence, as they would to a predator (Laurie and Seidensticker 1977, this study).

Distribution and Population Status

The sloth bear is endemic to the Indian subcontinent and is found in India, Nepal, Bhutan, and Sri Lanka (and perhaps in a few areas in Bangladesh). It is widely distributed in India, it occurs in most low-altitude, non-arid areas where forest cover still remains. In India, sloth bear ranges from the southern tip of the Western Ghats mountain ranges to the foothills of the Himalayas. Its western distribution is limited by the desert regions of Rajasthan. To the east, its range is bounded by the wet forests of the north-eastern India. The forests of the Western Ghats mountain range and central India are currently its strongholds of distribution, in terms of population abundance and habitat availability (Yoganand *et al.* in press). The sloth bear is found in a variety of habitats ranging from wet evergreen forests, to dry deciduous and degraded scrub forests. However, their abundance varies in the different habitats, probably depending on resource availability.

Reliable data on its abundance and other population parameters that are essential to determine its exact status are not yet available. Yoganand *et al.* (in press) mapped its distribution, assessed threats to its habitat and estimated population size for India, by carrying out a questionnaire based survey. They estimated that secure habitat of high quality for sloth bears is only about 10% of forest area in India and population size for all of India to be between 6,000 and 11,000. Its populations have declined and its range has shrunk over the past century, primarily due to habitat loss. Although it appears to be secure in some parts of its range, overall, the sloth bear is threatened. The sloth bear has been listed as “Vulnerable” by the IUCN red lists (IUCN 1996, 2004 Global Mammal Assessment, IUCN/SSC Bear Specialist Group, *personal communication*), listed under Appendix I of CITES (all trade and export are banned), and is protected under Schedule I of the Indian Wildlife (Protection) Act of 1972.

Conservation Issues

Habitat loss, degradation and fragmentation are some primary issues affecting the continued existence of sloth bear, all across its range (Garshelis *et al.* 1999). Inadequate coverage of sloth bear habitats in India as protected reserves is another important concern (Yoganand *et al.* in press). Degradation and loss of forest habitats, especially outside protected areas, pose a major threat to sloth bear populations, and most populations occurring outside protected areas are probably declining. Degradation, in the form of overgrazing, tree-felling, fire, conversion and reclamation for other uses, and over-extraction of forest resources that are essential for sloth bear survival, appear to be occurring throughout the sloth bear range, particularly in the dry forests (Yoganand *et al.* in press). Forest patches are getting fragmented and connections between patches are getting lost, and this may lead to isolated, non-viable bear populations.

Garshelis *et al.* (1999) reported that sloth bear populations in India appear to be significantly threatened by poaching for trade in body parts, particularly gall bladders. Poaching has reportedly caused a decline of sloth bear populations in western central India, terai areas, eastern and north-eastern India (Yoganand *et al.* in press). Capture of cubs from the wild to be reared and used as performing bears also poses a significant threat to bear populations (Santiapillai and Santiapillai 1990, Seshamani G. and Satyanarayan K., World Society for Protection of Animals, *personal communications*). Conflict occurs wherever bears and humans co-exist, in the form of crop depredation by bears, extraction of forest resources by humans, degradation of forest habitats by other human activities, and encounters between bears and humans, which sometimes leads to serious injuries to humans and bears. Sustained or severe conflict situations puts the concerned bear populations under threat from human persecution, or management actions that may include removal of such populations. Lastly, inadequate documentation of distribution and population status of the sloth bear is a problem that has major implications for planning its range-wide conservation.

Plate 1. The sloth bear possesses many physical, physiological and behavioural adaptations to its tropical habitat and a myrmecophagous (feeding on ants and termites) niche. The long, almost naked muzzle, long claws on forelegs, low metabolic rate, and nocturnal habits are some such adaptations. The sloth Bear is widely distributed in India, where large patches of tropical forest habitats still exist. But its populations have declined and its range has shrunk over the past century, primarily due to habitat loss.

CHAPTER 3. STUDY AREA DESCRIPTION

Location

Panna National Park (NP) is located between 24°27’ to 24°46’ North and 79°45’ to 80°08’ East, in the northern part of the state of Madhya Pradesh in central India (Fig. 3.1). It covers a 543 km^2 expanse of dry deciduous forests of the Vindhyan tracts, which are some of the last remaining relatively intact forests in the northern part of the peninsular India.

Topography

Panna NP is characterised by vast plateaus separated by steep escarpments. The elevation ranges from 200 m at the level of Ken River in the North, to about 550 m on hilltops in the southern parts. About half of the Park is comprised of two flat plateaus at different elevation levels, bordered by steep escarpments, which together form a step-like topography. This has made the area friendly for conducting ground-based radio tracking study. I selected these two plateaus as my primary study area (where I trapped for bears), which covers an area of about 250 km^2. The relatively flat terrain resulted in lower habitat heterogeneity in the study area, and allowed me to compare the space and habitat use among radio-tagged bears, with smaller number of variables influencing them.

The Park contains numerous caves and crevices along its long rocky escarpments, which provide excellent shelters for sloth bears and other animals. Ken River is a perennial source of water and has its catchment area in the Park. The soil types of Panna NP belong to the Vindhyan formations and are shallow, with low humus and water holding capacity. The underlying red sandstone, shale rocks and red ferruginous soil, along with climatic factors dictate the types of vegetation the area supports.

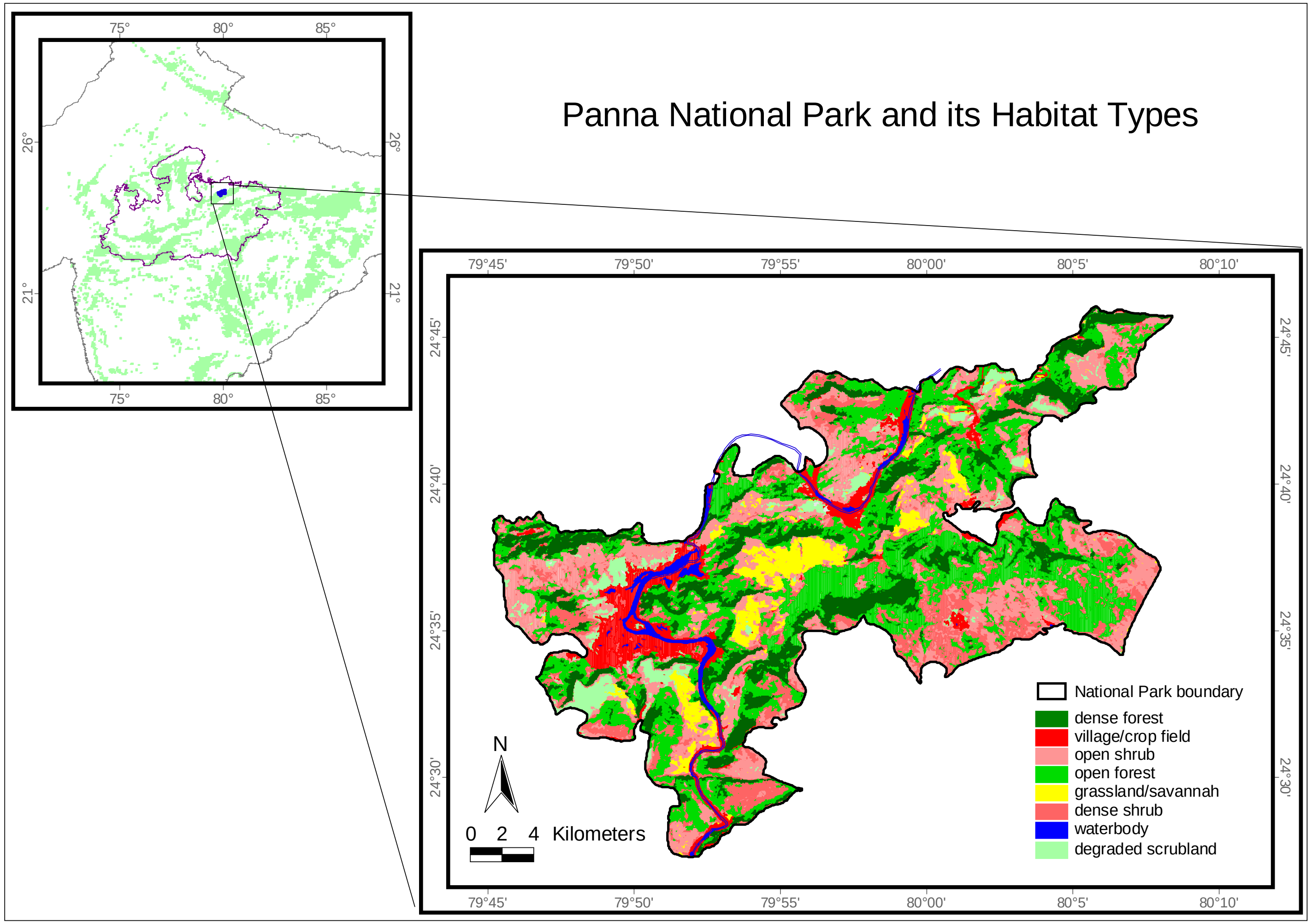


Fig. 3.1. Location of Panna National Park (Madhya Pradesh State, central India) shown with distribution of forest cover (light green patches) in central India (left top). Extent of Panna National Park and the distribution of various habitat types that were identified in the field and mapped using satellite imageries (right).

Climate

Panna NP receives a mean annual rainfall of about 100 cm, most of it from the southwest monsoon during July to September. It faces a dry and hot period (mean daily temperature ranging from 30^{o}C to 40^{o}C) between March and June and a cold period (temperature ranging from 15^{o}C to 25^{o}C) between December and February.

Vegetation types

The vegetation types of Panna NP can be broadly classified into dense (closed canopy & high tree density) forests, which occur mostly along the escarpments, stream courses and some less-disturbed patches; the most common open forests with grass and shrub under-storey; short-grass/open savannah habitat occurring on shallow, drained plateaus; tall grasslands that grow in relocated village sites; dense shrub habitat dominated by *Lantana camara* shrub patches, open shrub habitat with sparse patches of *L. camara* and open areas, and degraded scrub vegetation, the latter types occur mostly in the southern parts of the study area, the peripheries of the Park, and around villages (Fig. 3.1).

The main tree species found there are *Tectona grandis* (teak), *Terminalia tomentosa*, *T. arjuna*, *Diospyros melanoxylon, Madhuca longifolia*, *Buchanania lanzan*, *Anogeissus pendula, A. latifolia, Lannea coromandalica, Boswellia serrata, Acacia catechu, Cassia fistula, Laegestromia parviflora, Aegle marmelos, Sterculia urens, Flacourtia indica, Limonia acidissima, Gardenia latifolia, Manilkara hexandra, Ficus spp., Phyllanthus emblica, Schleichera oleosa, Butea monosperma, Zizyphus xylopyros,* and *Z. mauritiana*. Common shrub and straggler species are *L. camara*, *Zizyphus* spp., *Carissa opaca, Helicteres isora*, and *Acacia* sp.. The area is considered to have originally had *T. tomentosa* and *A. latifolia* dominated forest, and was later transformed to a teak-dominated forest due to forestry operations of the past century.

Plant phenology cycle

After the first spell of monsoon rains, by end of June, the ground started to get clothed with new flush of grass and herbs, and in the degraded parts of the Park, with weeds. The plants that have not already started wearing new flush of leaves, in anticipation of rain, would start the cycle of leafing. July is the time when all of vegetation and ground layers look green and wet, after a long spell of dry season. For sloth bears, *C. fistula* would have ripe fruits that still remain on trees or have fallen to the ground. It also would have unripe fruits, as would the *D. melanoxylon* trees that would become ripe and available for bears the next dry season. Grass would grow taller and other vegetation denser with the progress of the wet season (Plate 2a). By mid-August, *Z. mauritiana, Z. oenoplia*, and *L. camara* would be in flower. By end of August, *L. camara* would be laden with unripe fruits, and some plants would even have ripened fruits. *A. marmelos* trees would have small unripe fruits that would grow and ripen the next March. The commonest trees in the forests, teak, would begin flowering and their crowns turn cream in colour with bunches of flowers. By September, grasses would flower and most *L. camara* plants would have ripe fruits.

With the start of the cold season, in November, *Z. mauritiana*, and *Z. oenoplia* fruits would begin ripening. *L. camara* would continue to have fruits. By end of January, *Zizyphus* spp. fruiting would get over and the ripe fruits that remain on plants would start drying up. *L. camara* fruits too would have dried up and it would start shedding its leaves. Leaves of many other plants, including teak, would begin to fall, grasses would have seeded and would start to wither, and the forests would start to open up, as if in preparation for the upcoming dry season.

With the onset of the dry season, by end of March, leaves of most plants would have fallen, and some plants, such as *P. emblica* and *F. indica*, would start the next leaf cycle with new flush of leaves. But the forests, on the whole, would remain bare and dry (Plate 2b). *M. longifolia*, the Mohwa tree, would flower and their fleshy petals fall to feed sloth bears and scores of other animals. *A. marmelos* and *C. fistula* fruits would start to ripen. Teak trees at the canopy level and Lantana at shrub level would be bare with their leaves and fruits having had fallen off. During May, the peak of the hot and dry season, main food plants of sloth bears, *D. melanoxylon, B. lanzan, A. marmelos*, and *C. fistula* would have ripe fruits available for bears to feed. By end of May, many plants, including *D. melanoxylon, B. lanzan, A. marmelos*, would start growing new set of leaves, while many others remain bare. By end of June, just as the monsoon rains start arriving, most plants, including teak would have new leaves, while the shrub level plants, *L. camara, Zizyphus* spp., would remain bare until the rains really pick up in July. With the arrival of monsoon rains that brings life to this dry forest, the plants would start cycling all over again.

Animal diversity

Several species of large carnivores occur in Panna NP, which include tiger, leopard, striped hyena, wolf, dhole, golden jackal and ratel. Some of these are potential predators on sloth bears. The ungulates that occur here are chital, sambar, Indian gazelle, four-horned antelope, wild boar, and nilgai. Several species of small mammals, including Indian fox, jungle cat, rusty spotted cat, ruddy mongoose, grey mongoose, small Indian civet, common palm civet, Indian pangolin, Indian hare, Elliott’s tree shrew, Indian porcupine, and many species of rodents and bats, occur in the Park. Over 230 species of birds, many species of reptiles, amphibians, and fishes have been recorded in the Park.

Conservation history

Panna NP was declared as a National Park in 1981 and was subsequently made a Tiger Reserve in 1994. Some parts of forests of this area and some adjoining protected forests in Chattarpur district were hunting preserves of the erstwhile royalty of Panna, Chattarpur and Bijawar, and thus were protected partially from human degradation for many decades. However, forestry operations have also been carried out for many decades, before the area was declared as a National Park. Although the area has been declared a National Park, the final notification to that effect is pending, because many villages enclaved in the Park are yet to be relocated, and rights of people who have been living in and using these forests are yet to be settled.

Conservation threats

Panna NP has fifteen villages located inside its boundary and several others on the periphery. Human presence and use is high in certain portions of the Park. The sustenance of most people of these villages is dependent on using the resources of the Park. These villages have a high cattle population, and they exert a severe grazing pressure on the Park. Overgrazing has lead to degradation of a considerable portion of the Park, and perhaps has also led to invasion of weeds. Additionally, the collection of non-timber forest products (NTFP) and livestock grazing inside the Park leads to an increased human presence in forests, and thus the chances of human-animal conflicts. Wild animals depredating crops and killing livestock also leads to a serious conflict. Unless these conflicts are managed effectively, it could pose an increasingly serious problem for the Park in the future. Although not reliably quantified, a considerable amount of poaching probably occurs in the peripheral areas and in the western parts of the Park. Overgrazing, suppressed regeneration, tree felling, ground fire and over-extraction of forest products are some factors causing significant habitat degradation.

Inadequate field-level staff for the Park, a generally low level of motivation of Park staff, an apparent shifted focus of Park management towards tourism management, and the consequent diversion of crucial Park resources that are needed for protection and habitat management for tourism activities are serious issues that concern the Park management. Lack of a buffer belt of forest land around the Park, which could absorb some of the impacts directed at the Park itself, is a critical concern. Lastly, inadequacy of the Park management plan, and flawed or arbitrary implementation of the plan pose serious concerns.

Plate 2a. Forests of Panna NP in wet season. Rains were frequent, streams flowed, yet sun was strong. Plants regenerated, vegetation grew dense, and insects became abundant and accessible for sloth bears to forage on them.

Plate 2b. Forests of Panna NP in dry season. Sun scorched, water became limited to a handful of springs and River Ken. Most plants shed leaves, and many key food-plants produced fruits in plenty, and thus provided sloth bears.

CHAPTER 4. GENERAL METHODS

A brief account of the methods that I followed in this study, particularly the ones that are common to many chapters of this dissertation and the ones not described in other chapters, is given here. Methods that require detailed descriptions are given in the respective chapters.

Capture and Radio-tagging of bears

I captured sloth bears using spring-activated foot snares and barrel traps (Plate 3a, b). The traps were baited mainly with honey, although I tried various other baits such as molasses, mohwa flowers, etc. during the first year of trapping. I conducted trapping during the dry season months of March to May and cold season months of November to January. Radio transmitters were attached to both types of traps and the transmitters were set up to send signals once the traps were triggered. This aided me to attend to traps as soon as they were triggered. The captured bears were immobilised with either of the drug mixtures (Ketamine HCl – Xylazine HCl or Tiletamine HCl – Zolazepam HCl), delivered remotely with an air-powered pistol (Telinject, GmbH, Germany). While the bears were in immobilised state, physical measurements were taken, and body condition was monitored by measuring rectal temperature, pulse, and respiration rates at frequent intervals. The bears were fitted with VHF radio transmitters mounted on urethane collars. After fitting the radio collars, the bears were either given an antidote drug (Yohimbine HCl in the case of Ketamine-Xylazine) to revive them, or were let to revive on their own while I monitored them. The choice of drug and the decision to use a reversal drug were made depending on ambient temperature and trap-site habitat conditions. 12 sloth bears were fitted with radio-collars between March 1996 and May 1999 (Plate 4a).

Radio tracking

The transmitters (Mod-450; Telonics Inc., Mesa, Arizona, U.S.A.) that I used sent out radio pulses in the frequency range of 150 – 151 MHz. Each transmitter had a unique frequency, which enabled me to identify individual animals. I used portable radio receivers and handheld 2- or 3-element “Yagi” antennas to receive the signals and to find the direction of signal (by maximum gain method; Plate 4b). The transmission units had a pulse interval modulation system, which varied the pulse interval depending on head movement and hence enabled me to detect motion and judge whether the bears were active or resting. The signals switched between a pulse interval of 800 msec when active, and 1200 msec when inactive (75 or 50 pulses per minute, respectively).

Direct observations

The radio-collared bears, and occasionally untagged bears, were homed-in to make direct observations (Plate 5a). These were mostly done during evenings and mornings, and less frequently in the nights. Once a bear was sighted, observations were made for as long as possible, which ranged from a few minutes to a few hours. For each observation, information on the type of habitat the bear was found, geographical location (coordinates obtained from GPS units), time, activity, food item eaten, etc. were recorded. If a bear was feeding, then the substrate from where the food item was consumed (e.g., fruits on trees, fallen on the ground, ants on trail, under rocks, etc.) was recorded. I also identified the food items using binoculars or by closer examination after the bear moved away. Interactions with other bears, and other animals, reactions to animal and human sounds, reactions to the presence of observers when detected by the bear, were also recorded.

Habitat classification

Habitat map of the study area was classified from satellite imageries (Indian Remote Sensing Satellite - 1C, LISS 3, spatial resolution 23.5*23.5 m) acquired during Oct/Nov 1996. The images were geo-corrected, geo-referenced and processed using ERDAS Imagine v8.2 software. A supervised classification was done using field-collected data on habitat characteristics. The habitat types were identified based primarily on structure of vegetation communities (canopy cover, tree and under-storey density). A map comprised of nine habitat types: dense forest, open forest, short-grassland / open-savannah, dense shrub, open shrub, degraded scrubland, barren land, village/crop field, and water body, was prepared. Habitat patches of <1 ha area were smoothed out during image processing to increase habitat homogeneity.

Habitat quality mapping

I evaluated the habitat quality of the study area (composite of 99% adaptive kernel home ranges of all radio tagged bears, ca. 240 km^2) with regard to sloth bear resource requirements. I sampled at all the intersections of even numbered UTM co-ordinate grid (2-km spacing) that fell within or adjoining the boundaries of the study area. Forty-eight such locations were sampled for various habitat parameters, food plant densities, and abundance of social insect colonies. Sampling locations were located in the field with the help of a GPS unit. Habitat parameters such as grass, shrub, canopy cover, litter, humus, dead wood, rock availability in the area were estimated visually and classified on an ordinal scale. Indicators of human disturbances such as livestock grazing, grass collection, tree felling, fire occurrences, and physical presence and usage by humans were also ranked. Macro-habitat parameters such as proximity to villages, water sources, and escarpment areas were measured from topographic maps.

Food plant abundance

Food plant densities and size classes were measured in 50m X 50m (0.25 ha plots) in each of the sampling locations. Keeping the location co-ordinate as the origin of the plot, plots were marked out using a compass and a hip-chain. Numbers of plant species (trees & shrubs) that were consumed by sloth bears in Panna, along with other potential food plant species were measured in the plots. Tree (food plant) species were classified as large, medium and small, based on the girth at breast height (gbh) and canopy spread, and the number of trees of each species was counted. Saplings (gbh <20 cm) were counted separately. Shrub (food plant) species were also classified as large, medium and small size classes depending on the crown spread. Teak and all other non-food species of trees in the plots were grouped together and counted.

Food plant phenology

Phenology of sloth bear food plants was monitored along trails at fortnightly intervals. Ten phenology trails of lengths ranging from 500 m to 2 km were laid, covering at least three different patches for each food plant species, to represent spatial variation within the study area. Also, the trails were spread out widely to represent the whole study area. All the individual plants of all food plant species were marked along the trails. Total number of individuals monitored varied between species, depending on the abundance of a species, but ranged from 50 to 200 individuals for each species. The phenophase of a plant, number of plants that had fruits, ripening stage of fruits, fruit-crop size (grouped into abundance classes – 0-25%, 25-50%, 50-75%, 75-100% fruiting) and plant size-class (large, medium and small based on gbh and canopy spread) of each marked plant was recorded. An estimate of mean fruit-crop sizes was made for samples of plants (10 or more) for each combination of plant size-class and fruit abundance-class. These fruit-crop size estimates were used as calibration values to estimate total fruit biomass.

Fruit biomass estimation

Fruits of the various food plant species were weighed to obtain fresh and dry weights. Using the food plant densities, proportion of plants that fruited in a sampling period, proportion of plants in each of the fruit-abundance classes, the fruit-crop size estimates, and fruit weights, the total biomass of fruits that was produced in the study area in a year (1999-2000) was calculated. Further, for each species, the ingestible pulp biomass was estimated after removing seeds, fruit rind and other indigestible fragments. The fruit biomass values were converted into ingestible pulp biomass for each species of food plant.

Social insect abundance

Social insect (ant, termite, and honeybee) colony abundance was estimated in 50m X 2m (100 m^2) plots, placed in each of the sampling locations, where other habitat variables and food plant abundance were sampled. Social insect sampling was conducted during the wet season, on sunny days, when the ants and termites were most active excavating nests, caring for brood, etc.

In the plots, an “all-out search” method was used to count social insect colonies. The micro-habitats where insect colonies were likely to be found and which were accessible for sloth bears, such as among leaf litter, under rocks, around root regions of plants, inside dead logs, inside tree hollows, among under-storey foliage, and around visible holes in the ground were searched intensively to locate colonies. Once located, the taxa (up to species level for most ants, and genus level for termites), colony size, brood presence, brood size, life stage, and other colony characteristics were recorded. Since honeybee colonies and termite mounds were rare in the sampled locations, they were also enumerated in larger, 50m X 50m plots. Specimens of insects were collected for identification, weighing and calorimetric analyses. However, by this all-out search method, the entirely subterranean ants like *Dorylus labiatus*, *Aenictus* spp., and non-mound-living subterranean termites could not be sampled adequately.

Insect biomass estimation

To estimate colony sizes of prey species and other common species of social insects, samples of colonies of each species were excavated and enumerated (Plate 5b). The various castes and life-stages of social insects and their numbers were counted. Abundance of termite alates was assumed for each colony. The colonies were categorised into relative size-classes, large, medium, small, and founder colonies, and the mean adult and brood numbers in each size-class for each species was determined. Adults and brood of insects were weighed (fresh and dry weight). Whole insect remains of different species were extracted from sloth bear scats and weighed. Pupal shells of various *Formicinae* and *Ponerinae* (sub-family) members were also weighed.

Using the colony densities of various species, proportions of colonies in each of the colony size-classes, mean colony size for each size-class and insect weights, the biomass of social insects were calculated. Further, using the proportion of ingestible mass (to chitinous and other indigestible parts) in an individual insect adult and brood of each species (estimated by taking the difference in weights of insects collected from nests and the ones from scats), total ingestible biomass available for consumption was estimated. This estimate was made for the monsoon season of the year 2000. Colony densities and sizes might vary over seasons and from year to year. Considering the enormous effort involved if I were to study this temporal variation, social insect sampling was restricted to one season. I made an estimate for a season, when social insects were available at their highest densities and when they contributed most to sloth bear diet.

Definitions of certain key terms used in this study

Seasons

Dry – months from March to June. It was the hot and dry period in Panna. There was little rainfall during that period and water availability was restricted to some perennial springs, a reservoir and the Ken River. Most trees remained leafless during a major part of that season and it was the main fruiting period for most plant species. There were frequent forest fires and a high presence and usage of humans and cattle in the forest.

Wet – months from July to October. It was the wet period, when most rainfall was received in Panna. A majority of days were either partly or fully cloudy. All the plants wore new flush of leaves and it was the period of regeneration of vegetative cover. Some plant species like *L. camara* fruited during that season. There was a high abundance of cattle, in the peripheral areas, grazing on fresh vegetation during that season.

Cold – months from November to February. It was the post-wet period and there were only occasional rains. Days were warm and nights cold with considerable dew formation. Most plants had leaves during the first half of that season and during the later half, most shed their leaves and the forests opened up. Some plants such as *Zizyphus* spp., fruited during that season. There was considerable cattle grazing pressure and associated human presence in the forest during that season.

Diet-based seasons. – In addition to climate-based seasons, I classified a year into diet-based seasons, so as to assess changes in various behavioural attributes in relation to changes in diet. I classified the months from April to July and November to December as ‘fruiting’ season, and months from January to March and August to October as ‘non-fruiting’ season.

Time of day

I classified a day into time periods in two different ways: 1) with two classes – day and night; 2) with three classes – day, night and crepuscular periods. In the 2-class scheme, ‘day’ starts from 45 minutes after sunrise time and ends at sunset time, and the reverse of it was considered as ‘night’ (coded using median sunrise and sunset times of each month). In the 3-class scheme, ‘day’ starts from 2 hrs 15 minutes after sunrise time and ends 2 hours 15 minutes before sunset time, i.e., 8:31 to 16:00 hrs for March. ‘Night’ period starts from 45 minutes after sunset time and ends 45 minutes before sunrise time, i.e., 19:01 to 5:30 hrs in March. The intervening period was considered as ‘crepuscular’ period.

Plate 3a. Bears were captured for radio-collaring in barrel traps baited with honey. Although these traps did not have a high success rate, they were very safe for the bears and for the researchers.

Plate 3b. Bears were also captured with spring-activated foot-snares. A careful planning and execution is required to use this capture method efficiently and safely.

Plate 4a. An immobilized bear being fitted a radio-collar in Panna NP. With the help of the radio transmitter the bear was located at any required time and observations were made. This enabled us to study bear behaviour and ecology systematically, and in detail. (Photo courtesy: Gary Koehler).

Plate 4b. Using mobile receivers and hand-held antennas, radio-tagged bears were tracked in Panna NP for many years. Radio signals were obtained from vantage points like this ledge, and were approached closer or their locations were estimated by method of triangulation. (Photo courtesy: Cliff Rice).

Plate 5a. Radio-tagged and untagged bears were observed from treetops and ledges, and by following them on foot at a distance, to record their food habits, social interactions, responses to humans, and other behaviour.

Plate 5b. Samples of termite mounds and ant nests were dug up in the sampling plots to estimate insect colony sizes and biomass. Using these and the estimates of colony densities, biomass of social insects available for sloth bears was estimated.

CHAPTER 5. SLOTH BEAR ACTIVITY PATTERNS AND UNDERLYING ECOLOGICAL INFLUENCES

5.1. INTRODUCTION

Animals perform various activities, primarily related to their survival and reproduction, for various lengths of time during their daily and seasonal cycles. The time they perform the activities, the factors that cause them and the survival value of the activities have significant physiological and ecological underpinnings. The patterns seen in timings of activity are largely a reflection of interactions between physiology and ecology of an animal. A study on this aspect of behavioural ecology that deals with describing the patterns in activity and examining their functional significance will have important conservation implications. For example, knowing an animal's peak activity time can be used to improve the chances of viewing the animal by visitors to wildlife reserves, or to restrict usage of its habitat by humans during those times and thereby reduce the chances of direct conflict between them.

There may be several physiological and ecological factors that influence the activity timings of animals. These include, the need to maintain body temperature, water balance, the need to accumulate energy reserves, other physiological constraints, food availability, predation risk, competition for food or mates, human-caused disturbances, and importantly, endogenous circadian rhythm linked to photoperiod. The factors that influence activity timings also influence the selection of habitats or microhabitats to perform the activities. The performance of an activity in a particular habitat may accentuate or moderate the effect of primary influencing factors. For example, the magnitude of cost for an animal to regulate its body temperature may depend on whether activity is performed in an open habitat or a shaded habitat.

The sloth bear exhibits several adaptations to its sub-tropical and tropical habitat. For example, to suit tropical thermal conditions, it has no underfur, has a long, sparse coat, and has naked soles. It has a large surface of nasal turbinates that may help reduce respiratory (evaporative) water loss (Schmidt-Nielsen *et al.* 1970, Schmidt-Nielsen 1972). The upper limit of its thermo-neutral zone is high (38.5 ^{o}C), or in other terms, has a higher thermal conductance (137%) than expected from mass, presumably to facilitate heat loss (McNab 1992). The sloth bear is large, aggressive in nature, possesses strong canine teeth and long claws on its forelegs that could be used for its defence. In addition, it has a large muscle mass. Dunbar-Brander (1923) called it immensely powerful for its size.

Early naturalist accounts of sloth bear reported it to be active primarily during the night and resting during the day (Dunbar-Brander 1923, Prater 1965). However, these authors also observed that the bears were active at day time, particularly in cool weather or in places remote from human interference. In Chitwan National Park, Nepal, sloth bears were found to be active at all times of the day, however, the main period of activity was during the evening and night (Laurie and Seidensticker 1977, Sunquist 1982, Joshi *et al.* 1999). In addition, Joshi *et al.* (1999) observed that sub-adult bears and females with dependant young generally limited their activity to day and rested at night. Chauhan *et al.* (2004) reported that the sloth bears in a degraded forest area in eastern central India were nocturnal and crepuscular. In general, the sloth bear seems to be mainly nocturnal in many parts of its range, but with variability supposedly related to weather conditions, human disturbance and social factors. However, systematic data on activity patterns is generally lacking, and most data hitherto available are biased by predominantly day time observations, and relatively few night time observations.

Joshi *et al.* (1999) did not assess the possible causes or benefits of timings of activity observed in the sloth bears they studied, but proposed that the subadult bears and females with cubs were diurnal to temporally avoid older bears or predators, which were assumed to be nocturnal. However, from the data the authors present, adult bears seemed to be active substantially at all times of day, except in the early afternoons (which they mention as probably due to high ambient temperature). Also, only a few observations were made on night activities of subadult bears or females with cubs. Similarly, Chauhan *et al.* (2004) simply assumed that the bears they studied were nocturnal because of human disturbance in the day, and did not assess other possible influences on diel (both day and night) activity. Although the factors proposed by these studies possibly influence activity, considering the results of studies conducted on other species of bears elsewhere (see below), comprehensive assessments of factors influencing activity were lacking in either study. Notably, the early naturalists (Dunbar-Brander 1923, Prater 1965) hypothesised, although simplistically, that the fundamentally constraining weather factors were major causes of changes in sloth bear activity timings.

The well-studied, temperates-distributed American black bear (*Ursus americanus,* distributed in North America) and brown bear (*U. arctos,* distributed in holarctic region) are known to be primarily diurnal and crepuscular (Amstrup and Beecham 1976, Garshelis and Pelton 1980, Lariviere *et al.* 1994, Craighead *et al.* 1995, Machutchon *et al.* 1997, White *et al.* 1998, Gende *et al.* 2001, Beckmann and Berger 2003), but some populations or some individuals in populations were also more nocturnal than diurnal (Craighead and Craighead 1965, Clevenger *et al.* 1990, Holm *et al.* 1999, Kaczensky *et al.* 2001, Klinka and Reimchen 2002, Beckmann and Berger 2003). Also, some populations showed increased nocturnal activity in some seasons while being mainly diurnal in others (Amstrup and Beecham 1976, Garshelis and Pelton 1980). In general, these bears seem to have been adapted for diel activity. The factors that were considered to affect activity patterns in these bears are: breeding season (Amstrup and Beecham 1976, Garshelis and Pelton 1980), availability of nutritious food (Garshelis and Pelton 1980), need for accumulation of energy reserves (Amstrup and Beecham 1976, Garshelis and Pelton 1980), vision limitations on food acquisition (Garshelis and Pelton 1980), temperature (Garshelis and Pelton 1980), human activity (Ayres *et al.* 1986), anthropogenic food combined with human activity (Beckmann and Berger 2003), predation risk (Aune 1994), prey (salmon) capture efficiency (Klinka and Reimchen 2002), prey activity (White *et al.* 1998, 1999), and intra-specific aggression and risk of infanticide

(Egbert and Stokes 1976, Klinka and Reimchen 2002). Kaczensky *et al.* (2001) reported that the activity patterns changed with age of bears, with younger bears being highly active during day, and the older adults being more nocturnal and that was probably because the bears learned to avoid humans as they grew.

Activity patterns of sloth bear and the factors that influence the patterns have not been studied in detail to date. Joshi *et al.* (1999) and Chauhan *et al.* (2004) addressed this aspect briefly, but were superficial in both describing the patterns and assessing the influences. It appears that the sloth bear is primarily nocturnal in many parts of its range. Anecdotal reports and preliminary observations indicated that they were mainly nocturnal in Panna NP too. There could be several possible factors influencing such a pattern and I attempt to examine some of them in this study. Additionally, sloth bears are widely believed to rest commonly in caves and crevices on hillocks during daytime. Patterns in usage of such resting sites and the factors that may influence the selection of sites are little known. There have been studies on selection of sites for winter denning in temperate bears (Craighead and Craighead 1972, Judd *et al.* 1986, Groff *et al.* 1998, Linnell *et al.* 2000, Martorello and Pelton 2003), however, in surveying the literature, I am yet to come across studies on usage of sites for resting during daily activity cycles of bears. In this study, I describe the patterns in usage of microhabitats for day-resting by sloth bears in Panna NP and assess the factors that may influence the patterns.

Bunnel and Harestad (1989) summarised that the daily activity pattern of an animal is influenced by three major factors: energy requirements (and consequent energy acquisition and processing), predators and thermal stress. Endothermic mammals maintain relatively high and stable body temperature, irrespective of variation in environmental temperature (Crompton *et al.* 1978, McNab 1978). This temperature maintenance facilitates physiological and biochemical functions of the body, enables high activity rates, ensures ability to respond readily to external stimuli, and consequently allows animals to be active for longer periods and over a wider range of habitats (Bartholomew

1977, Heinrich 1977, Crompton *et al.* 1978, Schmidt-Nielsen 1990, Robbins 1993).

In hot environments, ambient temperatures are often higher than body temperatures of mammals. Under such conditions, animals will be heat sinks, and will passively gain heat from the environment. Reducing or stopping activity will minimize metabolic heat gain. The avenues of heat loss are evaporative cooling, or moving to an environment where ambient temperatures are lower than body temperatures. In such environments, heat can be lost by conduction, convection, and evaporative cooling. By these means, the animals should decrease heat gain and increase heat loss from their bodies to maintain body temperature. Animals do this by both physiological and behavioural means (Schmidt-Nielsen 1990, Robbins 1993, Tracy and Walsberg 2000, 2002). Heat gain could be decreased by reducing metabolic heat production and by preventing heat gain from the surroundings, primarily by avoiding solar radiation and hot winds. When an animal is in rest, its metabolic heat production is up to 10 times lower than when it is active (Bennett and Ruben 1979, Schmidt-Nielsen 1990). Therefore, by avoiding being active during hot periods, and by selecting appropriate microhabitat to rest, animals can greatly reduce heat gain. At high temperatures, evaporation is the key means of heat loss (Schmidt-Nielsen 1990, Robbins 1993, Wolf and Walsberg 1996, Walsberg 2000), and this puts a demand on water requirement for an animal. Water availability may be a constraint in dry forest habitats such as Panna NP, and therefore, evaporative heat loss cannot be relied upon entirely. I hypothesized that sloth bears in Panna NP would reduce activity during the day to avoid heat stress conditions. Additionally, they would select microhabitats with low heat gain and high heat loss possibilities to rest during the day, particularly during seasons of high thermal stress.

Tigers attack and kill sloth bears only occasionally (Laurie and Seidensticker 1977, Joshi *et al.* 1999 and the references therein), however encounters between them are fairly common (unpublished data). For sloth bears, avoiding being active in the times when tigers are active may provide the benefit of decreased encounters with them and thereby decreased predation or risk of predation, and this might translate to an increased investment of their time and energy for survival and reproduction. I examined if sloth bear activity timings were related to tiger activity in Panna NP. Human disturbance is probably perceived by sloth bears similar to predation risk. The human disturbance stimuli, similar to predation risk, have been known to affect the survival and reproduction of animals, by affecting their energy intake and increasing their investment in anti-predatory behaviour (Gill and Sutherland 2000, Frid and Dill 2002, Beale and Monaghan 2004). Sloth bears react to humans aggressively, as they would to a predator, when encountered suddenly and at close distances (Laurie and Seidensticker 1977, *personal observations*; see Chapter 8: Bear – Human Conflict). In addition to the disturbance (predation risk), sloth bears probably have been having frequent adverse interactions with humans for a long time, perhaps spanning several centuries. Sloth bear attacks on humans are common throughout the range where bears and humans co-occur (Garshelis *et al.* 1999, Rajpurohit and Krausman 2000, Yoganand *et al.* in press). In this study, I examined if sloth bear activity timings had a relationship with human activity timings.

Changes in food availability, prey activity and food acquisition efficiency over a day may also influence daily activity patterns of animals. Sloth bears fed predominantly on fruits and social insects in Panna NP (see Chapter 7: Feeding Behaviour). Efficiency of foraging on fruits over the day may be influenced by vision limitations. American black bears have been reported to depend on colour vision to feed on fruits and probably for this reason they limited their activities to daylight in the seasons when they fed on fruit (Garshelis and Pelton 1980). However, their nocturnal foraging efficiency on fruits remains to be evaluated. Capture efficiency of salmon were higher at night than during the day, and American black bears and brown bears were reported to become more nocturnal during seasons of salmon availability (Klinka and Reimchen 2002). But to capture salmon at night, bears relied on tactile and auditory senses rather than vision. Considering their phylogeny, sloth bear may be dichromatic (but whether they actually are dichromatic is unknown), and therefore they may have a higher efficiency of visual foraging on fruits if they were diurnal during the fruiting season. In addition to fruits, sloth bears fed mainly on subterranean ant and termite nests and for foraging on insect nests a well-developed olfactory sense may be needed rather than vision. Also, since they feed on nests of insects, it may not make much difference whether the insects are active or not. Observations were made on these and some other food-habit related factors that may potentially influence sloth bear activity, and they are discussed in this dissertation.

Daily activity patterns of many animal species are known to follow endogenous circadian rhythms, rather than responding to concurrent environmental stimuli (Aschoff 1966, Enright 1970). Aschoff (1966) and Enright (1970) suggest that the environmental conditions may not produce activity pattern anew each day, and they probably only modify a pattern that already exists in an animal. They further cautioned that the correlations found between animal behaviour and concurrent environmental conditions based on field observations must be interpreted cautiously, because they might not have been a result of external stimuli, but might have just been caused by an internal physiological rhythm. I investigated if such a circadian rhythmic activity pattern existed in sloth bears in Panna NP.

The objectives, questions investigated and research hypotheses tested in this study are:

- To describe daily and seasonal activity patterns of sloth bears in Panna NP and assess the factors that may influence the patterns.
- To describe seasonal patterns in usage of microhabitats for day-resting by sloth bears in Panna NP and assess the factors that may influence the patterns.
- I hypothesised that sloth bears in Panna NP would reduce activity during daytime to avoid heat stress conditions.
- I hypothesised that the bears would select microhabitats with low heat gain and high heat loss possibilities to rest during day, particularly during seasons of high thermal stress.
- I examined if sloth bear activity timings were related to tiger activity in Panna NP.

- I examined if sloth bear activity timings were related to human activity timings in Panna NP.
- I examined if food-habit related factors had any major influences on bear activity patterns.
- Finally, I investigated if the activity pattern shown by sloth bears in Panna NP could have been caused by an endogenous circadian rhythm, rather than the external ecological factors stated above.
- Additionally, I report on the cubbing period of sloth bears in Panna NP.

5.2. METHODS

Activity detection from motion sensor

The radio transmitter units that I had fitted on sloth bears were equipped with a motion sensor (S6B Mortality-Motion Sensor, Telonics, Inc., Mesa, Arizona, U.S.A.). This type of reset-sensor fitted transmitters improve locational accuracy, activity determination from weak signals, distinguishing true activity from comfort movements, and are more sensitive to localised movements than measurements from radio locations (Garshelis *et al.* 1982). This sensor was set to transmit signals at a slower pulse rate (1200 msec interval or 50 pulses per minute (PPM)) when the animal was resting and switch to a faster pulse rate (800 msec interval or 75 PPM) when the animal was active, with a delay of 30 seconds. If the bear was in constant motion as in walking, the signals were transmitted continuously at a faster rate. If the bear was intermittently active, as if while grooming or moving only its head while resting, the transmitted signals changed between the two rates, but more often there was 'resting' pulse than 'active' pulse. However, when the bear was intermittently resting, as if while feeding or digging insect nests, the signals changed between the two rates, but there was more of active pulse than resting pulse. These different states could be discerned by monitoring the radio signals. However, for this study, only the two primary activity states, 'active' and 'resting' were used.

Manual activity logging

I recorded whether a bear was in one of the two states of activity, by listening to the signals for two minutes every 15 minutes throughout the day during the first year of the study. This kind of continuous activity logging was done for each radio collared bear, for about 2 – 7 days each month. When the bear activity patterns became more familiar, from the second year onwards, activity logging was done during parts (different hours) of the day, ensuring a sampling coverage of all periods of the day. Activity logging was also made during radio-tracking sessions for monitoring bear movements and space use patterns (see Chapter 6: Space Use and Habitat Selection).

Activity Receiver-Recorder Unit (ARU)

In addition to manual logging of activity, an automated “activity receiver-recorder unit (ARU)” (a prototype developed by William Cochran, Illinois, U. S. A.) was deployed to log activities of radio collared bears during the study. This battery-operated unit recorded the pulse interval and the signal strengths received from the motion-sensitive transmitters fitted on the bears, and recorded it on a memory module, facilitating periodic retrieval of data through a PC connection. The transmitter frequencies, scanning interval, pulse width and other parameters for the ARU were set through a PC. The unit scanned for the various transmitter frequencies at preset intervals, and on receiving a signal, it recorded the pulse interval and signal strength and moved on to the next frequency. After scanning for all the input frequencies, it cycled back to the next scanning sequence and so on, continuously monitoring the signals, until the battery ran out, memory got filled or until it was turned off to download data. For this study, I set the scanning interval of the unit between 30 seconds and 4 minutes, depending on the number of animals within range of reception and the period before my next scheduled visit to the unit. Preliminary analyses showed that the data collected from an interval of 30 sec up to 4 min gave similar results. From the pulse interval and the changes in the signal strength, it was discerned if the animal was resting or active.

One ARU unit was deployed in the field during 1997, 1999 and 2000, for a period of four to six months in a year, during cold and dry seasons. The ARU was set at vantage points (such as cliffs, hilltops, watch towers, etc.) with a receiving antenna raised high up on a tree or a pole (between 10 – 30 m above ground level). The unit was moved around in the study area every few days, so as to collect data on different bears ranging different parts of the study area, and to get representative data for all bears for each season. Every year at about April, when the temperature or the combination of temperature and relative humidity conditions became unsuitable, the unit failed. It was repaired and put back in the field the following post-monsoon (cold) season. Therefore, such intensive data on activity was unavailable for the monsoon season.

Day-resting (day-bed) habitats of bears

The sites where bears rested during midday were recorded by homing in or by triangulation and the resting sites were grouped into four different habitat cover classes: escarpment, knolls/hillocks, dense *Lantana* shrub thicket and other dense habitat. Each bear with a functioning radio collar was recorded at its resting site for at least 10 days each month, usually for over 20 days each month, throughout the study period.

Thermal conditions of habitat

I made measurements of temperature and relative humidity (RH) in different microhabitats used by sloth bears (dens, cliff tops, dense shrub cover, closed tree cover, escarpments, open spaces in forest, etc., Plate 6) by placing automatic temperature and RH loggers (Hobo® Pro, Temp, RH models, Onset Computer Corp., Bourne, MA, U.S.A.). In addition, temperature loggers were suspended inside black copper globes and were placed in forest and escarpment habitats to measure globe temperatures (Keuhn *et al.* 1970). The loggers were all placed at a height of 1.5 to 2 feet above the ground, to reflect the temperatures experienced by the bears at mid-body height. Since temperature and RH by themselves may not reliably indicate the thermal stress that was likely experienced by bears in the hot periods, and hence the associated thermoregulatory costs for them, more reliable indices based on combinations of both were used. From the temperature and RH measurements, I calculated vapour pressure, wet-bulb temperature and other heat indices (see below). I related activity/resting in the different microhabitats during different times of day or seasons with the thermal (temperature, vapour pressure, heat indices) profile of the particular microhabitat. However, as the energy expended or heat transferred by bears to regulate their body temperature could not be measured, the thermal conditions were assumed to indicate the potential energetic/heat transfer costs.

Out of the dens regularly used by bears in Panna NP as day beds, I examined about 30 and out of those chose 5 dens that best represented the different kinds of dens used (simple den with one room and one entrance, den with multiple nested chambers, dens on top of cliff, dens mid-way down the slope, etc.). Thermal loggers were placed in those 5 dens and measurements taken for over a year in each den. In three dens, measurements were taken at an interval of 15 minutes and in other two, every 2 hours. For this study, data from thermal loggers placed in open space (no tree/shrub cover) within forest habitat (Forest-Open) and in shade formed by tree and shrub cover in forest habitat (Forest-Shade) were analysed.

Heat stress indices

As indices of heat stress that is probably experienced by sloth bear, I calculated wet-bulb temperature (WBT), wet-bulb globe temperature (WBGT; Keuhn *et al.* 1970), Bianca's effective temperature (Bianca's ET; Bianca 1962), and temperature humidity index (THI; Armstrong 1994). Among these, WBT was found to be similar to WBGT and Bianca's ET, and similarly, THI was found to be similar to Bianca's ET. So, WBT and THI were not used in further analyses. WBGT combines the effects of air temperature, humidity, air flow and radiant heat, and has been used as a heat stress index (e.g., Olympics equestrian event forecasts).

For outdoors, WBGT = $0.7\ T_{wb} + 0.2\ T_g + 0.1\ T_{db}$;
where, T_{wb} – wet-bulb temperature,
T_g – globe temperature, and
T_{db} – dry bulb temperature.

For indoors, WBGT = $0.7\ T_{wb} + 0.3\ T_g$.
In shade, T_g is approximately equal to T_{db}, so the WBGT indoors model, with T_{db} replacing $T_{g,}$ was used for forest-shade and den microhabitats.

Bianca's ET combines the effect of temperature and humidity and is calculated as,
Bianca's ET = $0.35\ T_{db} + 0.65\ T_{wb}$.

Tiger and Human activity

Activity patterns of four radio collared tigers (the main predator of sloth bear) in the study area, (including one tiger that was accidentally trapped in a foothold snare set for bears and radio collared by me, and three others radio collared by colleagues from Wildlife Institute of India for a contemporaneous study on tiger ecology), were monitored during two seasons with the ARU, as described above for bears (Plate 7a). Human activity was assessed by direct observations and interviews (for details, see Chapter 8: Bear – Human Conflict, Methods section). Diel and seasonal usage of the forest habitats by humans was recorded by mapping the locations and by assessing at uniformly spaced sampling points across the study area.

Other explanatory variables

Methods used for assessing monthly diet composition of sloth bears are given in Chapter 7: Feeding Behaviour. Methods used for measuring monthly fruit productivity of sloth bear food plants in the study area are given in Chapter 4: General Methods. Monthly diet diversity was calculated using Shannon's Index (Krebs 1989), by including the diet items that contributed to > 0.5% of the monthly diet.

Data analysis and statistical issues

For each bear, activity during each hour of the day was marked active or resting depending on the predominant activity during that hour. Activity start and end times were recorded manually or obtained from the ARU logs. Location and habitat use data from the radio-tracked bears were pooled to describe the overall diurnal, monthly and seasonal activity and habitat use of bears.

For this study, only the hourly, monthly or seasonal means of bear, tiger and human activities, and the thermal measurements were used for assessing relationships. Therefore, correlation rather than regression analyses were used. Wherever the relationships were *a priori* expected to be non-linear or where the variables were not on interval scale, rank correlations were used. For frequency data, the percentages were arcsine transformed

(=$\sin^{-1}$ (√proportion); Sokal and Rohlf 1995) before analysing them with parametric models.

For statistical hypothesis tests, $\alpha = 0.05$ was used, unless stated otherwise. For multiple comparisons, family-wise type I error rates were controlled by using Tukey's HSD test. In circumstances requiring statistical null hypothesis testing, emphasis was placed on parameter estimates, estimates of effect sizes, confidence intervals of effect sizes and biological significance, rather than making decisions merely based on statistical significance. In addition, if there were failures to reject null hypotheses, careful interpretations have been given based on sample sizes, variability in data, and effect sizes. For a discussion of these issues, see Yoccoz (1991), The Wildlife Society (1995), and Johnson (1999).

Plate 6. Bear day-bed dens were monitored for usage by tagged and other bears. Temperature and RH loggers were placed in various micro-habitats, including dens, and daily and seasonal changes in their thermal characteristics were monitored. (Right Photo courtesy: Gary Koehler).

5.3. RESULTS

Diel activity pattern

A total of 10,526 activity logs, each separated by a minimum of one hour, were used in describing the activity patterns of sloth bears. Bears were found to be active during night and crepuscular hours and resting during daytime (Fig. 5.1). This pattern of activity was similar among all radio collared bears, although with some variability (Fig. 5.2). A female bear F76 showed the most dissimilarity, but was still comparable to others. Even the differences in diel activity patterns among climatic and fruiting seasons were small (Figs. 5.3a, b). In the wet and cold seasons, bears extended their activity into the day hours and reduced their activity in the post-midnight, pre-morning hours, as compared to the dry season. Consequently, the day resting period was shorter by about 2 – 3 hrs in the wet and cold seasons as compared to dry season. There was no appreciable difference in diel activity between fruiting and non-fruiting seasons, except for a slight reduction in activity during night hours in the non-fruiting season. Within the cold season, there was considerable variability among individual bears in their diel activity (Fig. 5.4a). Some bears showed substantial reduction in activity during midnight hours, while others were highly active. Morning and evening activity were also considerably different among bears. Whereas, in the dry season, the diel activity was similar, except for some differences among bears in the night hours (Fig. 5.4b). In the wet season too, except for two bears (F76 and F80), the diel activity pattern was similar (Fig. 5.4c). Similarly, during the fruiting and non-fruiting seasons too the activity patterns of individual bears were more or less in harmony, except for a marginally discordant pattern shown by bear F76 in the non-fruiting season (Figs. 5.5a, b). Bears (except the cubbing females) were active almost every day of the year, and for several (>10 h) hours each day. Only rarely were they active for merely a few hours (<6 h) in a day.

Overall, bears were active for 48% to 54% of the whole day (out of 24 h) in all seasons. At the level of individual bears, the percent of time active in a day was quite similar within seasons, except for the cold season, when there was high variability (Fig. 5.6). When the means were considered, dry season activity was marginally lower than other two seasons. The dry season activity was also consistently lower than wet season at the individual level.

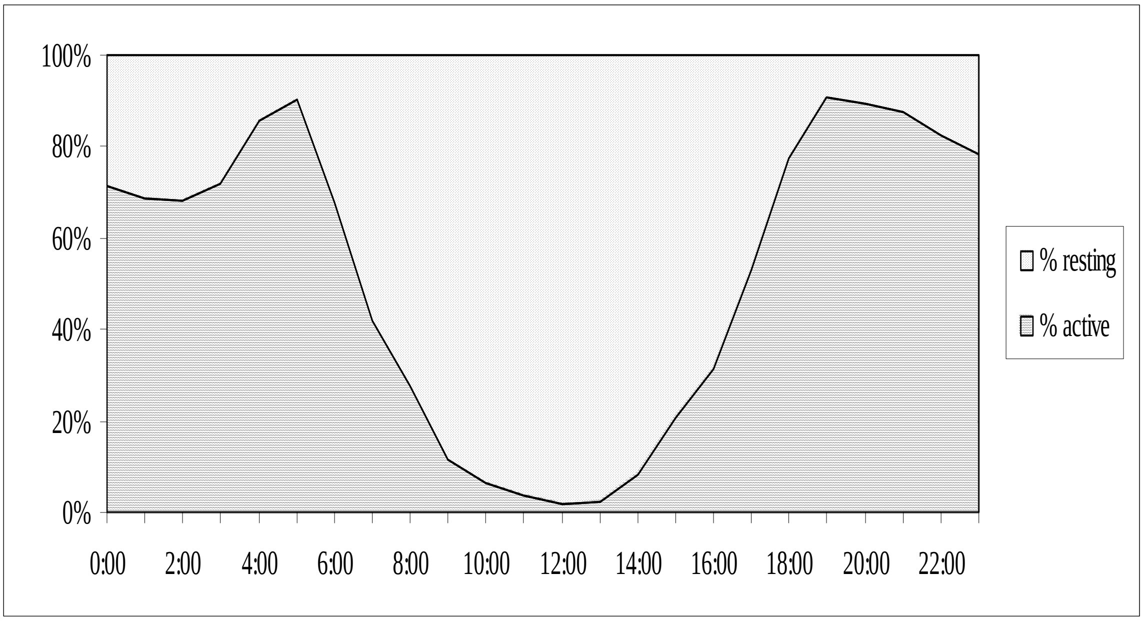


Fig. 5.1. Annual mean of percent of time (hours of day) sloth bears in Panna NP were active (cross-shade) or resting (dots).

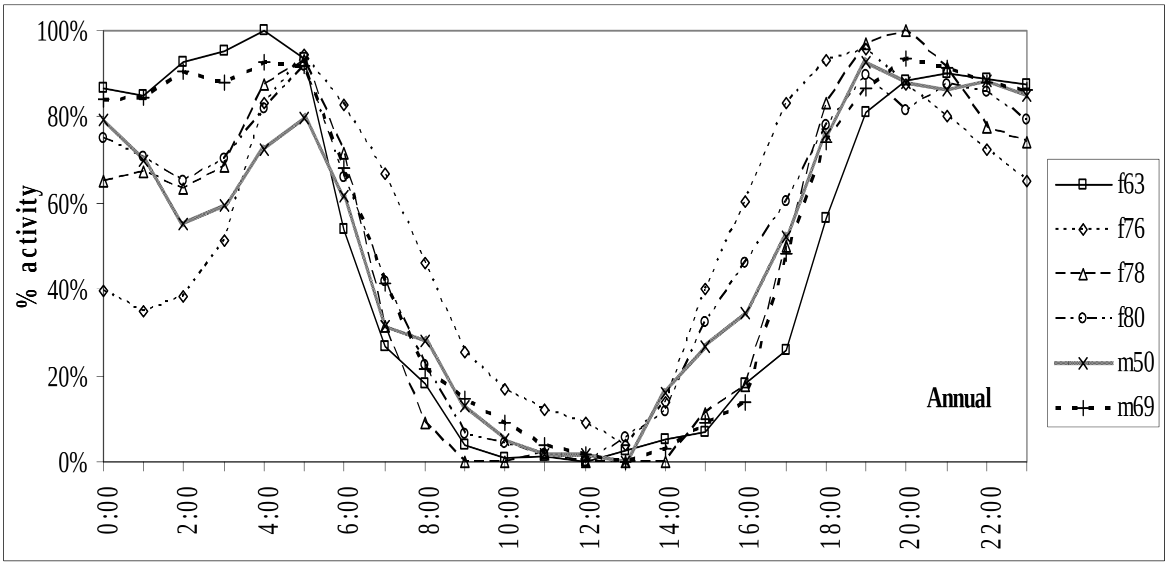


Fig. 5.2. Similarities in annual diel activity of radio-collared sloth bears (that were studied > 1 year) in Panna NP. The bear names that start with ‘f’ are females and ‘m’ are males.

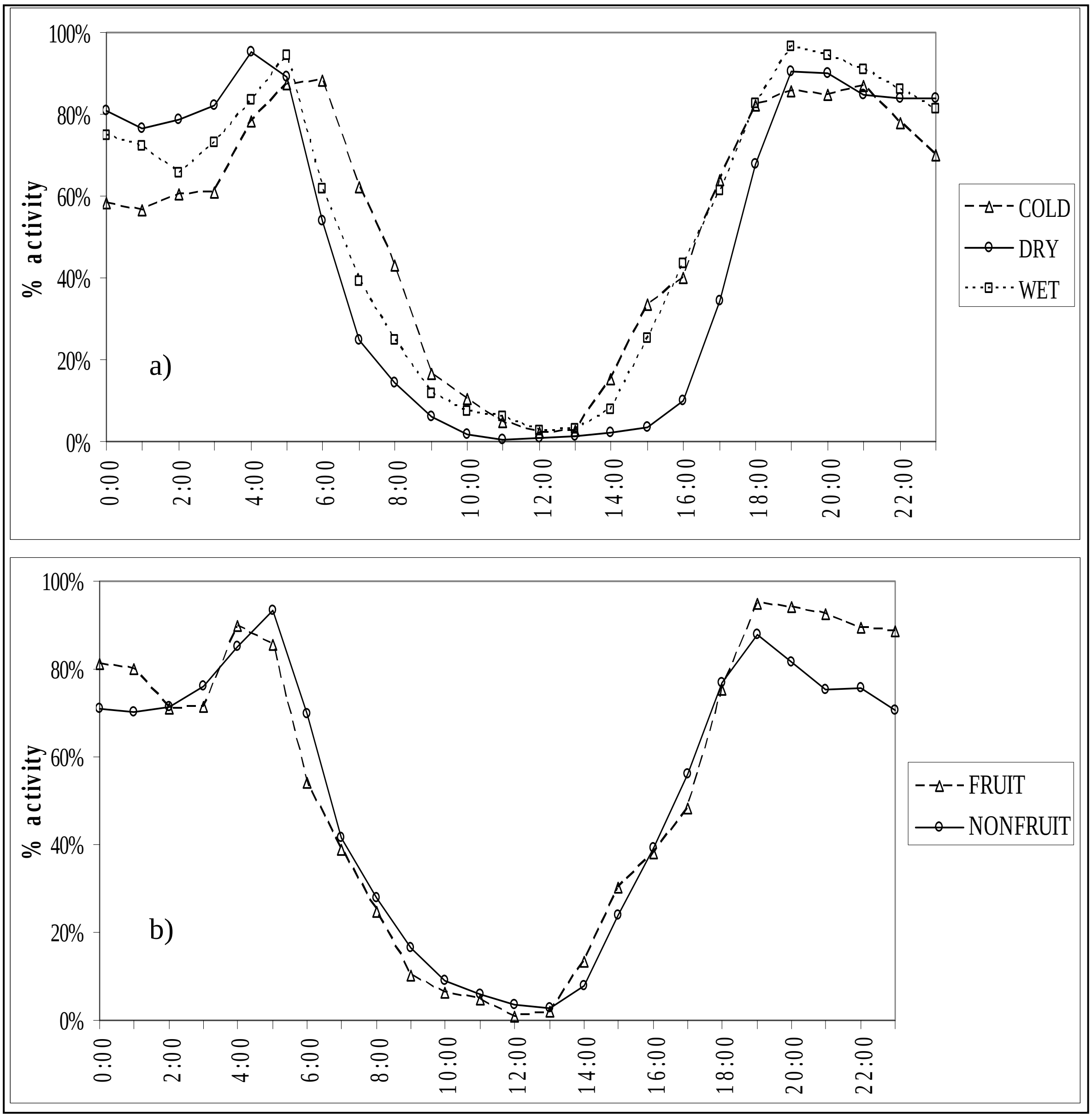


Fig. 5.3. Differences in mean percent diel activity of sloth bears in Panna NP, among (a) climatic and (b) fruiting seasons (fruiting months: April to July, November and December; other months compose non-fruiting season).

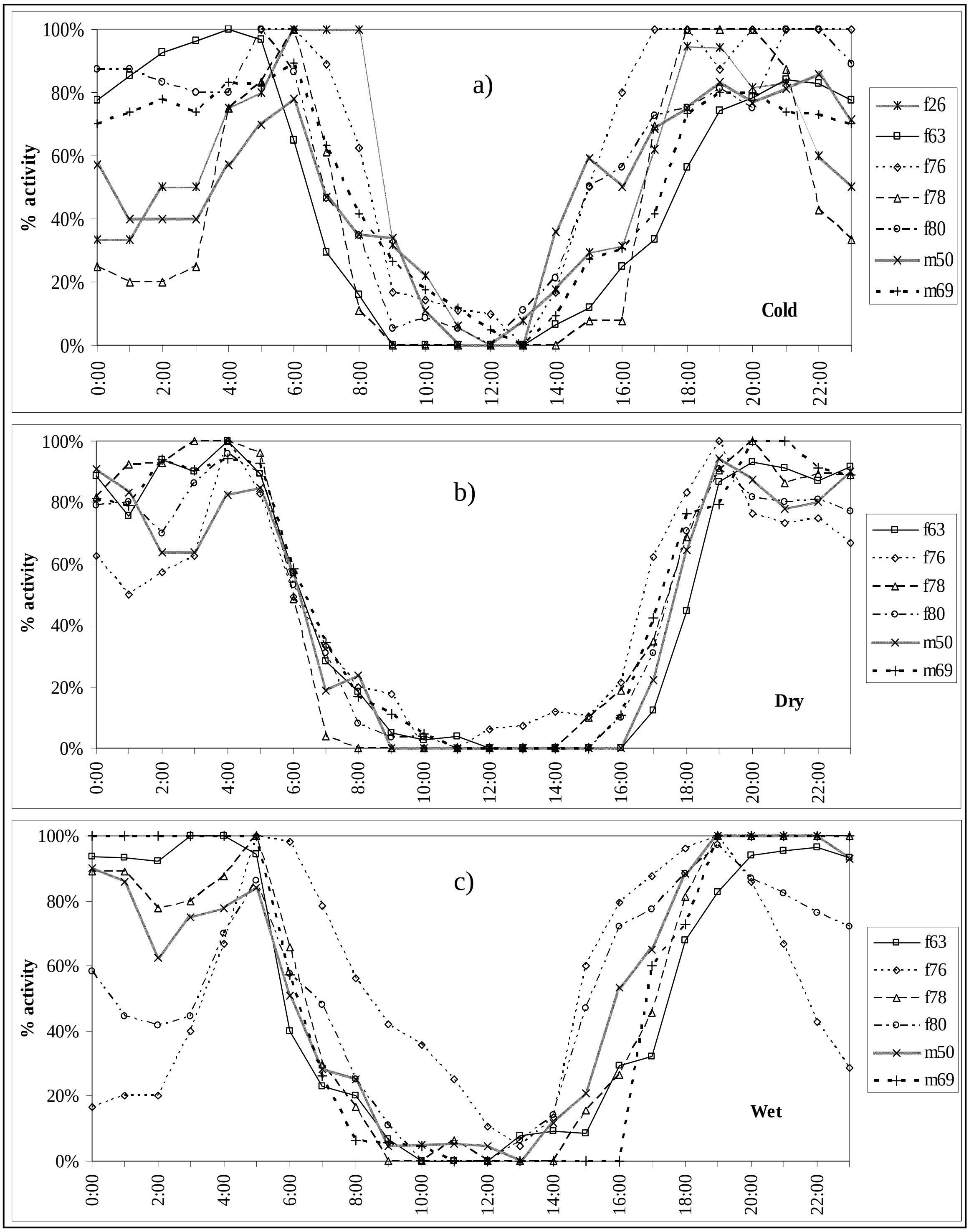


Fig. 5.4. Variability in diel activity of radio-collared sloth bears in Panna NP, during (a) cold, (b) dry, and (c) wet seasons. The bear names that start with ‘f’ are females and ‘m’ are males.

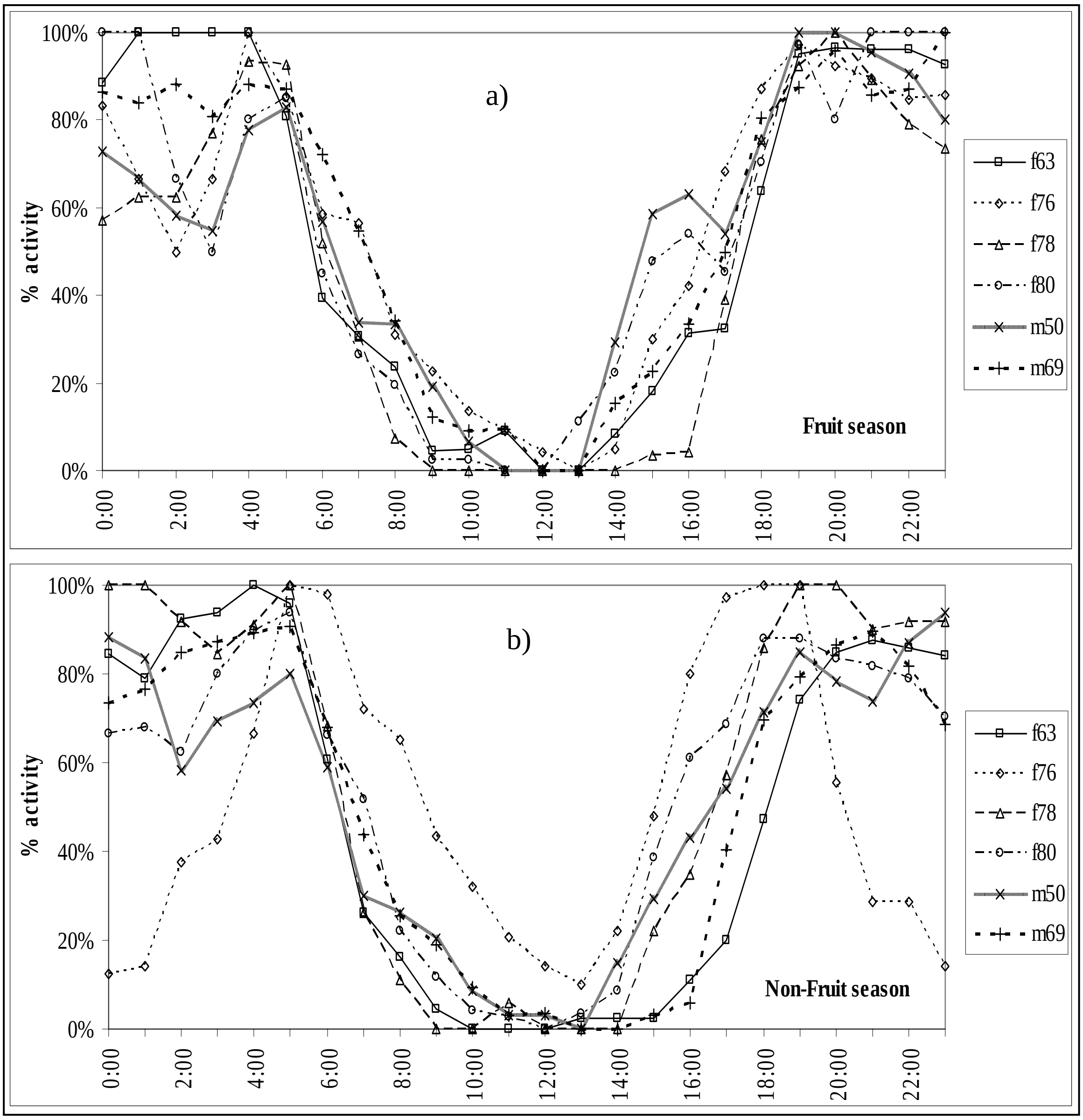


Fig. 5.5. Variability in diel activity of radio-collared sloth bears in Panna NP, during (a) fruiting, and (b) non-fruiting seasons. The bear names that start with ‘f’ are females and ‘m’ are males.

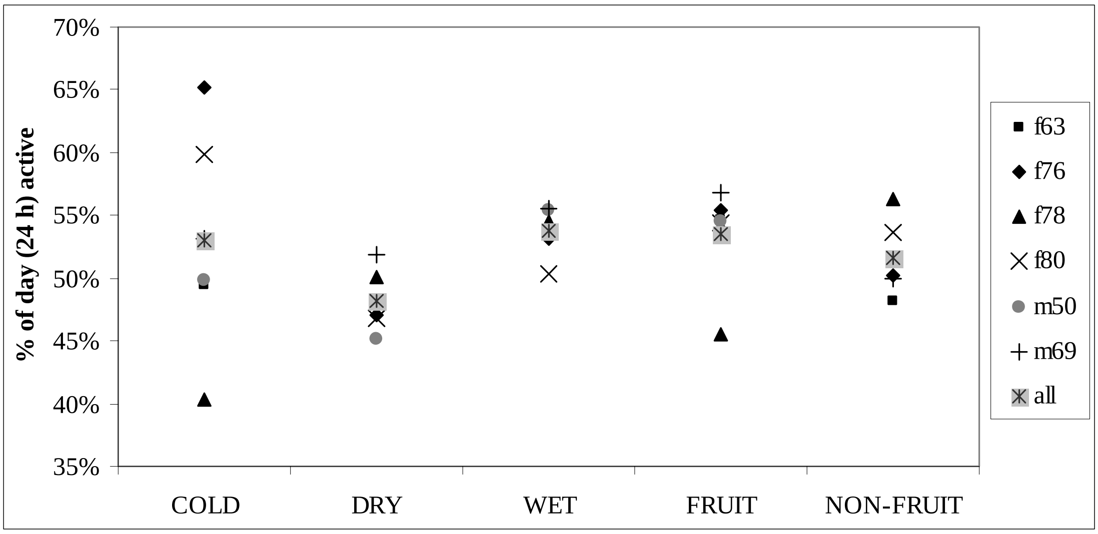


Fig. 5.6. Percent of day (out of 24 hours) radio collared sloth bears in Panna NP were active during different seasons. The bear names that start with ‘f’ are females and ‘m’ are males. ‘All’ denotes the mean of all bears within each season.

When examined by paired samples Wilcoxon signed-rank test (Table 5.1), the difference was statistically significant, but the size of difference was only about 5%, which may not be significant in a biological sense. For other seasonal comparisons, the differences were not statistically significant and were small. When the differences were assessed after separating the different periods of day, there still did not seem to be any substantial seasonal differences, except that the difference between percent of crepuscular period active in cold and wet seasons was statistically significant, and the difference (median = 11.8%) was considerable (Table 5.1). This was largely contributed by a higher activity in the evening period of wet season. The difference between percent of night time active in cold and wet seasons seems substantial (median = 17.1%), but the high variability among individual bears in their night time activity in these seasons renders this difference to be statistically not significant. There were no large differences seen among months in percent of whole day, percent of day time, percent of night time, and percent of morning time the bears were active (Fig. 5.7). However, percent of evening time active showed some large differences, with activity <40% in February and March and >70% from August to October.

Table 5.1. Comparisons of seasonal values of percent of time active in whole day (24 h), daytime, crepuscular and night times of radio collared bears in Panna NP. Seasonal values of individual bears (N=6, radio collared bears with data for all seasons) compared using paired samples Wilcoxon signed-rank test.

Response Variable	Seasonal comparisons (mean ± 1 SE)	Median of differences	Statistic [a]	*P*
% of whole day (24 h) active	Dry – Wet (48.2±1.0) – (53.7±0.8)	4.76	2.10	0.04
	Dry – Cold (48.2±1.0) – (53±3.5)	3.00	1.26	0.21
	Cold – Wet. (53±3.5) – (53.7±0.8)	3.10	0.21	0.83
	Fruit – Non-fruit (53.6±1.65) – (51.6±1.21)	4.18	0.84	0.40
% of Daytime active	Dry – Wet (4.53±1.23) – (11.14±4.25)	5.07	1.68	0.09
	Dry – Cold (4.53±1.23) – (7.72±2.36)	3.38	1.05	0.30
	Cold – Wet (7.72±2.36) – (11.14±4.25)	4.59	0.84	0.40
	Fruit – Non-fruit (9.56±2.23) – (12.15±4.25)	1.41	0.00	0.99
% of Crepuscular period active	Dry – Wet (60±2.3)– (63.7±6.2)	2.94	0.42	0.67
	Dry – Cold (60±2.3) – (52.7±6.9)	8.68	1.47	0.14
	Cold – Wet (52.7±6.9) – (63.7±6.2)	11.81	2.10	0.04
	Fruit – Non-fruit (57.5±2.9) – (62.9±6.8)	3.37	0.00	1.00
% of Night time active	Dry – Wet (84±3.6) – (81.8±8)	1.95	0.00	1.00
	Dry – Cold (84±3.6)– (78.1±5.9)	10.79	0.84	0.40
	Cold – Wet (78.1±5.9) – (81.8±8)	17.11	0.42	0.67
	Fruit – Non-fruit (84.3±3.1) – (76.4±7.7)	8.08	0.84	0.40

[a] Continuity correction applied

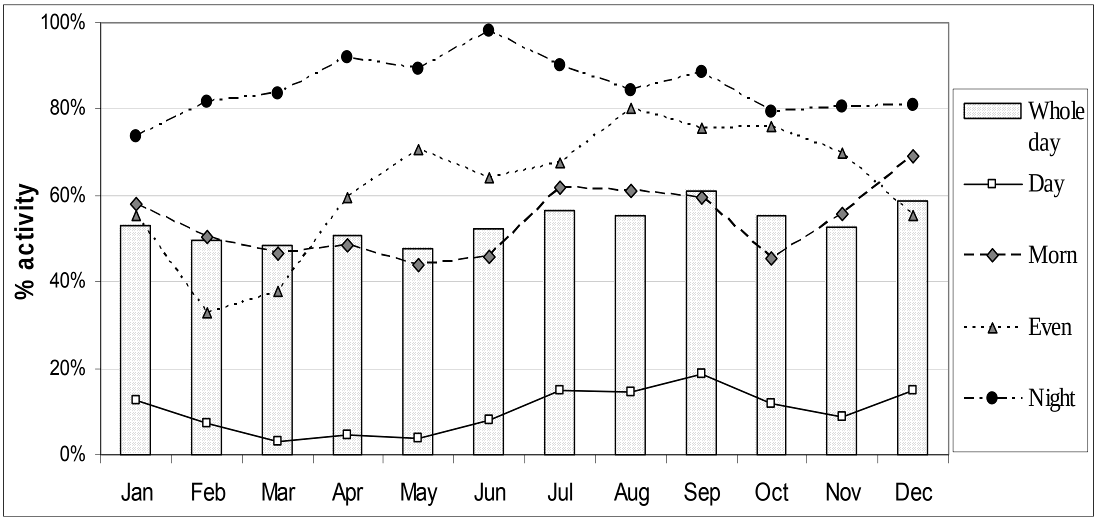


Fig. 5.7. Percent of whole day (bar) and percent of different periods of day (lines) radio-collared sloth bears in Panna NP were active during different months. For definitions of different time periods, see Chapter 4: General Methods.

Times of start and end of bear diel activity

The times bears started their activity after their long, continuous mid-day resting, and the times they ended their activity after their night-long activity varied within and among months (Figs. 5.8a, b). However, certain general patterns were seen. The bears started their activity generally later (medians between 17:30 and 18:30) in the months of February to August and earlier (medians between 16:00 and 17:00) in the months of September to December. Within-month variability in activity start time was lower with a range of about 2 h during the dry season months of April to June, but during other months had a range of about 3 – 6 h. Bears ended their activity generally earlier (medians between 6:00 and 7:00) and within-month variability was lower during the dry and wet season months of March to October, and generally later (medians between 7:00 and 9:00) and with higher within-month variability during the cold season months. Box plots of monthly activity end times identified several outlier and extreme values for many months (Fig. 5.8b), mostly in the positive tails of the distributions, indicating that a few bears ended their activity consistently later than the general activity end times.

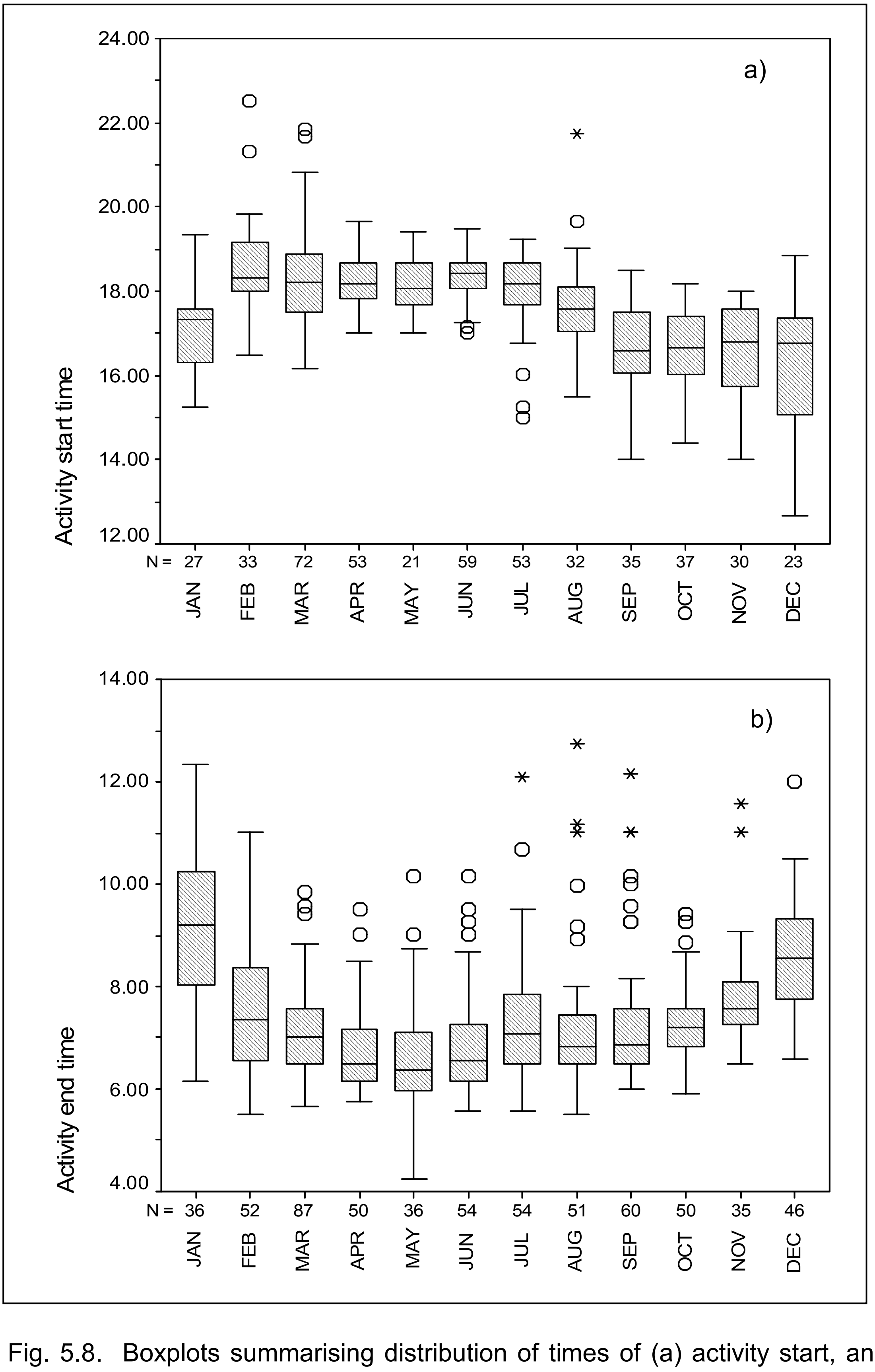


Fig. 5.8. Boxplots summarising distribution of times of (a) activity start, and (b) activity end, of sloth bears in Panna NP during different months. Circles indicate outliers, and stars extreme values.

The differences in activity start and end times among individual bears within seasons were large in certain seasons, and differences among seasons of a bear and were large for certain bears (Figs. 5.9a, b). Also, certain bears in some seasons were more consistent in their timings (smaller standard deviations; but SE are shown in Figs. 5.9, 5.10), while others or the same bears in other seasons had higher variability. Differences in means of activity start and end times among bears were small during dry season and large during cold and wet seasons. However, the large difference in activity end time in wet season was primarily due to bear F76 having ended activity much later than the rest (Fig. 5.9b). Bears such as F63, F78, and M69 did not show much difference among seasons, while others such as F76, F80 and M50 showed large differences. Also, many bears showed higher variability in cold and wet seasons than dry seasons, particularly in activity start times. A similar assessment of activity start and end times comparing fruiting and non-fruiting seasons showed a different pattern (Figs. 5.10a, b). Differences among bears in activity start times in fruiting season were minimal, whereas, large differences were seen in the non-fruiting season. Differences among bears in activity end times were considerable in both seasons. While bears such as F76 and F80 had substantial differences in activity start and end times between the two seasons, others showed similar timings in both seasons.

Bears, in general, started their activity later and ended it earlier in the dry season than the other two climatic seasons (Figs. 5.11a, b). The earliest activity start and latest activity end was in the cold season. The differences among climatic seasons in both timings were statistically significant (ANOVA; Table 5.2). Pair-wise comparisons showed that the differences in activity start times between dry and the other two seasons were statistically significant, the differences were large, and the 95% confidence intervals (CI) of effect sizes were also considerably narrow. For activity end time, all seasonal differences were found to be statistically significant. While the differences between cold and the other two seasons were large, that between wet and dry seasons was not large and the CI of effect size was wide, and so there was uncertainty about the actual size of difference. No substantial difference was found between fruiting and non-fruiting seasons in both the timings (Fig. 5.11a, b). Although the difference in activity start times was found to be statistically significant (Table 5.2), the difference was small and 95% CI wide, making the actual size of difference uncertain.

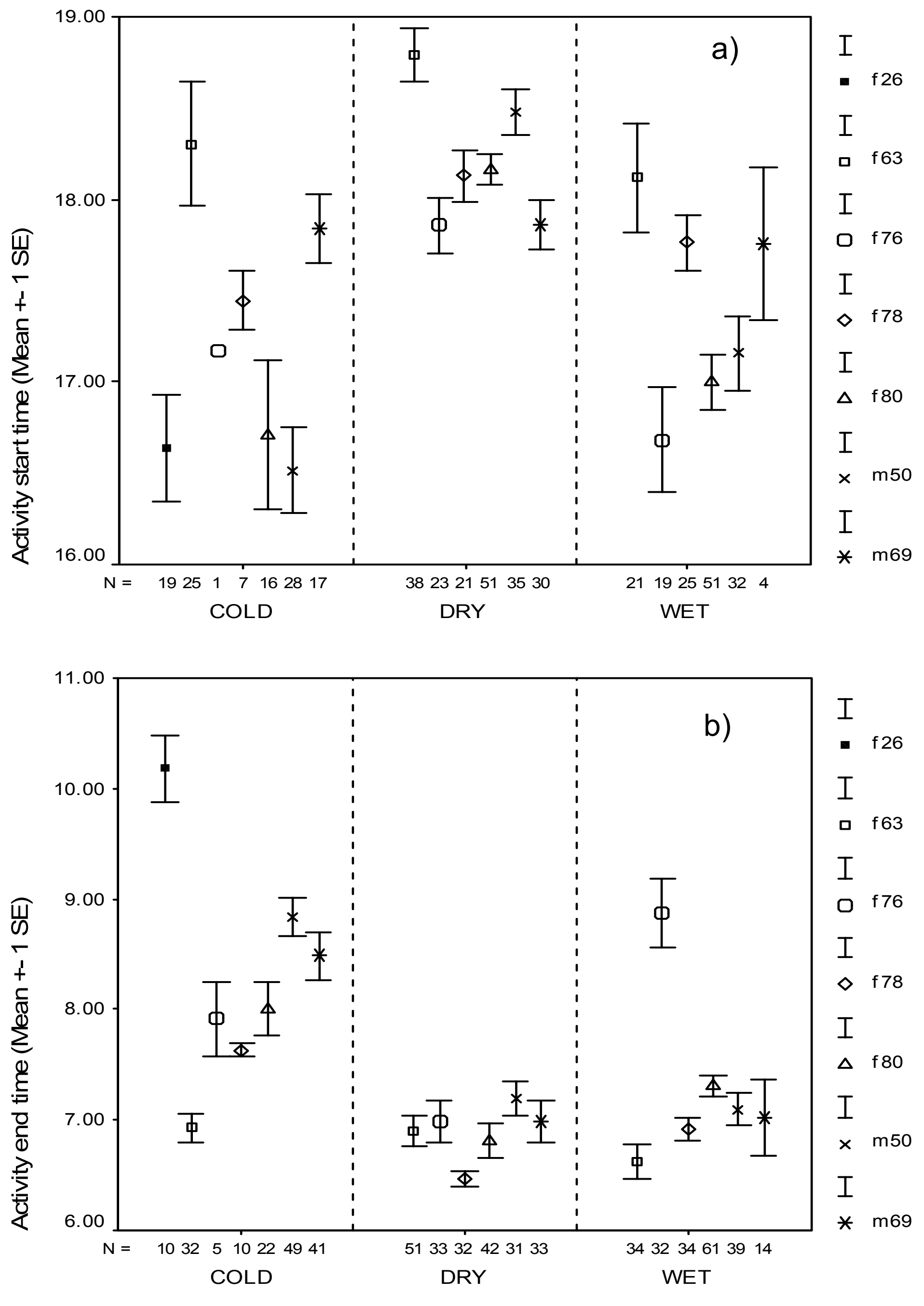


Fig. 5.9. Means and 1 S.E. of means of times of (a) activity start, and (b) activity end, of radio collared bears in different climatic seasons. Bear names that start with ‘f’ are females, and ‘m’ are males.

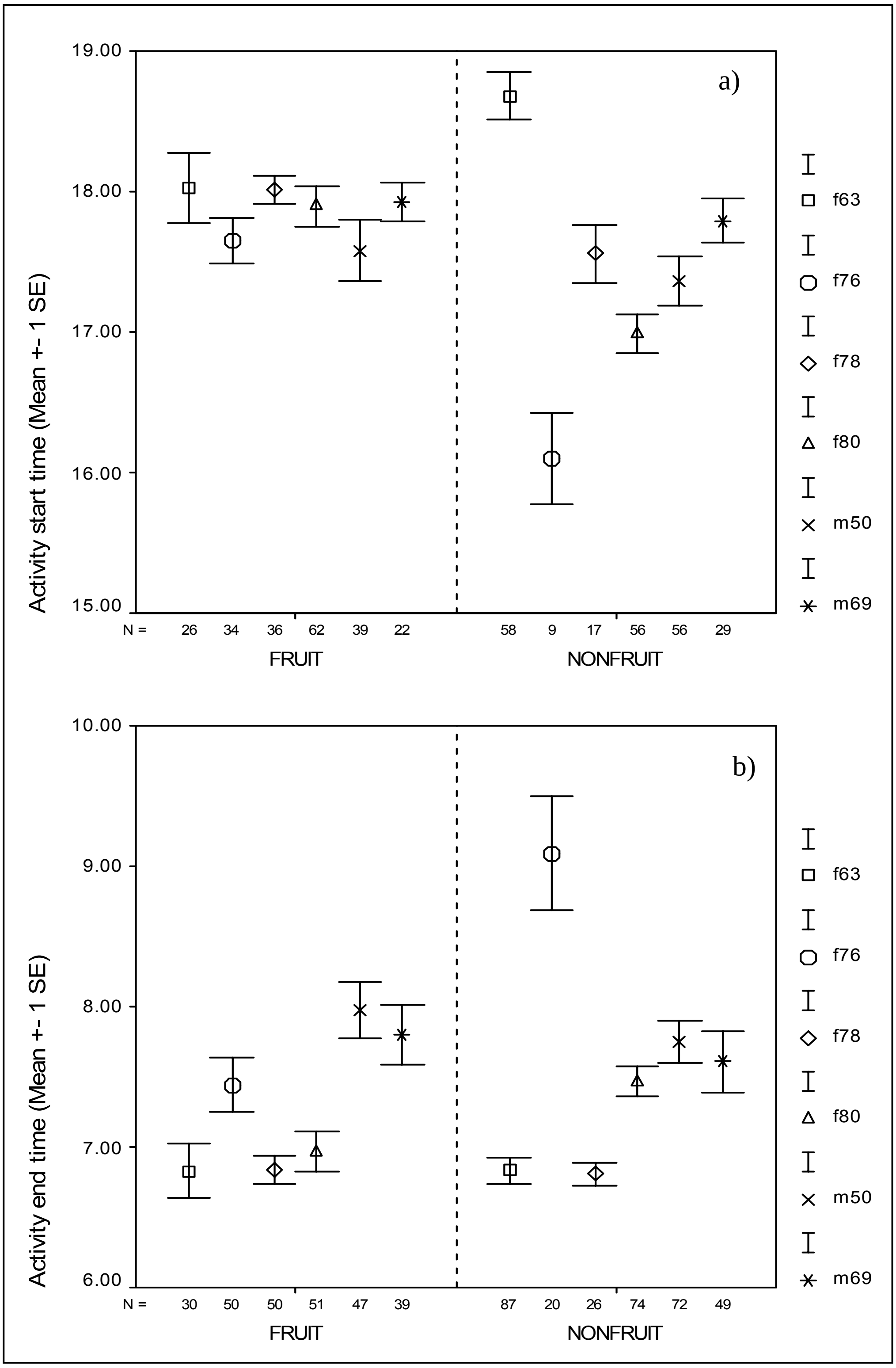


Fig. 5.10. Means and 1 S.E. of means of times of (a) activity start, and (b) activity end, of radio collared bears in fruiting and non-fruiting seasons. Bear names that start with ‘f’ are females, and ‘m’ are males.

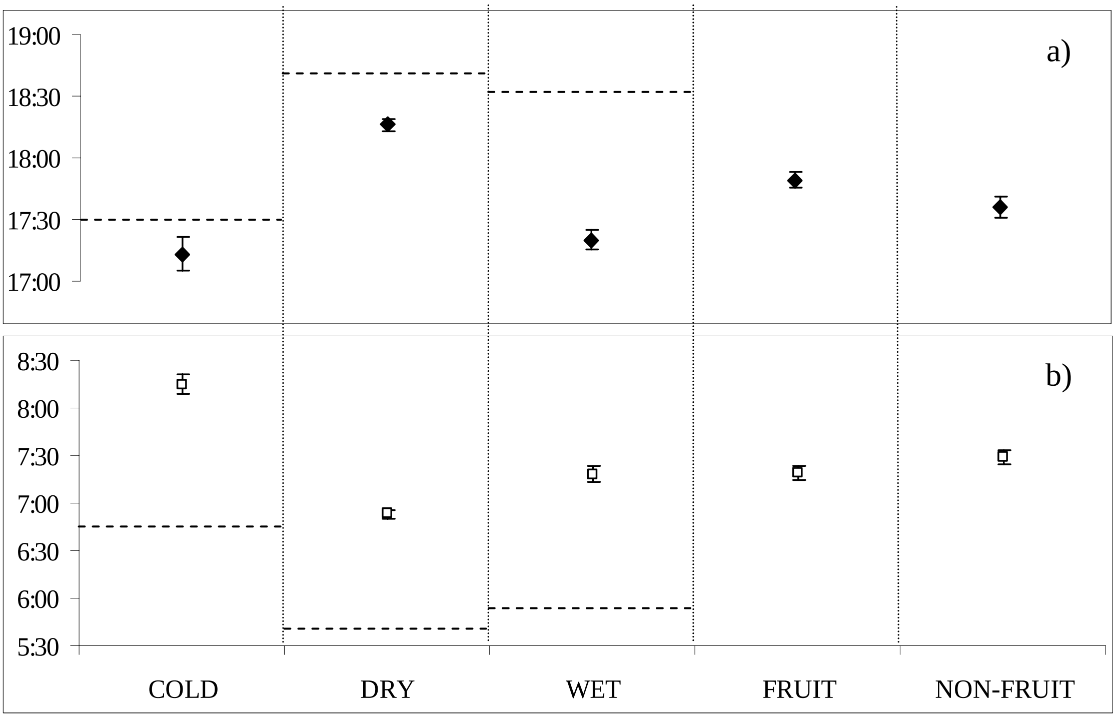


Fig. 5.11. Means and 1 S.E. of means of times of (a) activity start, and (b) activity end of all radio collared bears in the different seasons. Dashed lines denote mean sunrise and sunset times of the respective climatic seasons (since fruiting seasons contain non-contiguous months, seasonal means were not calculated).

When activity start and end times were adjusted for seasonal sunset and sunrise times, respectively, the patterns in seasonal differences in both the timings changed remarkably (Table 5.2). Wet season activity start times with reference to sunset were much earlier than the other two seasons, whereas the difference between cold and dry seasons was small and not statistically significant. This was in contrast to the result obtained before adjusting for sunset time, which showed a large difference between cold and dry seasons (Table 5.2). Similarly, difference in activity end times after sunrise between cold and wet seasons was small, uncertain and was not statistically significant, while the difference in activity end times before adjusting for sunrise time was large and significant. The difference in activity end times between cold and dry seasons too became much smaller after adjusting for sunrise time. The differences in both timings between fruiting and non-fruiting seasons did not change much after adjusting for sunrise and sunset times and they remained small.

Table 5.2. Effect of climatic and fruiting seasons on means of bear activity start and end times, before and after adjusting for sunset and sunrise times, as tested by ANOVA and T-tests. Pair-wise differences in means were assessed by Tukey's HSD test for > 2 groups.

Response (Bear activity variable)	Effect	Seasonal comparisons (means in parenthesis)	Effect size (difference in mean ± 1 SE)	*P*	95% CI of effect size	
					Low	High
Activity start $F_{(2,472)} = 44.75$, $P < 0.001$	Climatic Season	Dry – Cold (18:16) – (17:13)	1:03 (±0:08)	< 0.001	0:44	1:21
		Dry – Wet (18:16) – (17:20)	0:56 (±0:07)	< 0.001	0:39	1:12
		Wet – Cold (17:20) – (17:13)	0:07 (±0:08)	0.67	-0:12	0:26
Activity end $F_{(2,608)} = 66.6$, $P < 0.001$	Climatic Season	Cold – Dry (8:15) – (6:53)	1:22 (±0:07)	< 0.001	1:05	1:38
		Cold – Wet (8:15) – (7:18)	0:57 (±0:07)	< 0.001	0:40	1:14
		Wet – Dry (7:18) – (6:53)	0:24 (±0:07)	0.001	0:09	0:40
Activity start $T = 1.94$, $df = 473$	Fruiting Season	Fruit – Non fruit (17:49) – (17:36)	0:13 (±0:06)	0.05	0:00	0:26
Activity end $T = -1.5$, $df = 609$	Fruiting Season	Non fruit – Fruit (7:29) – (7:19)	0:09 (±0:06)	0.13	-0:02	0:21
Activity start before sunset $F_{(2,472)} = 28.2$, $P < 0.001$	Climatic Season	Wet – Cold (1:07) – (0:26)	0:41 (±0:08)	< 0.001	0:23	0:59
		Wet – Dry (1:07) – (0:20)	0:47 (±0:07)	< 0.001	0:32	1:03
		Cold – Dry (0:26) – (0:20)	0:06 (±0:07)	0.64	-0:10	0:23
Activity end after sunrise $F_{(2,608)} = 10.91$, $P < 0.001$	Climatic Season	Cold – Dry (1:32) – (1:03)	0:29 (±0:07)	< 0.001	0:12	0:46
		Wet – Dry (1:29) – (1:03)	0:26 (±0:07)	< 0.001	0:10	0:42
		Cold – Wet (1:32) – (1:29)	0:02 (±0:07)	0.91	-0:14	0:20
Activity start before sunset $T = 1.34$, $df = 473$	Fruiting season	Fruit – Non fruit (0:41) – (0:33)	0:08 (±0:06)	0.18	-0:03	0:20
Activity end after sunrise $T = 2.57$, $df = 609$	Fruiting season	Fruit – Non fruit (1:28) – (1:13)	0:15 (±0:05)	0.01	0:03	0:26

Day-resting habitats

Bears used certain kinds of habitats frequently for their extended mid-day resting. Escarpment habitat was most frequently used for day-resting by the radio collared bears in all months (Plate 7b), followed by *Lantana* shrub thickets (Fig. 5.12). Knolls and other forest habitats with dense undergrowth were also used, and frequently so in some months. The use of escarpment habitat was predominant in the dry season months and decreased in the monsoon and post-monsoon months (August to December), with a converse increase in the use of *Lantana* habitat as day-bed, which peaked in October to about 50% usage. Overall, usage of *Lantana* habitat as day-bed was highest in wet season at about 30%, and lowest in dry season at about 15%. Boxplots of monthly percent use of escarpment and *Lantana* habitats as day-beds reveals certain outliers to the general patterns of usage (Figs. 5.13a, b). While most bears showed predominant usage of escarpment for day-resting from January to July, bears F76, F80 and M50 showed low usage of escarpment and high usage of *Lantana* cover during the same period. From August to December, more bears were commonly using more of *Lantana* and less of escarpment habitats for day-resting as compared to the other months, while many bears continued to use escarpment highly. An associated feature of most resting locations, particularly the ones used in the dry and wet seasons was the availability of water within a range of a km.

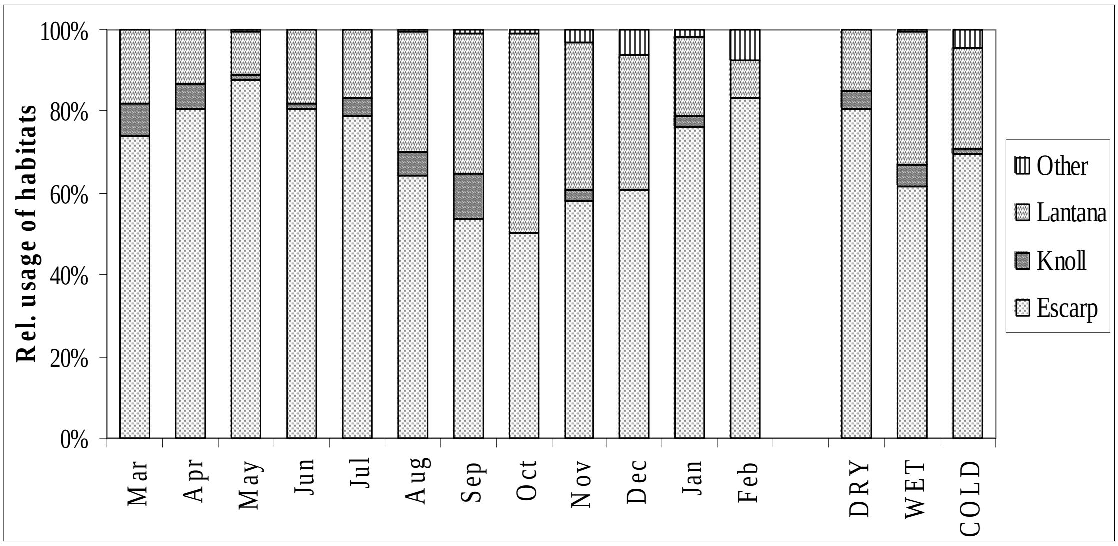


Fig. 5.12. Relative usage of different habitats by sloth bears in Panna NP for day-resting, in different months and seasons (N=2,553 bear-days).

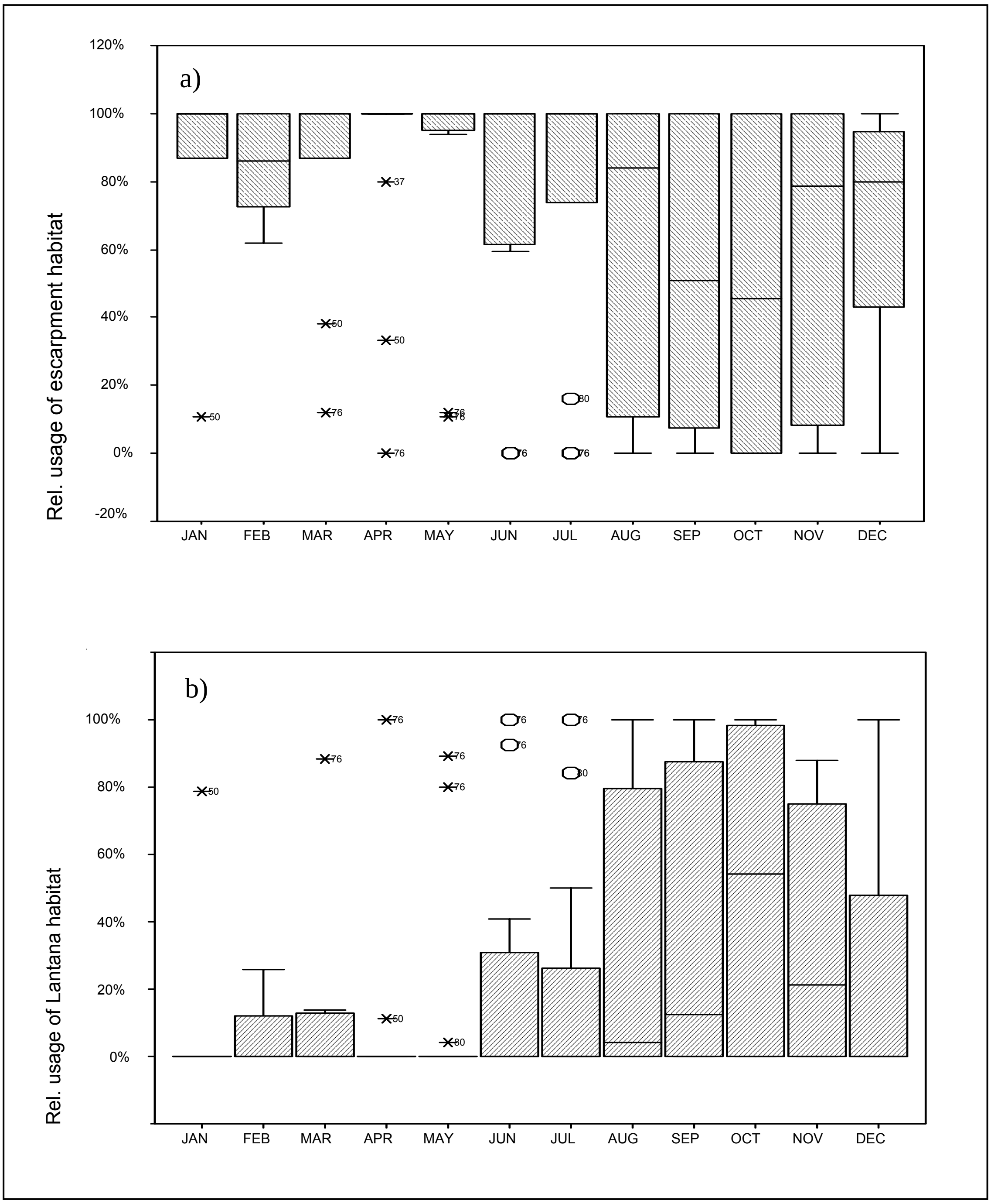


Fig. 5.13. Boxplots of monthly relative use of (a) escarpment habitat, and (b) *Lantana* habitat, by radio collared sloth bears in Panna NP. Circles indicate outliers and stars extreme values.

An analysis of data on relative usage of different habitats for day-resting by individual bears in the different seasons illustrates the individual behavioural differences (Fig. 5.14). Bears F63, F78, and M69 consistently used escarpment highly and bear F76 used *Lantana* highly in all seasons. Bears F80 and M50 were variable in their use across seasons. When the bears were grouped according to the location of their home-ranges (with respect to escarpment availability and habitat protection status of the study area – see Chapter 6: Space Use and Habitat Selection) as 'core bears' and 'peripheral bears' and the relative usage of habitats for day-resting assessed, the apparent individual behavioural differences were explained to a large extent by the location of their home ranges. The core bears, which had substantial escarpment habitat available to them, used escarpments for day-resting predominantly in all seasons, and the peripheral bears, which had low escarpment and high *Lantana* cover available within their home ranges, used these habitats for day-resting variably (Fig. 5.15).

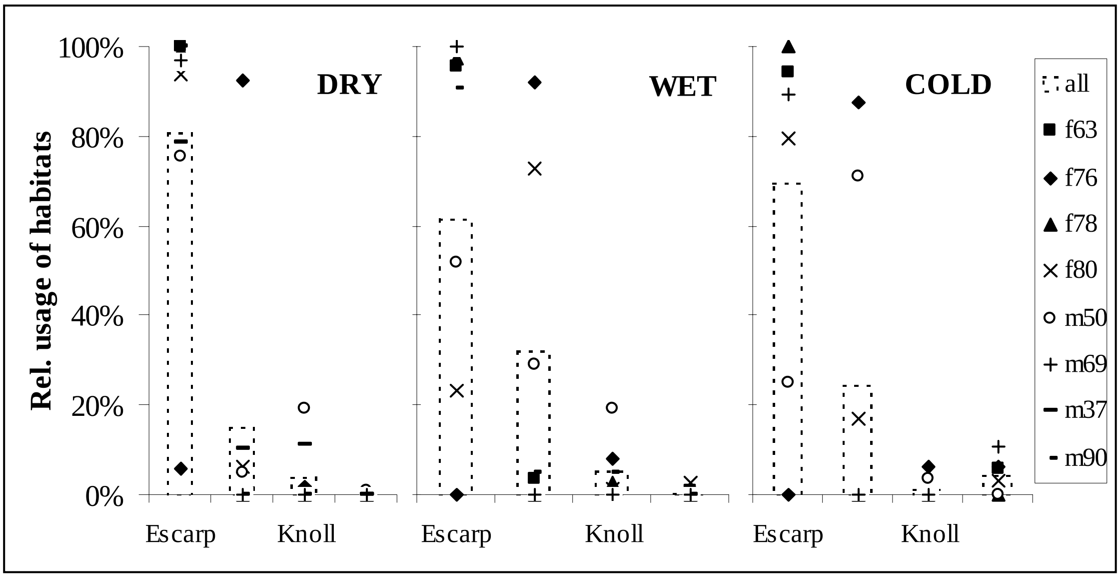


Fig. 5.14. Relative use of different habitats for day-resting by radio collared bears (mean of all bears – bars; individuals – markers) in Panna NP during different seasons. Bear names that start with 'f' are females, and 'm' are males.

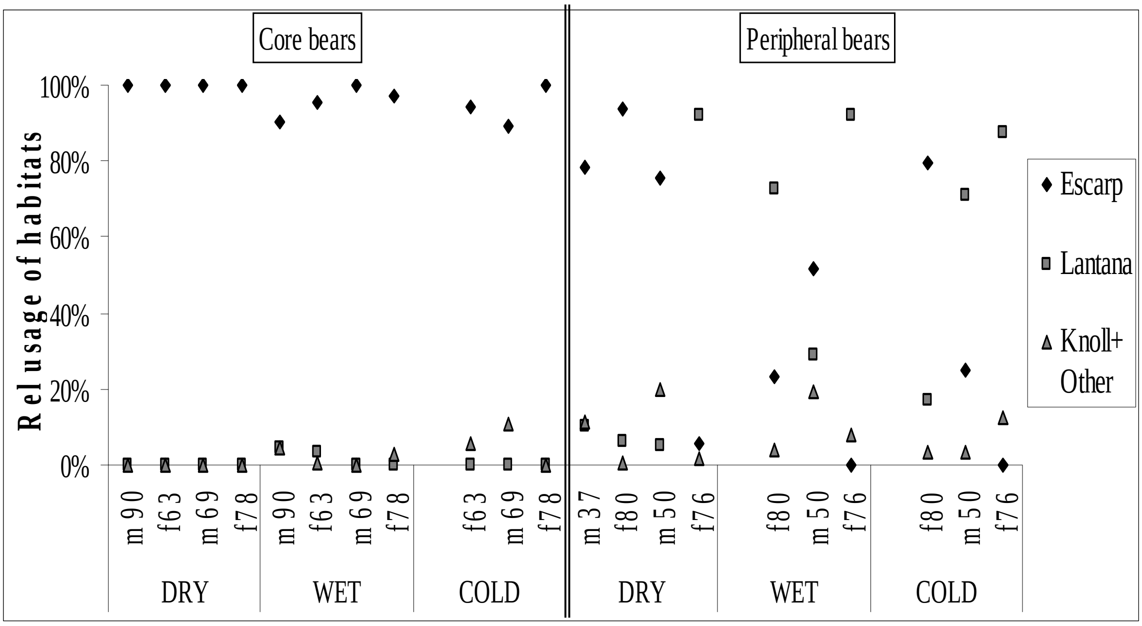


Fig. 5.15. Relative use of different habitats for day-resting by radio collared bears whose home ranges were in the middle areas of Panna NP, which had substantial amount of escarpment habitat within the area (core bears), and whose predominant part of home ranges were in the peripheral areas of Panna NP, which had high percent of *Lantana* habitat and low percent of escarpment habitat (peripheral bears).

Cubbing period of bears

The radio collared female bears in Panna NP gave birth during the cold season. The female bears entered secluded and protected dens (generally, crevices and caves along steep slopes in the escarpment habitat) before parturition and stayed inside the dens (termed “maternity dens”) caring for the cubs, without coming out for several weeks. They emerged for foraging only after the cubs grew up considerably. This period of staying inside den during and after parturition, that I termed “cubbing period”, was monitored manually and with the help of ARU for six radio collared females that cubbed during 1996 to 2000. In general, the cubbing period started towards end of November and continued until February, ranging from 9 to 12 weeks (Fig. 5.16).

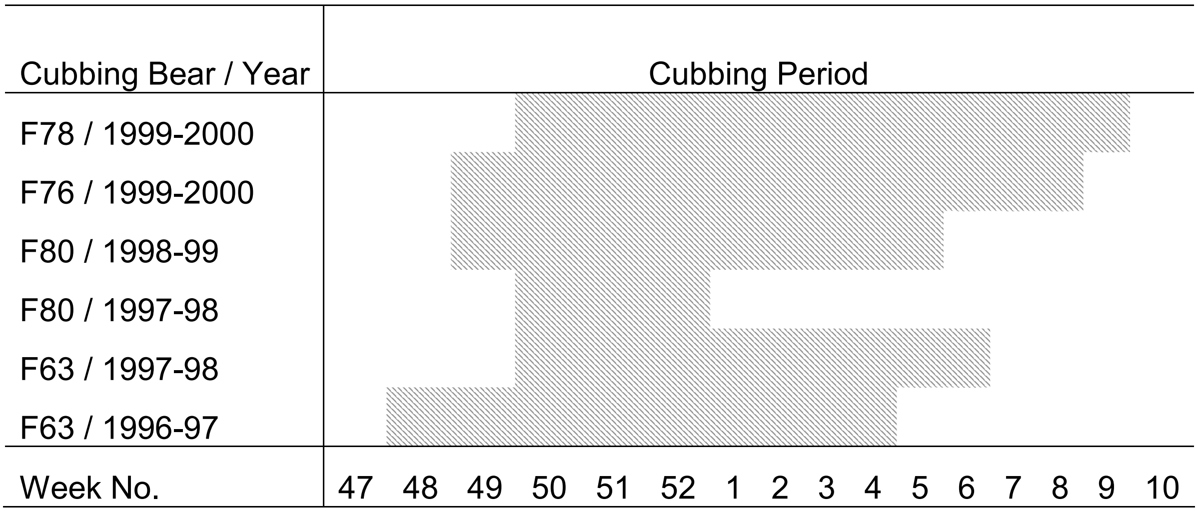


Fig. 5.16. Periods of cubbing observed in radio-collared female sloth bears in Panna NP, studied between 1996 and 2000. Cubbing by F80 failed during 1997 – 98, and so was exceptionally short.

Thermal characteristics of sloth bear habitat

In the forest-open habitat, monthly mean temperatures in the day time rose to about 40 ^{o}C in some months and were over 30 ^{o}C in most months (Fig. 5.17a). The monthly maximum temperatures were over 30 ^{o}C in all months and were close to 50 ^{o}C in April and May. The monthly minimum night temperatures dropped lower than 5 ^{o}C in cold season months. Night temperatures were much lower than day temperatures in most months and were also less varying. In the forest-shade habitat (Fig. 5.17b), night time mean temperatures were similar to forest-open habitat, day temperatures were lower by a few to several degrees than forest-open habitat, and both day and night temperatures had a similar pattern of change in the two habitats. Night time minimum temperatures were higher by a few degrees in forest-shade than forest-open habitat. Also, variability in day temperature during the wet season months was lower in the forest-shade habitat.

The pattern of change over months in the heat index WBGT was similar in forest-open and forest-shade habitats in the day (with forest-shade values consistently lower than forest-open). In the night, the WBGT values were lower than day and were similar in the two habitats (Fig. 5.18). WBGT showed a much different profile over months than the temperature, mainly caused by the wet season differences. While the temperature declined after May and remained lower in the wet season months of July to October, WBGT increased as the dry season progressed and stayed the highest in the wet season months (Fig. 5.18).

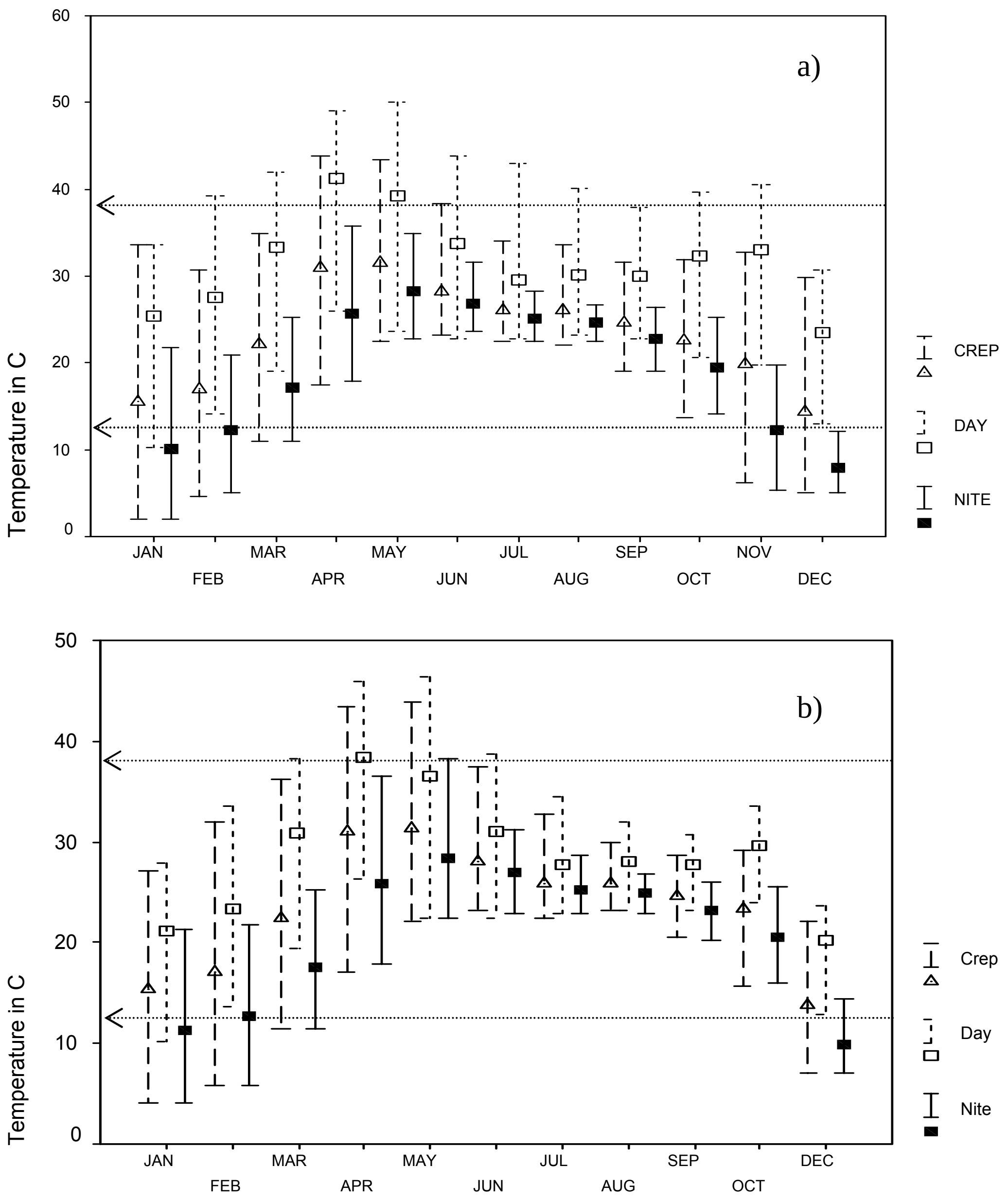


Fig. 5.17. Mean (markers), maximum and minimum (error bars) temperatures recorded in (a) forest-open, and (b) forest-shade habitats in Panna NP, during different times of day in different months. Dotted lines denote lower and upper critical temperatures of the sloth bear (McNab 1992).

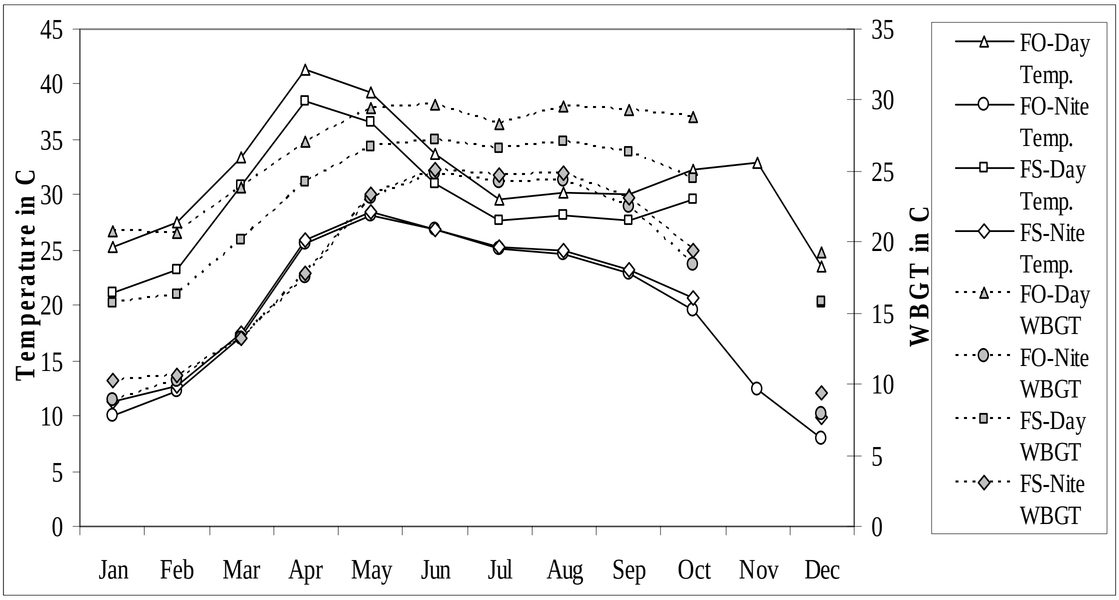


Fig. 5.18. Mean monthly day and night temperature (solid lines), and Wet Bulb Globe Temperature (WBGT; dotted lines), in forest-open and forest-shade habitats in Panna NP.

In the forest-open habitat, temperatures were the highest in dry season, followed by wet and then cold seasons, while the temperature ranges were the smallest in the wet season and the largest in the dry season (Fig. 5.19a). In all seasons, over a day, temperatures started rising at about 7:00, rose quickly and reached a peak between 12:00 and 14:00 and then dropped quickly until about 18:00, and then declined slowly through the night hours until about 6:00, when the temperatures were the lowest. Mid-day temperatures were not substantially different between the wet and cold seasons. RH values were the highest in wet season and the lowest in dry season (Fig. 5.19b). Relative changes in RH values over the day were similar to temperature, but in the opposite direction, i.e., reached the lowest during mid-day and the highest in the early morning. Mean RH values were above 80% during most parts of the day and above 60% even during mid-day in the wet season, whereas in the dry season, RH values were lower than 60% even in the early morning and were as low as 25% in the mid-day. In the cold season, RH values showed high variability, ranging from about 90% in the early morning to about 25% in the mid-day.

In the forest-open habitat, temperature and WBGT had similar patterns of change over a day in all seasons (Fig. 5.20a). WBGT in cold season was much lower than dry and wet seasons, similar to temperature (excepting midday when temperatures were not very different between cold and wet seasons). However, in contrast to temperature, WBGT was higher in wet season than in dry season at all times of day (except at afternoon hours when they were similar). The relative positions of temperature and WBGT profiles (absolute values can not be compared because they are on different scales) were similar between cold and dry seasons, but different in the wet season (Fig. 5.20a). Similar patterns of change in WBGT over a day, difference among seasons, and relative profile positions of temperature and WBGT were seen in the forest-shade habitat (Fig. 5.20b). Excepting that the day time WBGT values were lower, and night time values were slightly higher and so the profile was flatter in the forest-shade habitat as compared to the humped profile of forest-open habitat.

Den temperatures were the highest in dry season, followed by wet season, which is only marginally lower than the dry, and the lowest in cold season (Fig. 5.21). The mean of temperatures of all dens was about 27 ^{o}C in the dry season, 25 ^{o}C in the wet and 18 ^{o}C in the cold season. There were minimal differences in den temperatures among the periods of day in any season. The differences in mean temperatures among the different dens in a season too were not large (all were < 6 ^{o}C). The maximum temperature in any of the measured den in the dry season was not over 34 ^{o}C and the minimum in cold season was not lower than 15 ^{o}C. Dens had the lowest day time temperature among the three microhabitats important for sloth bear in all seasons (Fig. 5.22). At night, den temperatures were slightly higher than the two forest microhabitats in the dry and wet seasons and substantially higher in the cold season. Temperatures in the forest-open habitat were higher than forest-shade in the day time in all seasons and the reverse was seen in the night time.

Temperature variability in the different microhabitats, measured as range (maximum-minimum) of temperature and temperature (in ^{o}C) change per hour was the lowest in dens in both day and night in all months (Figs. 5.23a, b). Forest-open habitat in day time showed the highest variability, followed by forest-shade habitat. In the night, both the forest microhabitats showed similar variability. Temperature range during day was over 20 ^{o}C in forest-open habitat in many months, whereas it was less than 5 ^{o}C in dens in most months. Temperature range in day, even in forest-shade was above 15 ^{o}C from January to June and was lower in the wet season months (Fig. 5.23a). Temperature change per hour was low during night in both the forest microhabitats, in all months (Fig. 5.23b). Temperature change per hour during day was less than half that in forest-shade than forest-open habitat in most months. There was over 2 ^{o}C change per hour observed in forest-open during day in several months, except in the late dry and wet season months. Although the forest-open habitat had cold season day temperatures much lower than dry season and mid-day temperatures comparable to wet season, the temperature change per hour during day was higher in cold season months than the other months, and particularly much higher than the wet season months.

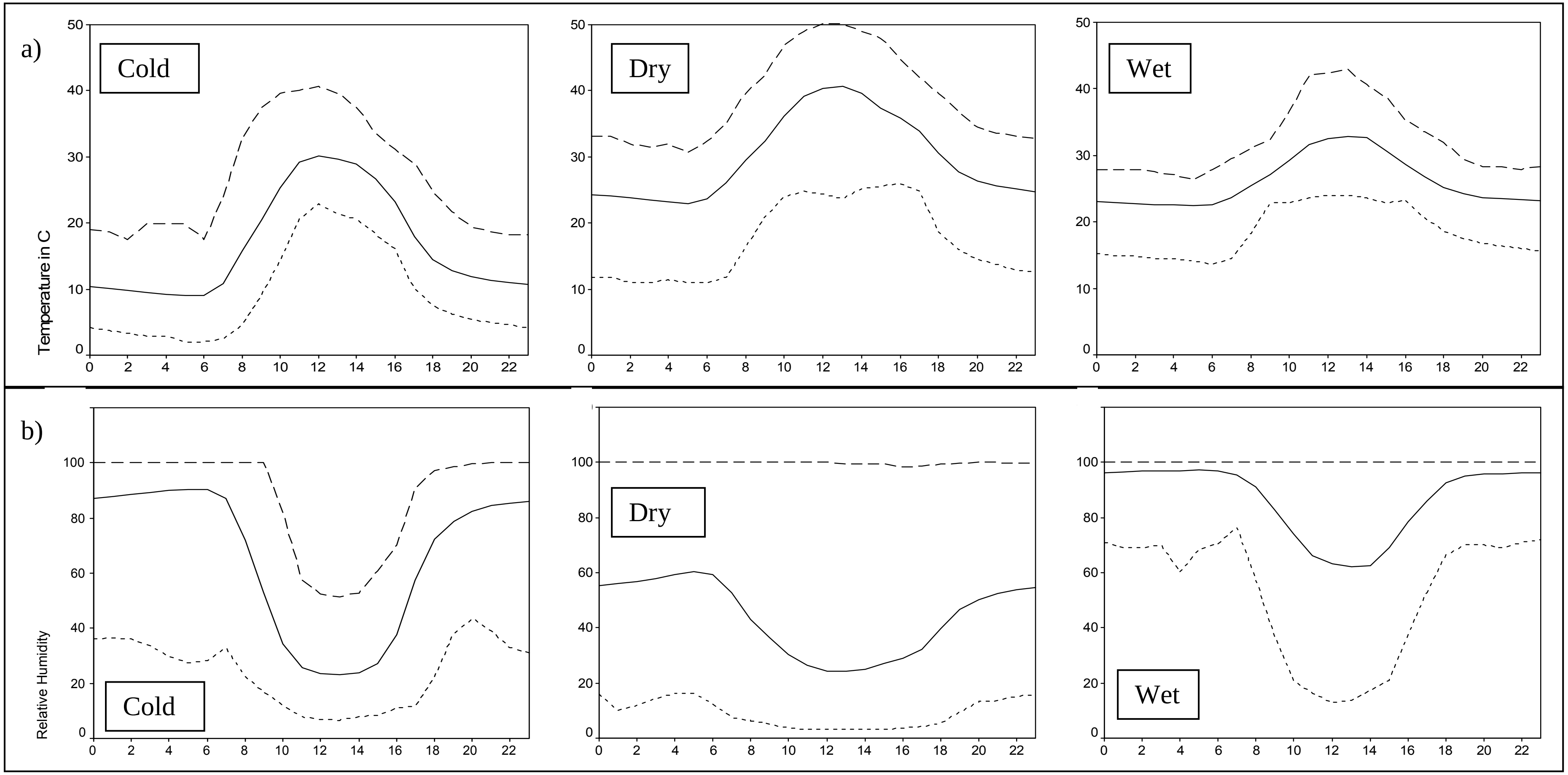


Fig. 5.19. Mean (solid line), maximum (broken line), and minimum (dotted line) of (a) temperatures, and (b) RH (%), during different hours of the day in different seasons, in forest-open habitat in Panna NP.

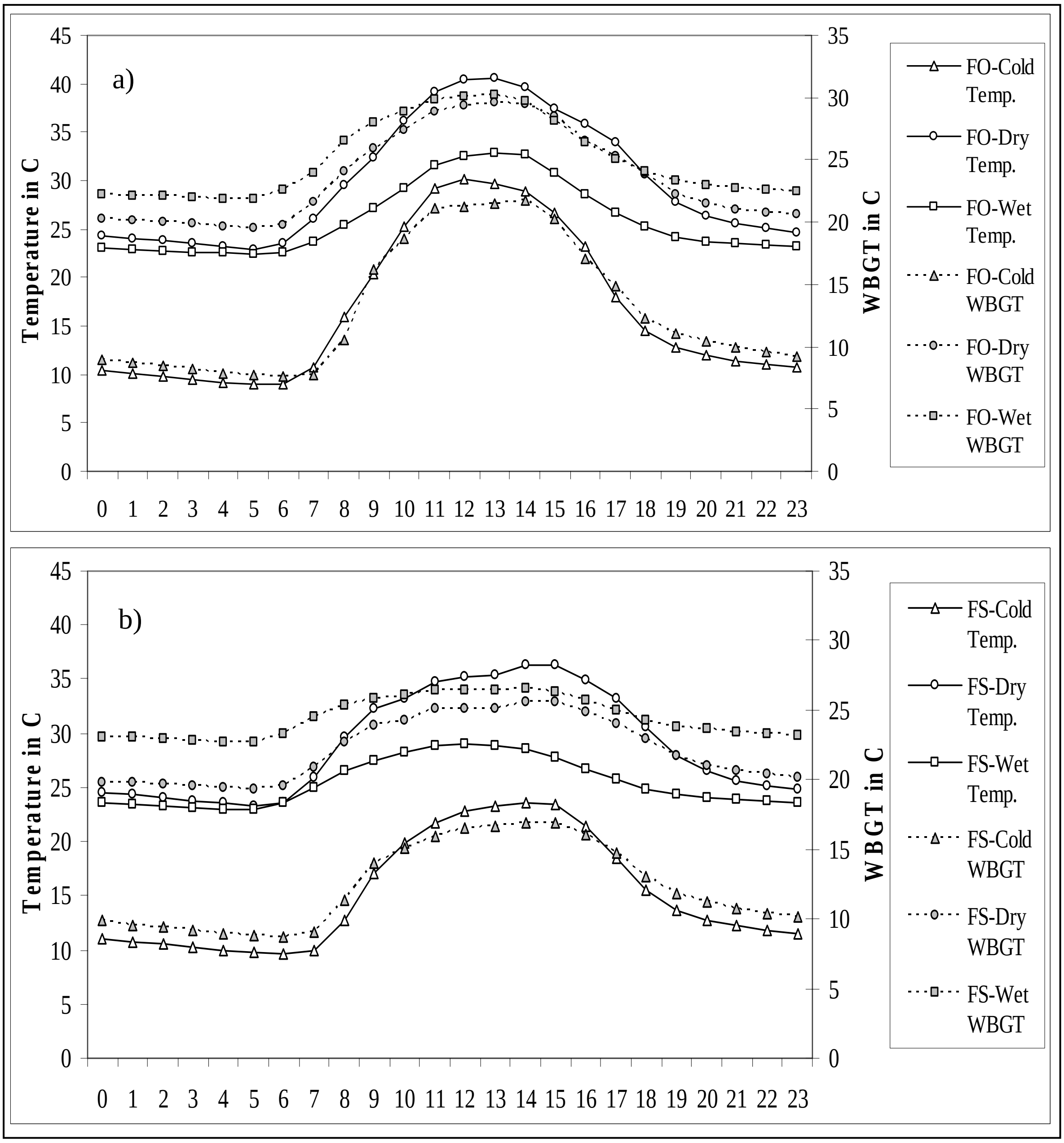


Fig. 5.20. Mean hourly temperature (solid lines), and Wet Bulb Globe Temperature (WBGT; dotted lines), in different seasons, in (a) forest-open, and (b) forest-shade habitats in Panna NP.

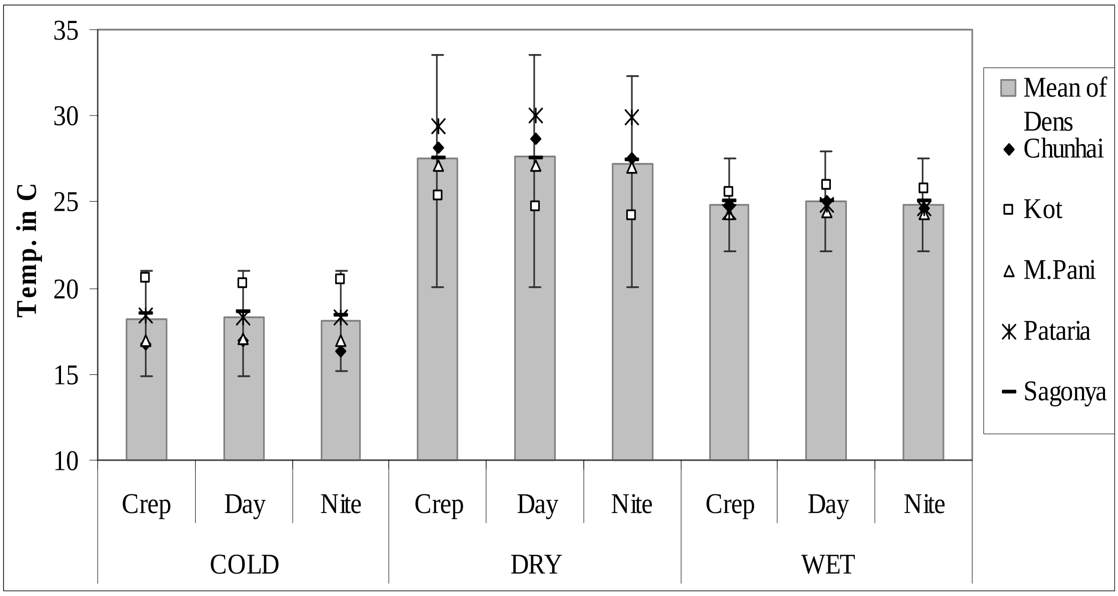


Fig. 5.21. Mean temperatures in different dens (markers) and mean (bars), maximum and minimum (error bars) of all dens during different periods of day in different seasons.

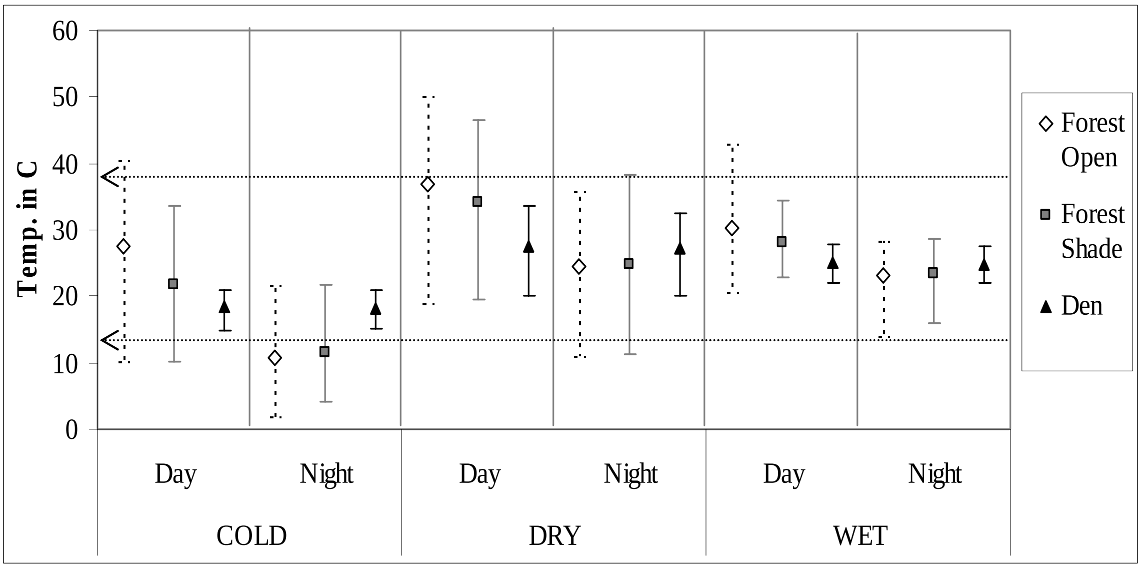


Fig. 5.22. Mean (markers), maximum and minimum (error bars) of temperatures recorded in forest-open (dashed line), forest-shade (grey line) and den (solid black line) habitats during day and night periods in different seasons. Dotted lines denote upper and lower critical temperatures of the sloth bear (McNab 1992).

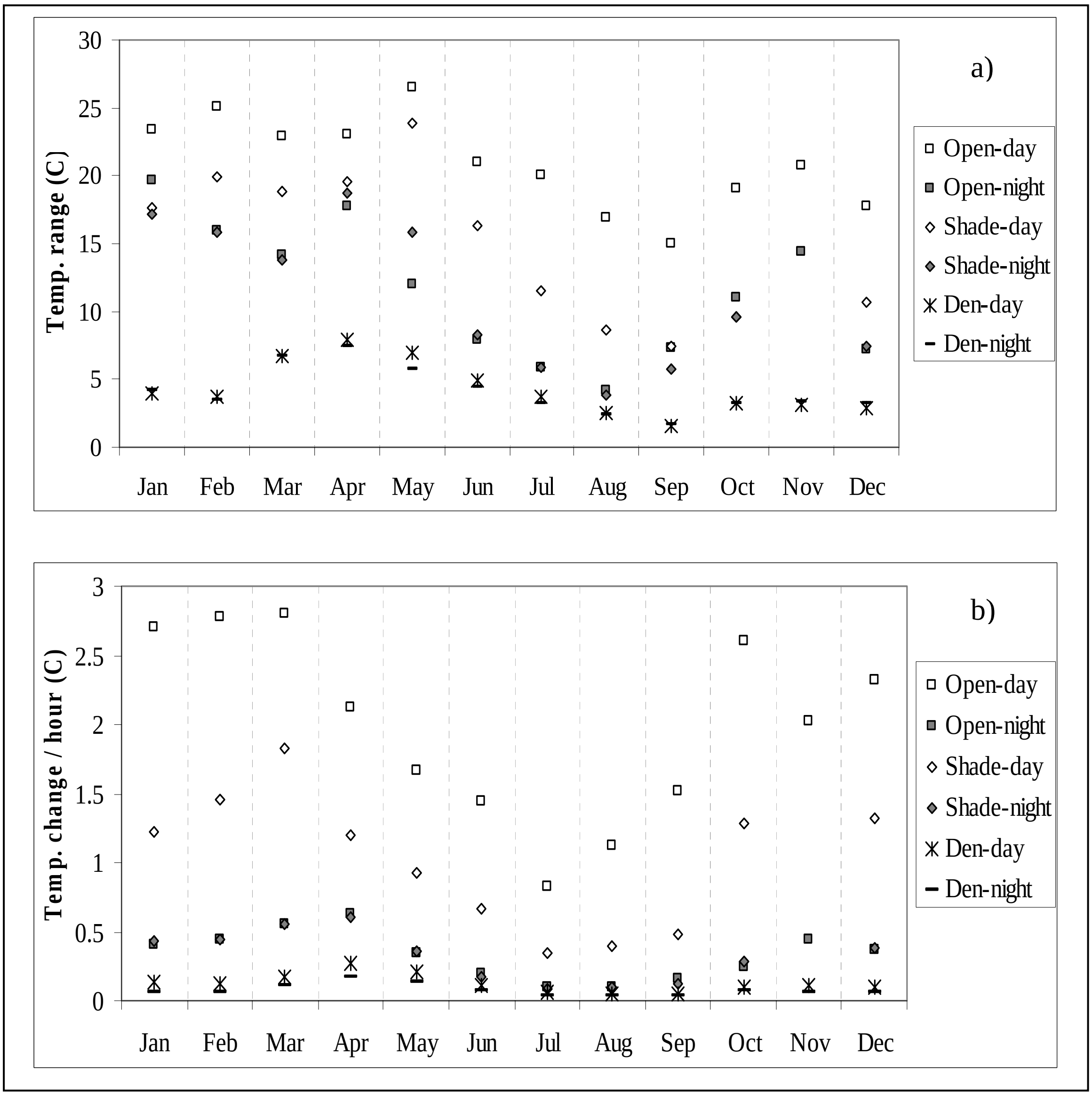


Fig. 5.23. Temperature variability measured as (a) range, and (b) change per hour, in different habitats, periods of day and months in Panna NP

Tiger activity pattern

The radio collared tigers that were monitored were generally nocturnal and crepuscular in activity during the dry and cold seasons (Fig. 5.24). The activity of tigers peaked during the crepuscular times, they predominantly rested during the mid-day, and they had a reduced level of activity in the post-midnight, pre-morning hours. The activity pattern was similar in the two seasons, except for a considerably increased activity in the day and decreased activity in the night during the cold season as compared to the dry season, thus approaching a bimodal pattern of activity. Tigers were active for over 80% of the time in the mornings, and over 60% of the time in the evenings and nights, in both seasons (Fig. 5.25). Day activity was only about 20% in the dry season and about 40% in the cold season. Out of the whole day, tigers were active for about 60% of the time in cold season and for a slightly lower percent of time in the dry season.

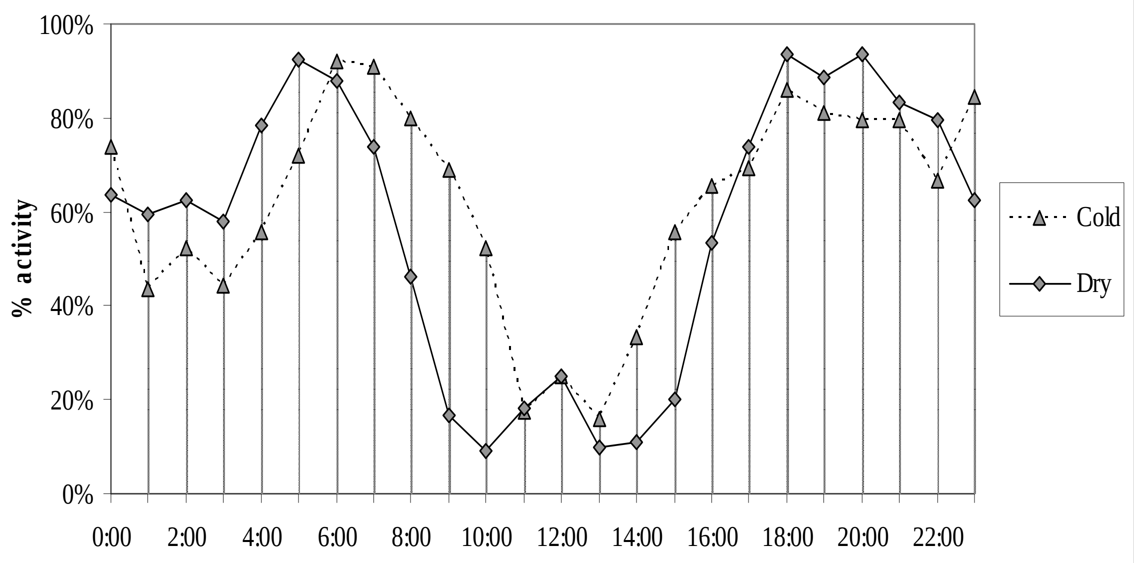


Fig. 5.24. Percent activity of tigers in different hours of day in cold and dry seasons.

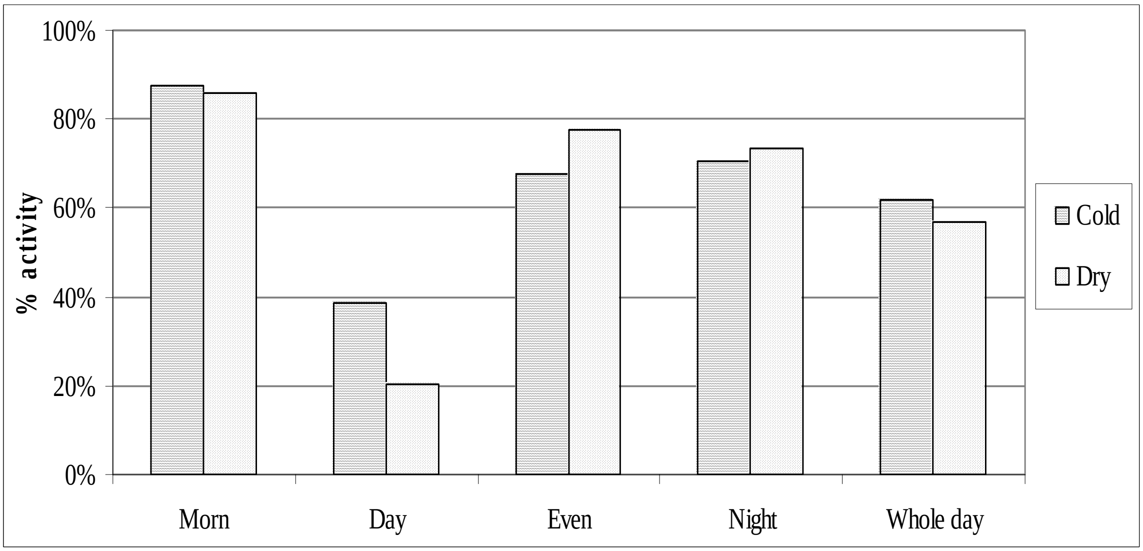


Fig. 5.25. Percent activity of tigers during different periods of day in cold and dry seasons.

Human activity pattern

Humans using the forest habitats in the study area, in general, showed a high level of activity in morning and evening, moderate level of activity in the mid-day, early mornings and late evenings, and a low level of activity in the immediate pre-morning and early night hours (Fig. 5.26). In the cold season, activity started later and ended earlier than wet and dry seasons. There was hardly any activity observed in the midnight hours. Humans were active for over 60% of the time in the morning, evening and day times in all seasons, day activity being lower than the crepuscular times (Fig. 5.27). Night activity was lower than 20% in cold and dry seasons, but was slightly higher in the wet season.

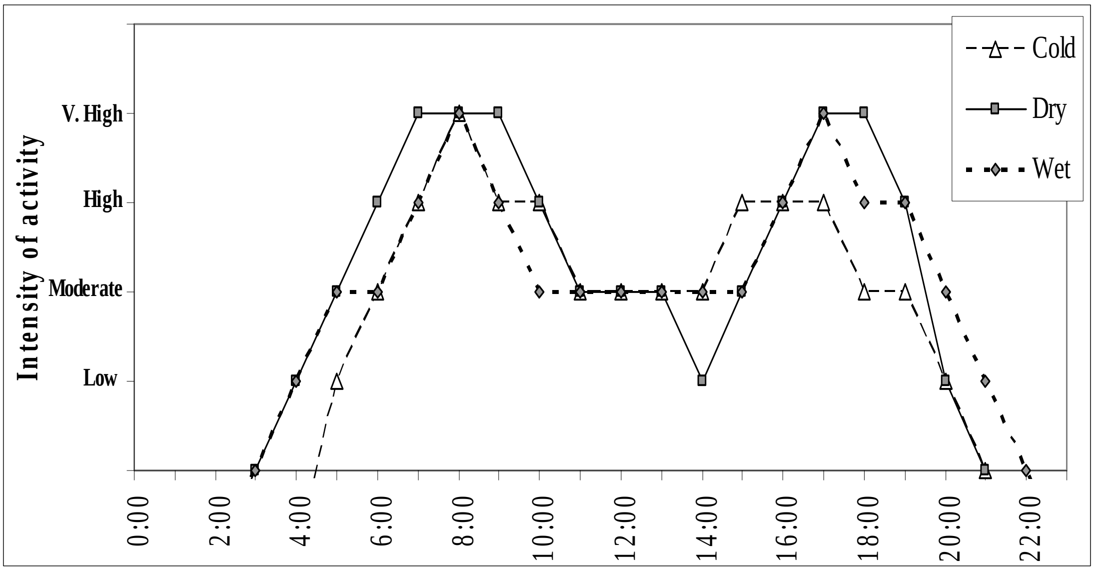


Fig. 5.26. Intensity of human activity during different hours of day in different seasons in the forest habitats of Panna NP

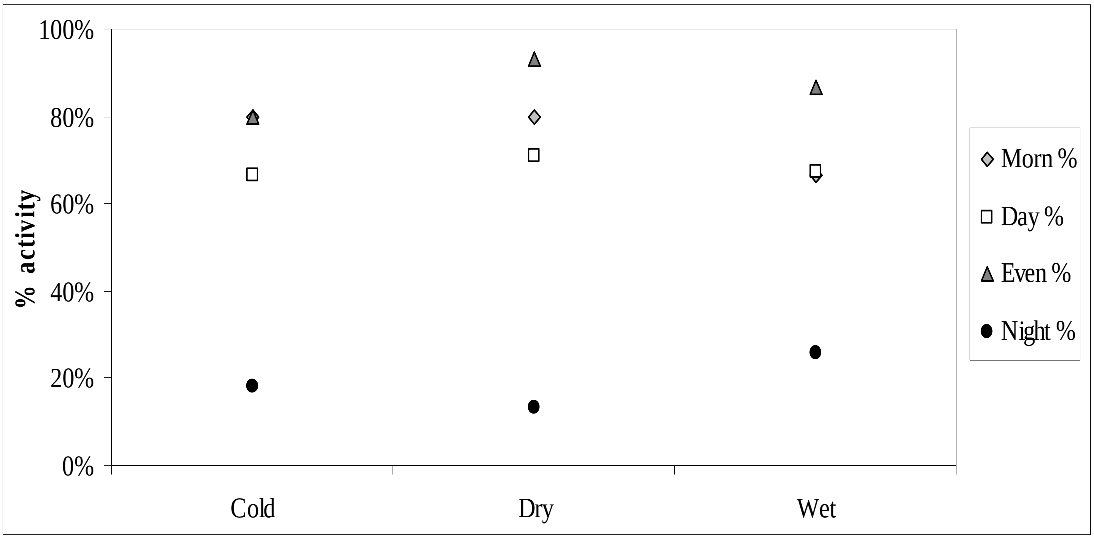


Fig. 5.27. Percent of time humans were active during different periods of day in different seasons.

Relationships between bear activity and thermal conditions of habitat

Bear activity in day time seemed to have an inverse relationship with the temperature observed in forest-open habitat, in all seasons (Fig. 5.28). However, the same relationship did not seem to hold for night activity. Sloth bear frequently experienced > 30 ^{o}C temperature, on any day over 20 ^{o}C temperature, and at times as high as 50 ^{o}C, during mid-day in the forest-open habitat. Their activity was minimal during that period of high temperature. In the night time, when bear activity was generally high, temperatures were commonly below 25 ^{o}C. Night temperatures in cold season were frequently about 10 ^{o}C or lower and in that season the bear activity declined to about 60% during midnight hours. But even at such low temperatures as 10 ^{o}C, or at high temperatures as 30 ^{o}C, if the period was crepuscular, bear activity nevertheless peaked. Mean hourly percent activity of bears in each season was strongly negatively correlated to temperature and heat indices of forest-open and forest-shade habitats (Figs. 5.29a, b; Table 5.3). In the wet season, WBGT showed a stronger relationship with hourly activity than did air temperature. The response of bear activity to temperature level differed between seasons. While activity was low in temperatures of about 25 ^{o}C in cold season, activity was very high at similar temperatures in wet and dry seasons.

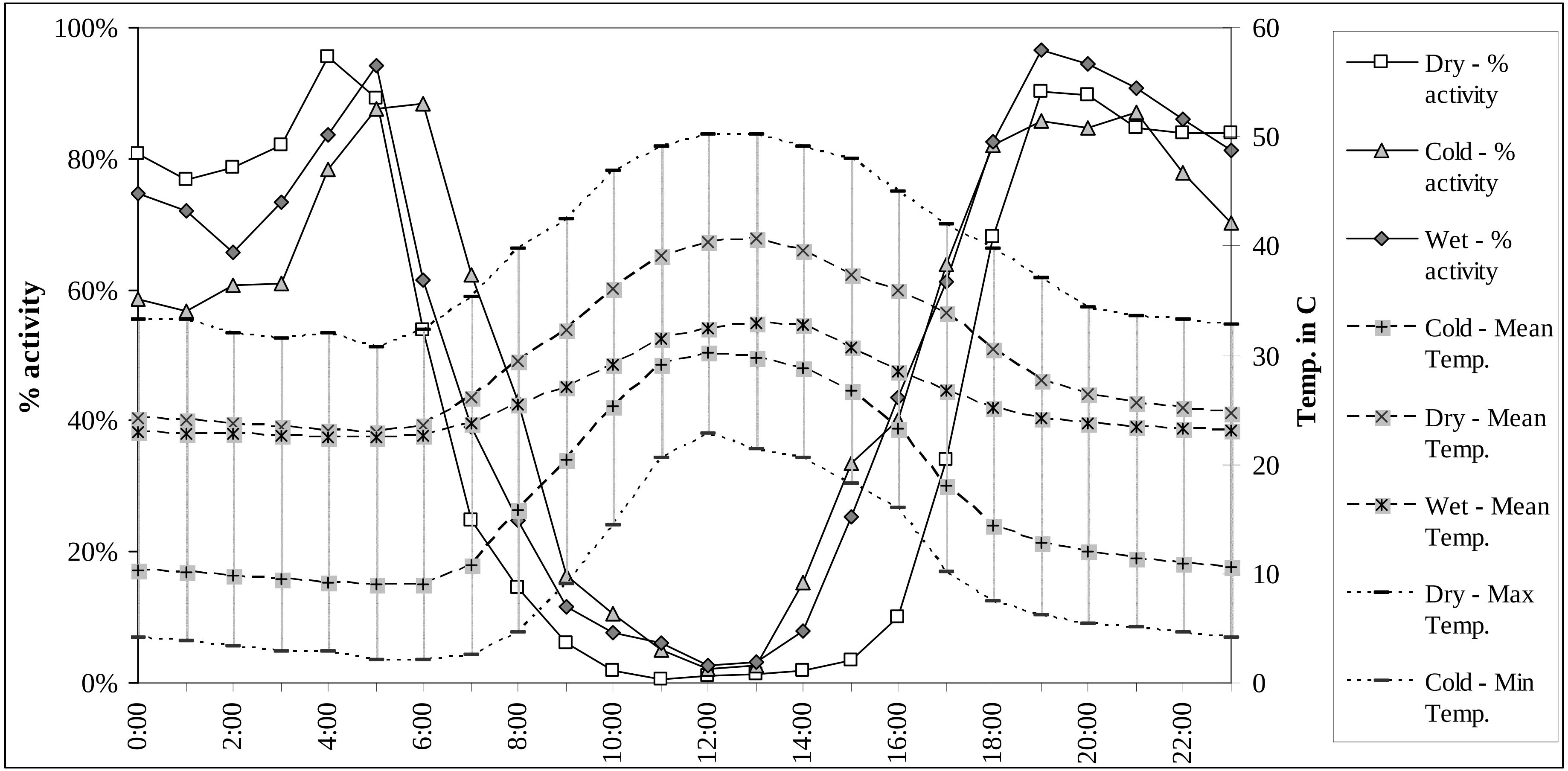


Fig. 5.28. Mean percent activity of radio collared sloth bears (solid lines, primary y-axis), mean temperatures in forest-open habitat (broken lines, secondary y-axis), during different hours of day in different seasons in Panna NP. Mean of maximum temperature recorded during dry season and mean of minimum temperature recorded during cold season (dotted lines) form the borders of the band of temperatures (marked with vertical lines) generally experienced by sloth bear in forest-open habitat in a year in Panna NP.

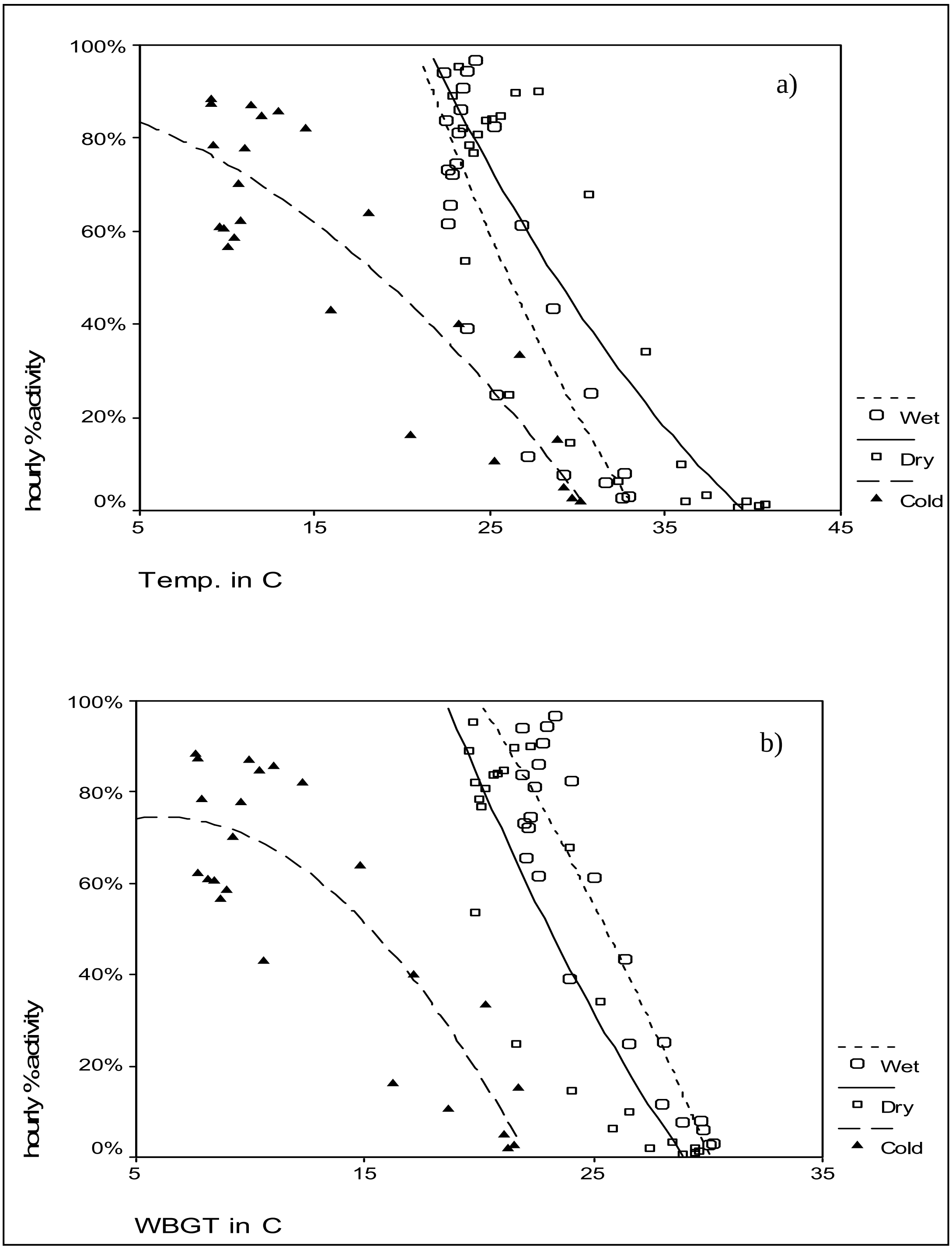


Fig. 5.29. Relationship between hourly percent activity of bears and (a) hourly mean air temperature, (b) WBGT, in forest-open habitat during different seasons. The tentative curve-fit lines are given only to indicate the direction and slope of relationships. The strength of relationships were measured by Spearman's rank correlation (see Table 5.3).

Table 5.3. Relationships of seasonal means of hourly percent activity of radio collared sloth bears in Panna NP with temperature and heat indices values in Forest-open and Forest-shade habitats (Spearman's r_s values were used as a measure of association; $P < 0.001$, N=24, for all correlations).

Seasons	Forest-open – Temp.	Forest-open – Bianca's ET	Forest-open – WBGT	Forest-shade – Temp.	Forest-shade – Bianca's ET	Forest-shade – WBGT
Cold	-0.74	-0.74	-0.71	-0.69	-0.69	-0.69
Dry	-0.80	-0.80	-0.81	-0.76	-0.78	-0.78
Wet	-0.71	-0.71	-0.77	-0.77	-0.77	-0.77

Percent activity of bears and mean temperatures in forest-open habitat during different hours of day were negatively correlated in all months, although not as strongly in a few months (Fig. 5.30; Table 5.4). Hourly activity was also strongly negatively correlated with Bianca's ET heat index in forest-open habitat and the temperatures and heat index values in forest-shade habitat in most months. Activity during midnight hours showed a weak positive correlation with temperature (Spearman's r_s =0.48, P<0.001, N=98; Fig. 5.31). However, hourly percent activity values were widely spread around the tentative regression line, indicating that at any level of temperature the activity levels varied considerably. A similar pattern of spread was repeated in each season, each of which showed nearly distinct midnight temperature levels. Overall, the midnight activity increased from cold to wet and then to dry seasons when temperatures too increased. However, within each season the relationship does not seem to hold. In a similar analysis, mid-day activity showed a weak negative correlation with temperature (Spearman's r_s = -0.49, P<0.001, N=68; Fig. 5.32). Mid-day temperatures overlapped among seasons, and up to about 35 ^{o}C, activity level varied considerably at each level of temperature. Overall, bear activity decreased as temperature increased across seasons. However, for all levels of mid-day temperature, there often were times (hours) when activity was very low or none.

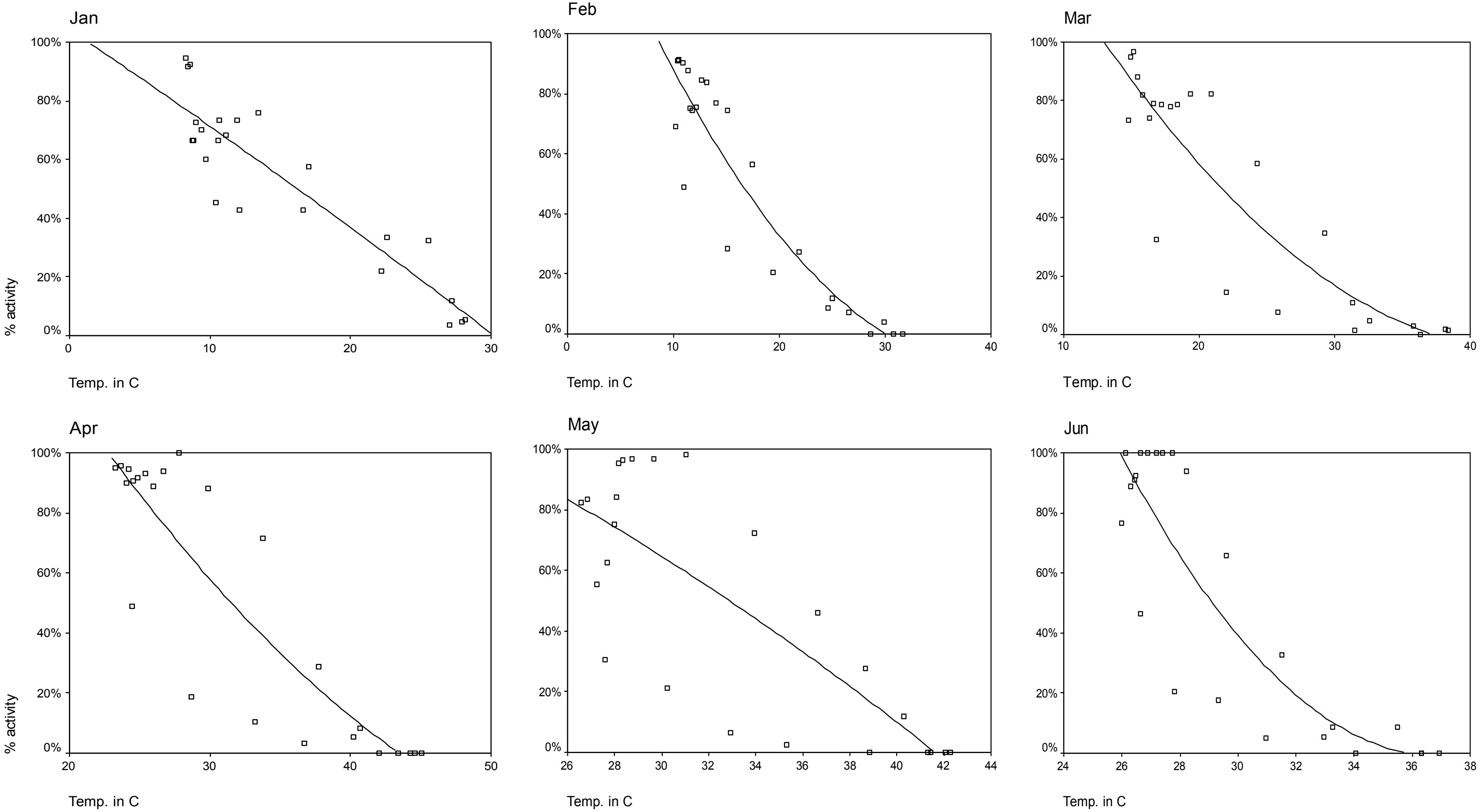


Fig. 5.30. Relationships between hourly percent activity of bears and hourly mean temperatures in forest-open habitat, in different months in Panna NP. The tentative curve-fit lines are given only to indicate the direction and slope of relationships. The strength of relationships were measured by Spearman's rank correlation (see Table 5.4).

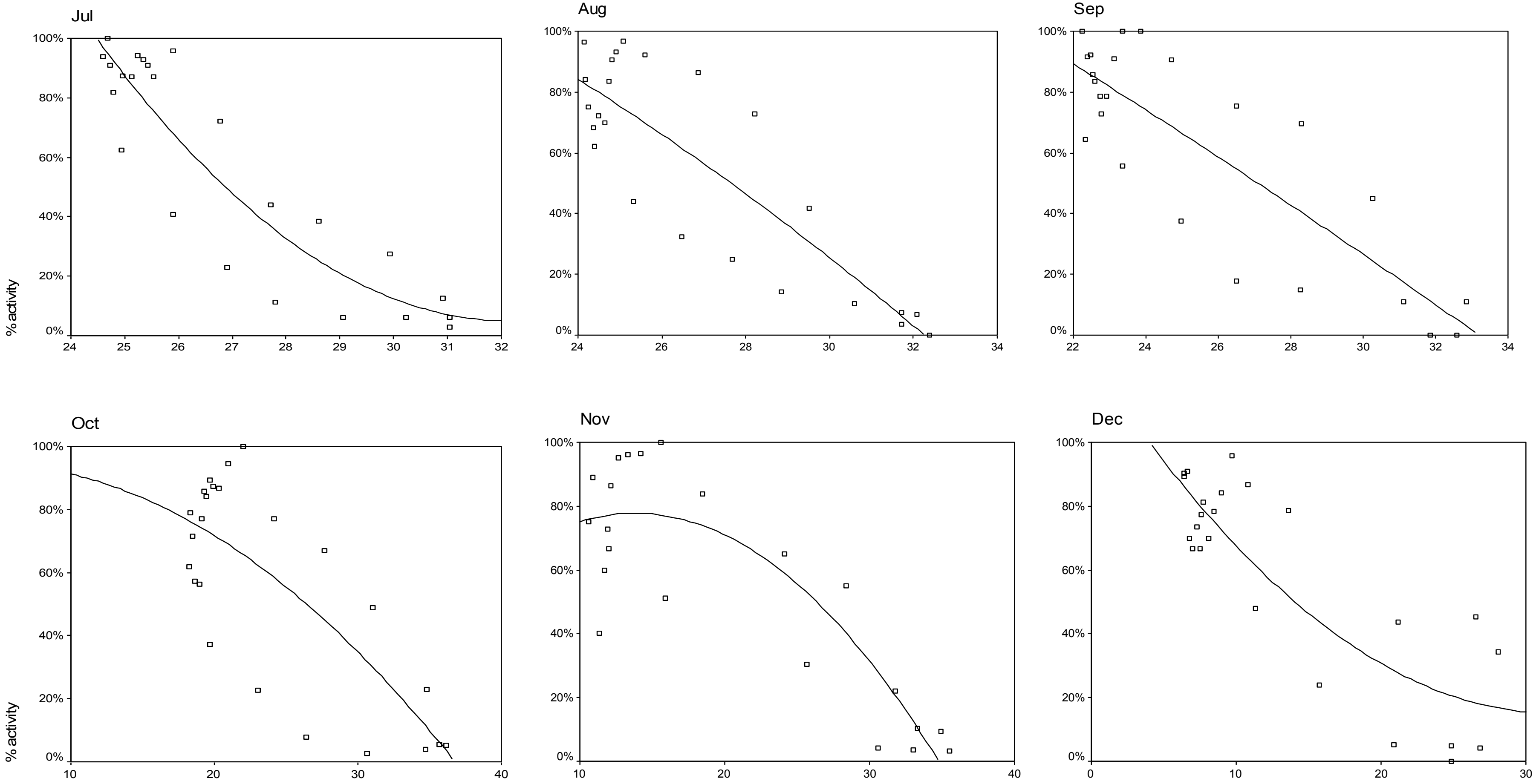


Fig. 5.30. Continued from previous page.

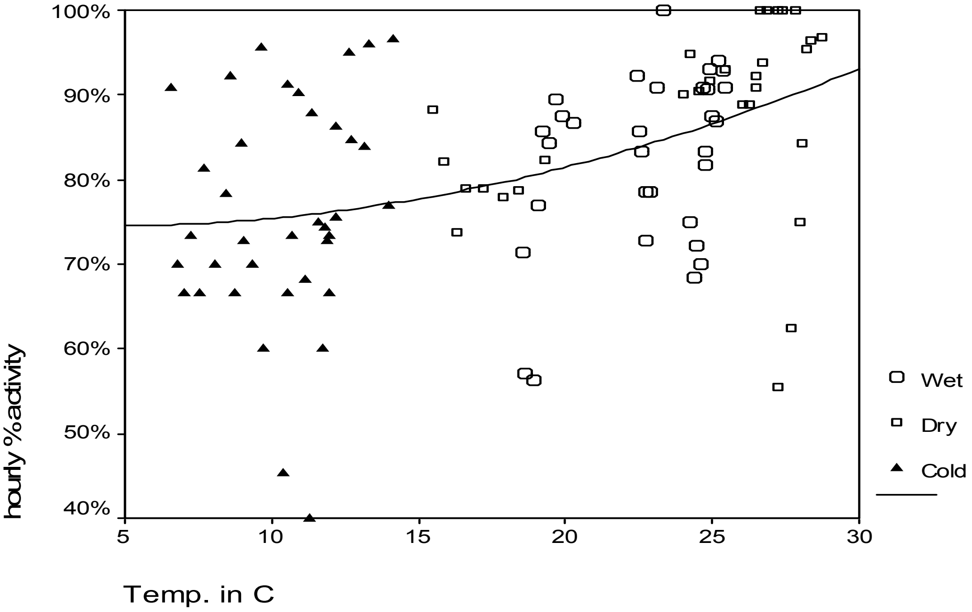


Fig. 5.31. Relationship between hourly percent activity of bears and hourly mean temperatures in forest-open habitat during midnight hours of each month (Spearman's r_S = 0.48, P<0.001, N=98). Points from different seasons are marked differently (Cold – solid triangle; Dry – hollow square; Wet – hollow circle).

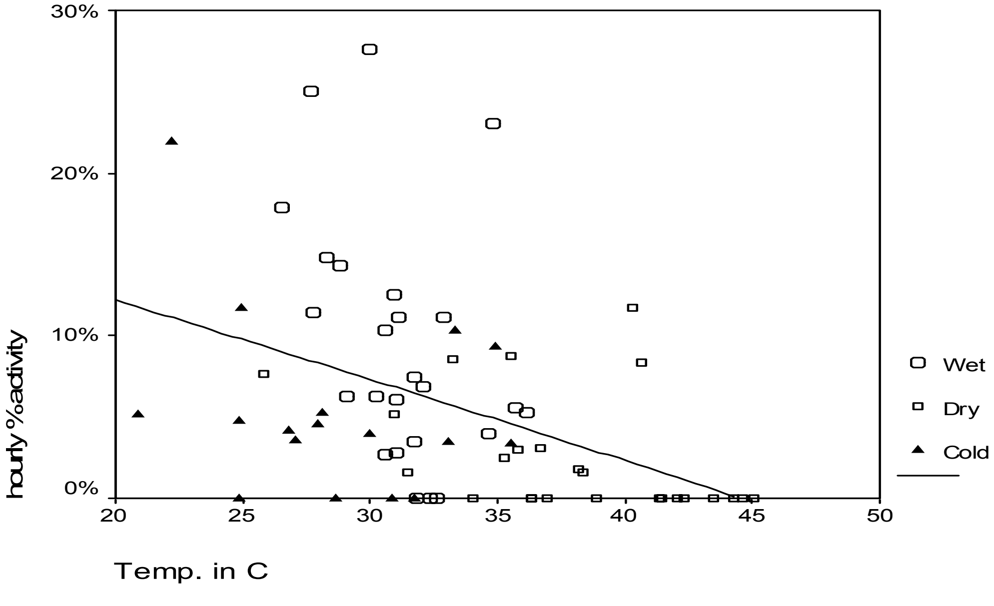


Fig. 5.32. Relationship between hourly percent activity of bears and hourly mean temperatures in forest-open habitat during mid-day hours of each month (Spearman's r_S = -0.49, P<0.001, N=68). Points from different seasons are marked differently (Cold – solid triangle; Dry – hollow square; Wet – hollow circle).

Table 5.4. Relationships of monthly means of hourly percent activity of radio collared sloth bears with temperature and Bianca ET heat index in forest-open and forest-shade habitats. Spearman's r_s values were used as a measure of association (for all correlations, $P < 0.001$, $N = 24$, except where given).

Months	Forest-open Temp.	Forest-shade Temp.	Forest-open Bianca's ET	Forest-shade Bianca's ET
January	-0.83	-0.78	-0.83	-0.78
February	-0.86	-0.83	-0.86	-0.84
March	-0.84	-0.82	-0.84	-0.84
April	-0.87	-0.86	-0.88	-0.87
May	-0.69	-0.65 ($P = 0.001$)	-0.70	-0.67
June	-0.78	-0.74	-0.76	-0.73
July	-0.84	-0.87	-0.82	-0.87
August	-0.70	-0.72	-0.69	-0.71
September	-0.74	-0.82	-0.73	-0.80
October	-0.52 ($P = 0.01$)	-0.60 ($P = 0.002$)	-0.54 ($P = 0.007$)	-0.62 ($P = 0.001$)
November [a] ($N = 22$)	-0.66 ($P = 0.001$)	--	-0.67 ($P = 0.001$)	--
December	-0.71	-0.71	-0.70	-0.71

[a] 2 hours in November were excluded due to low sample size ($N < 10$ logs each)

Response variables characterising bear activity showed diverse relationships with the main ecological explanatory variables considered in this study. Variables representing heat conditions showed strongest relationship with monthly bear activity levels, activity start and end times, and usage of day-resting habitat. Bear activity variables were also related to variables denoting usage of day-resting habitat (Table 5.5). Other food-habit related variables, which were thought to influence bear foraging behaviour and consequently the activity characteristics, did not show any strong ($r_s \geq 0.7$ or ≤ -0.7) relationships.

Table 5.5. Relationships between variables denoting monthly bear activity and various ecological explanatory variables, as measured by Spearman's rank correlation, r_s (for all, N = 12).

Bear activity characteristics	Forest-open day temp	Forest-open night temp	Forest-open day temp. range	percent of fruit in diet [a]	Fruit productivity in study area	Diet diversity	percent day-resting in Escarpment	percent day-resting in *Lantana*
% of whole day (24 h) active	-0.59 (*P*=0.05)	-0.30 (*P*=0.34)	-0.85 (P<0.001)	-0.23 (*P*=0.47)	-0.19 (*P*=0.56)	0.06 (*P*=0.85)	-0.71 (*P*=0.01)	0.65 (*P*=0.02)
% of Daytime active	-0.69 (*P*=0.01)	-0.31 (*P*=0.33)	-0.78 (P=0.003)	-0.23 (*P*=0.47)	-0.22 (*P*=0.48)	0.04 (*P*=0.9)	-0.59 (*P*=0.05)	0.55 (*P*=0.07)
% of Morning active	-0.77 (*P*=0.003)	-0.46 (*P*=0.14)	-0.57 (P=0.06)	-0.21 (*P*=0.51)	-0.32 (*P*=0.31)	0.00 (*P*=1)	-0.32 (*P*=0.32)	0.24 (*P*=0.46)
% of Evening active	0.26 (*P*=0.42)	0.42 (*P*=0.18)	-0.57 (P=0.05)	-0.05 (*P*=0.88)	0.48 (*P*=0.11)	-0.07 (*P*=0.83)	-0.45 (*P*=0.15)	0.49 (*P*=0.11)
% of Night active	0.55 (*P*=0.07)	0.85 (*P*<0.001)	0.05 (P=0.88)	0.41 (*P*=0.18)	0.11 (*P*=0.75)	-0.32 (*P*=0.31)	0.52 (*P*=0.08)	-0.55 (*P*=0.06)
Activity start time	0.40 (*P*=0.2)	0.48 (*P*=0.11)	0.62 (P=0.03)	0.03 (*P*=0.93)	-0.26 (*P*=0.42)	0.02 (*P*=0.95)	0.80 (*P*=0.002)	-0.84 (*P*=0.001)
Activity end time	-0.85 (*P*<0.001)	-0.90 (*P*<0.001)	-0.20 (P=0.53)	-0.34 (*P*=0.29)	-0.37 (*P*=0.24)	0.25 (*P*=0.43)	-0.46 (*P*=0.13)	0.46 (*P*=0.13)
Activity start before sunset [b]	-0.30 (*P*=0.34)	-0.10 (*P*= 0.76)	-0.89 (P<0.001)	-0.12 (*P*=0.71)	0.10 (*P*=0.76)	0.04 (*P*=0.91)	-0.78 (*P*=0.003)	0.78 (*P*=0.003)
Activity end after sunrise[c]	-0.56 (*P*=0.06)	-0.25 (*P*=0.44)	-0.36 (P=0.25)	0.29 (*P*=0.37)	-0.13 (*P*=0.68)	0.28 (*P*=0.38)	-0.24 (*P*=0.46)	-0.33 (*P*=0.3)
% day-resting in escarpment	0.29 (*P*=0.37)	0.48 (*P*=0.11)	0.80 (*P*=0.002)	0.40 (*P*=0.2)	-0.03 (*P*=0.93)	-0.33 (*P*=0.3)	--	--
% day-resting in *Lantana*	-0.22 (*P*=0.48)	-0.46 (*P*=0.13)	-0.73 (*P*=0.007)	-0.26 (*P*=0.42)	0.17 (*P*=0.6)	0.36 (*P*=0.26)	--	--

[a] % of insect in diet is largely a complement of fruit in diet. So, it shows relationships similar in strength to fruit, but in the reverse direction

[b] activity start time, after adjusting for sunset time

[c] activity end time, after adjusting for sunrise time

Day temperature in forest-open habitat was strongly inversely correlated to percent of daytime, and percent of morning bears were active, and time of activity end. Night temperature was strongly positively correlated to percent of night time bears were active, and negatively correlated to time of activity end. Temperature range experienced in daytime in forest-open habitat was strongly negatively related to percent of whole day, and percent of daytime bears were active, negatively related to the interval prior to sunset time bears started their activity, and strongly positively related to percent day-resting in escarpment habitat. Percent of month sloth bears day-rested in escarpment habitat was strongly positively related to the time bears started activity and negatively related to the interval prior to sunset time bears started activity. Percent day-resting in *Lantana* cover, which largely complements resting in escarpment habitat, as expected, showed relationships inverse to that shown by escarpment resting.

Interestingly, the interval ahead of sunrise time bears ended activity did not show any relationships with the explanatory variables, although the time bears ended activity itself had strong inverse relationships with daytime and night temperatures (Table 5.5). Just as activity end and activity start times had relationships with temperature, sunrise and sunset times too showed strong relationships with temperature (Fig. 5.33). Monthly mean sunrise time was negatively correlated with monthly mean temperature (Spearman's rank correlation coefficient r_s = -0.92, P<0.001, N=12), and sunset time was positively correlated with temperature (r_s =0.81, P=0.001, N=12). Also, activity start time was positively correlated to sunset time and activity end time was positively correlated to sunrise time (Figs. 5.34a, b; Table 5.6). Partial correlation analysis of these interrelated variables revealed the relationships bear activity start and end times had with each of the explanatory variables, after the exclusion of the effect of other variables (Table 5.6). After controlling for the effect of temperature, activity start time was positively related to sunset time, while activity end time showed no relationship with sunrise time. When controlled for the effect of sunset time, activity start time did not show a relationship with temperature, but a strong positive correlation with range in daytime temperature in forest-open habitat. When controlled for sunrise time, activity end time showed a negative relationship with temperature, but had no relationship with range in daytime temperature. Activity start time showed a strong positive correlation with percent day-resting in escarpment habitat, even after controlling for both sunset time and mean temperature. However, when controlled for sunset time and range in daytime temperature, activity start time did not show a relationship with percent day-resting in escarpment habitat.

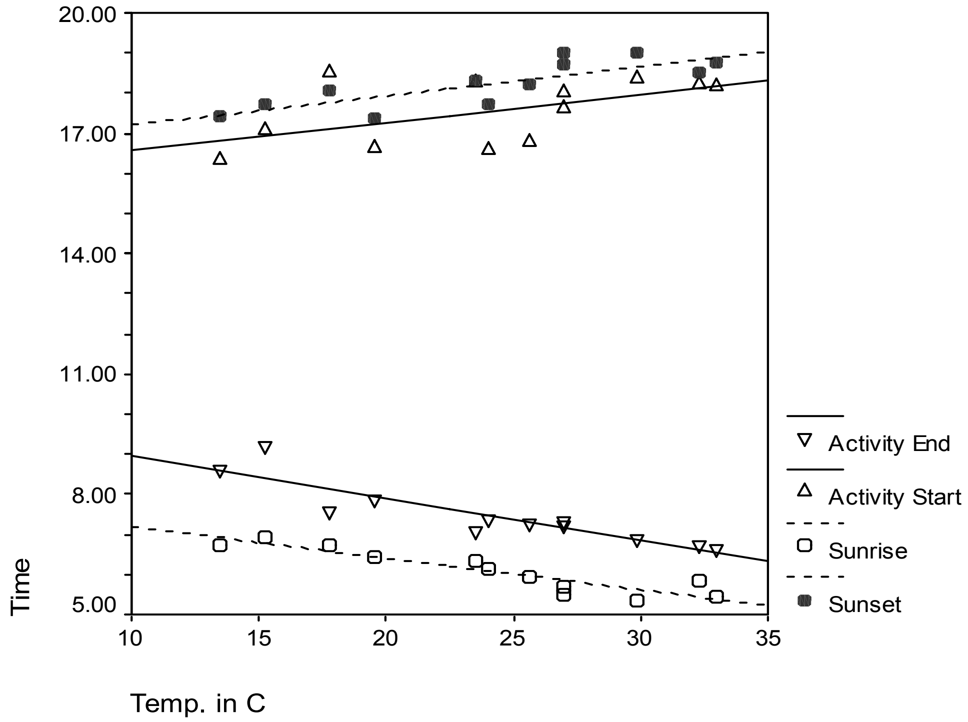


Fig. 5.33. Relationships of monthly mean bear activity start and end times with monthly mean temperatures in forest-open habitat in Panna NP (see Table 5.6 for strength of relationships; see text for relationships of monthly mean sunrise and sunset times with temperature).

Table 5.6. Relationships of bear activity start and end times with sunrise, sunset times, and temperature in forest-open habitat measured as Pearson's correlation coefficient *r*, and the relationships after controlling for other variables, by partial correlation analysis. *P*, and *df* are given in parenthesis.

Bear activity variable	Sunrise	Sunset	Sunrise [a]	Sunset[a]	Forest-open temp.	Forest-open – range in day temp.	% day-resting in escarp-ment [d]	% day-resting in escarp-ment [e]
Activity start time	--	0.76 (0.004, 10)	--	0.66 (0.03, 9)	-0.21 [b] (0.54, 9)	0.81 [b] (0.003, 9)	0.77 (0.009, 8)	0.22 (0.54, 8)
Activity end time	0.81 (0.001, 10)	--	-0.08 (0.81, 9)	--	-0.66 [c] (0.03, 9)	-0.35 [c] (0.3, 9)	--	--

[a] Controlling for temperature in forest-open habitat

[b] Controlling for sunset time

[c] Controlling for sunrise time

[d] Controlling for sunset time and temperature in forest-open habitat

[e] Controlling for sunset time and range in day temperature in forest-open habitat

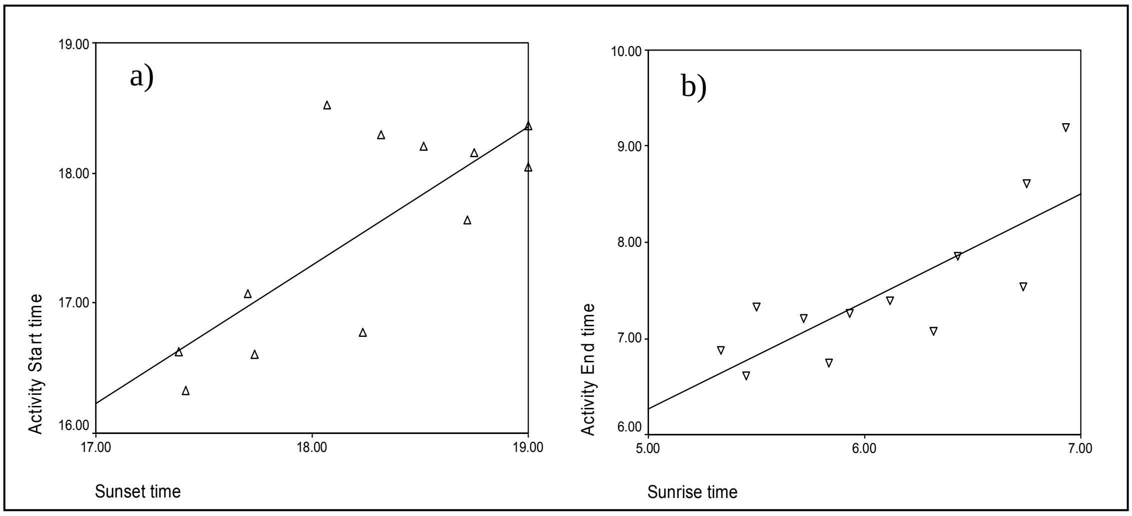


Fig. 5.34. Relationships between monthly means of (a) bear activity start time and sunset time, and (b) bear activity end time and sunrise time, in Panna NP (see Table 5.6 for strength of relationships).

Relationship between bear activity pattern and tiger and human activities

Diel activity patterns of bear and tiger were similar to a large extent, in the two seasons tigers were monitored (Fig. 5.35). The activity peaks of both species more or less coincided in the mornings and evenings. The differences were: tiger activity extended longer into the morning and day periods than bear's, midday rest period of tigers were shorter, they started their activity after midday resting earlier than bears, and their post-midnight, pre-morning activity were lower than that of bears'. Hourly percent activity of bears and tigers in the cold and dry seasons were strongly positively correlated (r_s =0.77, P<0.001, N=48). High levels of activity of both the species occurred in night and crepuscular times (Fig. 5.36). In the day hours when tiger activity was considerably high, bear activity remained low.

Human activity overlapped highly with that of bear activity during early morning and evening hours, in all seasons (Fig. 5.35). A low level of overlap occurred in the late mornings, afternoons, and early nights. Overlap period was longer and the activity peaks of both bears and humans coincided in the evenings of wet and cold seasons. A relationship between hourly percent activity of bears and intensity of human activity could not be seen with the available evidence (null hypothesis of no relationship could not be rejected; r_s= -0.24, P=0.08, N=56), but given the large sample size, the actual relationship is probably none or at the most weak. During night hours when bear activity was high, human activity was low and during the day and some crepuscular hours when human activity was high, bear activity remained low (Fig. 5.37). High level of activity of both occurred in the crepuscular (primarily evening) period.

Partial correlation analysis revealed the relationships bear activity had with tiger and human activities, after controlling for the effect of temperature, with which bear activity was strongly correlated (Table 5.7). Bear activity was positively correlated with tiger activity, at all periods. With data from the whole day (except midnight times when human activity in forest habitat was negligible), bear activity was weakly negatively correlated with human activity and strongly positively correlated to tiger activity. With data from daytime, bear activity was not shown to be related to human activity. Whereas, in crepuscular period, bear activity was negatively correlated with human activity and in the night time, it was positively correlated with human activity.

Table 5.7. Relationships between seasonal means of hourly percent bear activity (arcsine transformed), hourly human activity (ranked based on intensity), and hourly percent tiger activity (arcsine transformed), measured as Pearson's correlation coefficient *r*, after controlling for hourly mean temperature in forest-open habitat, by partial correlation analysis.

% Bear activity	Human activity	% Tiger activity [a]
Whole day [b]	-0.27 (*P*=0.05, *df*=53)	0.72 (*P*<0.001, *df*=45)
Daytime	0.31 (*P*=0.16, *df*=20)	0.65 (*P*=0.01, *df*=12)
Crepuscular period	-0.56 (*P*=0.02, *df*=15)	0.72 (*P*=0.01, *df*=9)
Night time	0.70 (*P*=0.006, *df*=12)	0.58 (*P*=0.008, *df*=18)

[a] tiger activity data was from two seasons

[b] midnight hours when human activity in forest habitat was negligible was excluded from analysis

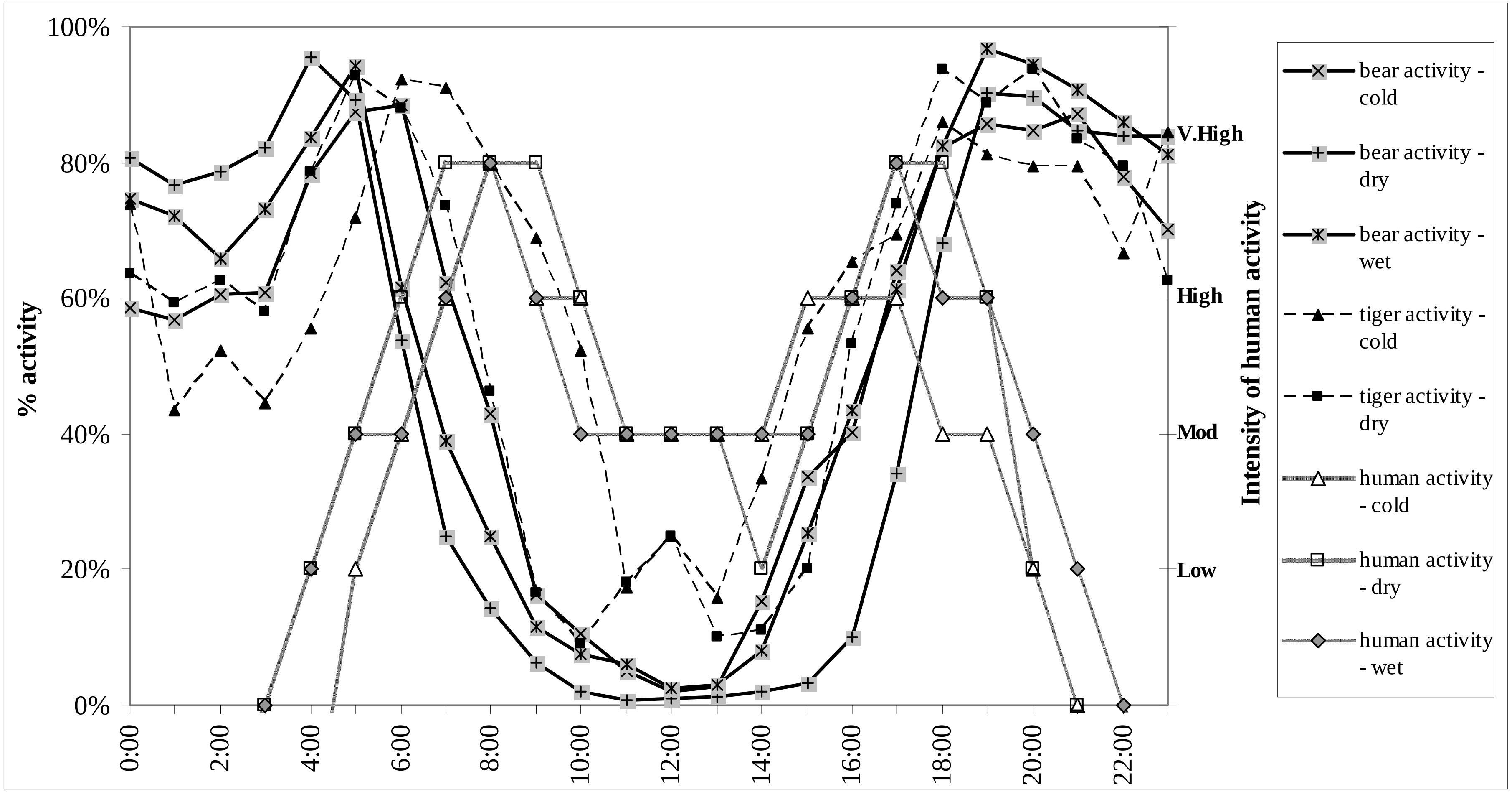


Fig. 5.35. Mean percent activity of bears (solid lines, primary y-axis), percent activity of tigers (broken line, primary y-axis), and intensity of human activity (grey shaded line, secondary y-axis), during different hours of day in different seasons.

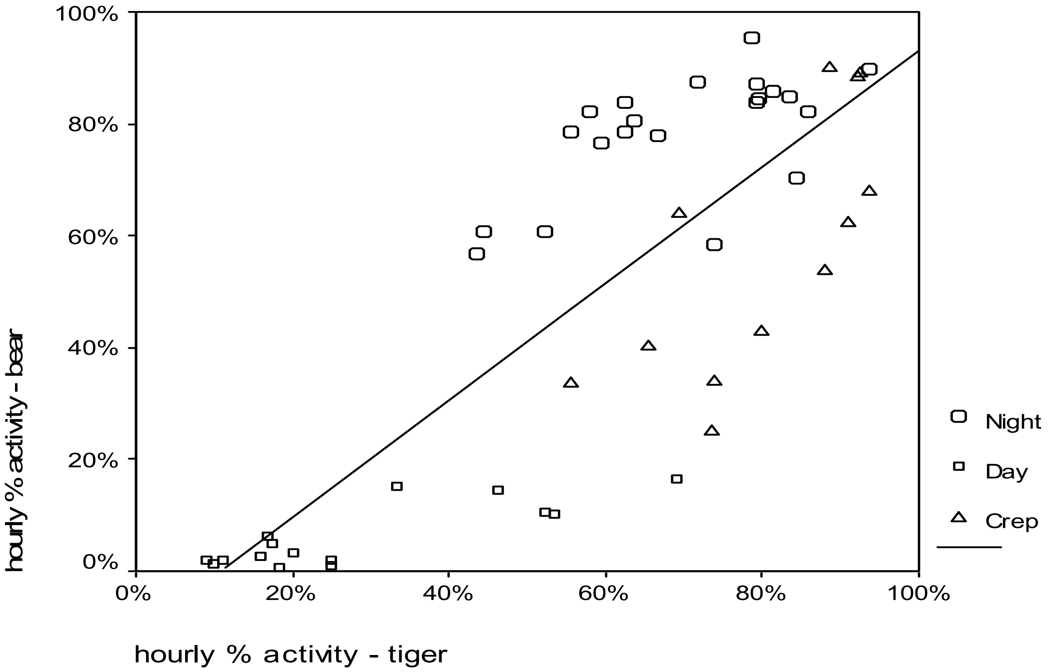


Fig. 5.36. Relationship between hourly mean percent activity of bears and tigers in cold and dry seasons in Panna NP. Scatter-points of different periods of day are marked differently. See text for strength of relationship.

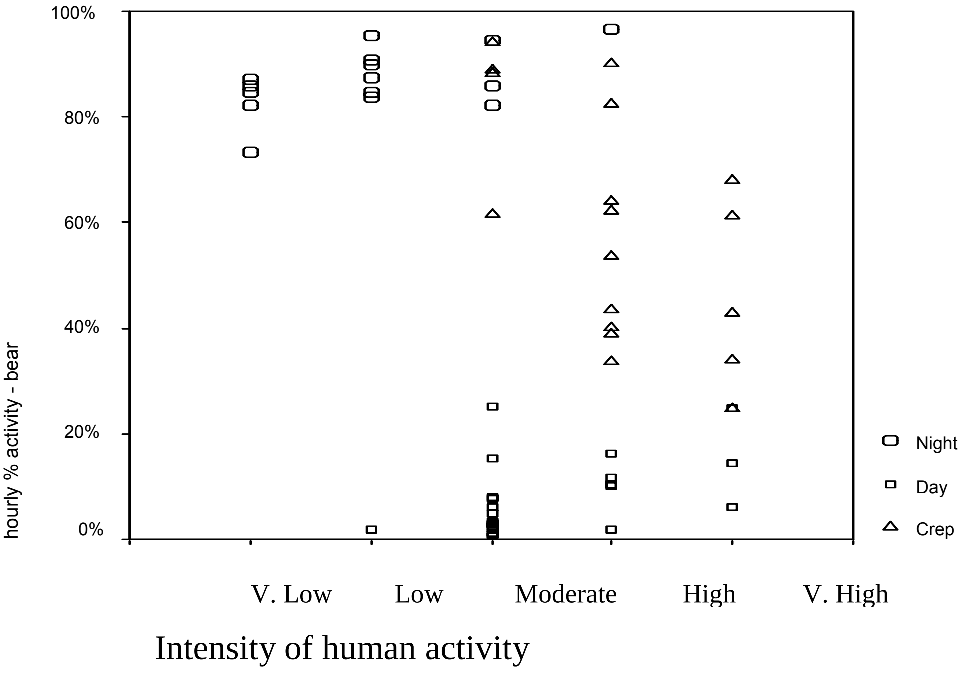


Fig. 5.37. Relationship between hourly mean percent activity of bears and intensity of human activity in all seasons (excluding midnight points when human activity was zero) in Panna NP. Scatter-points of different periods of day are marked differently. See text for strength of relationship.

Plate 7a. In addition to monitoring the activity of tagged bears using an automatic receiver-recorder unit, activity of 4 radio-tagged tigers, the main predators of sloth bears, were also monitored in Panna NP. Automatic trail monitoring cameras too were useful in monitoring the diel activity of bears and tigers.

Plate 7b. Sloth bears in Panna NP rested during mid-day, evidently to avoid adverse thermal conditions. They rested often under boulders, in caves, and such sheltered sites found in the escarpment habitat. After several-hours-long day-resting, the bears emerged in the evenings to forage during the crepuscular and night periods.

5.4. DISCUSSION

Sloth bears in Panna NP were essentially nocturnal and crepuscular in activity and they rested during midday, in all seasons. The bears started their activity in the evenings, after their long midday resting, were active through the night (sometimes with a few hours of rest during midnight, particularly in the cold season), and ended their activity in the mornings. They rested during day mostly in natural dens found commonly in escarpment habitat, and in dense cover provided by *Lantana* shrub thickets. The relative usage of these two microhabitats for day-resting by bears varied considerably among seasons and among individual bears. A few bears that had home ranges in peripheral areas showed considerably different activity patterns and usage of habitat for day-resting, but were still comparable with the general pattern.

What factors influence the bears to be active during night and rest during day?

In general, bear activity decreased when temperatures or heat index values increased and vice versa, in all seasons. High temperatures (> 30 ^{o}C) combined with or without high relative humidity during day time caused high thermal stress conditions and correspondingly the bear activity remained low during day. If the bears were to be active at such temperatures, the rate of metabolism may increase up to 6 times that of basal rate (Schmidt-Nielsen 1990, McNab 1992), and this would cause a need to remove a lot more heat from the body, than if they were resting. The sloth bear has a higher thermal conductance than expected from mass (McNab 1992), and therefore they might be efficient in removing heat from body through conduction. However, this characteristic may not help during the dry (hot) season, when temperature differential with the surroundings may not be suitable for heat removal. Also, in the dry season, water balance might be a constraint to effect large-scale evaporative heat loss. Therefore, the bears would be better off to rest during day and also to choose to rest in sites where they could decrease heat gain and increase heat loss. Even if temperatures are not too high in some seasons, but relative humidity is high, the bears cannot cool themselves effectively by evaporation (Schmidt-Nielsen 1972, 1990).

In contrast to daytime, night time temperatures were generally not high (< 25 °C), and probably within the sloth bear thermo-neutral zone (thermo-neutrality in sloth bear was reported from 13 °C to 38.5 °C; McNab 1992). The bear activity correspondingly remained high at night, largely irrespective of changes in temperature. However, when night temperatures in cold season fell below 10 °C frequently (i.e., below the probable lower critical temperature for sloth bear), bears reduced their night activity, perhaps to reduce heat loss. At cold temperatures, activity causes additional thermoregulatory cost above that occurring in a resting animal (Robbins 1993). Remarkably, even at such low temperatures in the early mornings and at relatively high temperatures in the late evenings, bears nevertheless showed peaks in activity. This apparent independence with temperature is probably caused by two factors: 1) the bears moved between their day-resting sites and foraging grounds during those peak periods, before ending and starting their daily activity; 2) Peaks in activity synchronised with dawn and dusk, probably maintained by an endogenous rhythm, as they have been observed for many other animals (Aschoff 1966, Mech *et al.* 1966, Enright 1970, Kavanau and Ramos 1972).

Further, the response of activity to temperature differed between seasons. For example, at around 25 °C temperature, the bear activity was low in cold season, while it was high in wet and dry seasons. It is apparently because 25 °C in cold season occurred during daytime, while it occurred in the night and crepuscular times in the other seasons, and it is likely that the bears avoid daytime as a routine (daily rhythm probably developed over a long period of time) and not respond to concurrent temperature on a seasonal or day-to-day basis. The bears avoided daytime perhaps based on probabilities (Enright 1970) of avoiding daytime harsh thermal conditions. It is also possible that this difference in activity responses could be caused by different heat tolerance or thermoregulatory capacity in different seasons (due to endogenous seasonal cycles or acclimatization). For instance, animals are known to have seasonal differences in thermal conductance levels (Robbins 1993), metabolic rate (Pengelley and Asmundson 1974, Robbins 1993), digestibility (Brody and Pelton 1988), body condition (Hellgren *et al.* 1989), body weight (Franzmann and Schwartz 1988), and other physiological characteristics (Hellgren *et al.* 1989). Similar seasonal changes in physiological characteristics could even have contributed to the development of fixed activity routine in sloth bears (or vice versa), rather than seasonally changing activity patterns. However, other factors that might be influencing bears in not becoming more diurnal or crepuscular and less nocturnal in the cold season are not clear. Similarly, the factors influencing bears in not being active, at least in shaded habitats, in much of daytime are not known. It might be that the bears need a single long stretch of time to rest, and another long stretch of time to forage. In such a case, the best period to avoid foraging is daytime, even in the cold season, due to the high temperatures experienced in the mid-day, high variability in day temperature, or both. The clue as to why they need to be active or resting for long stretches of time probably lies in their food habits and physiology. They may need to spend long periods for foraging (because of dispersed and low energy-density food) and may need to spend long periods for resting for conserving energy. Some animals are known to show daily torpor, which helps conserve energy (Wang and Wolowyk 1988, Robbins 1993). If not as effective as torpor, even a long stretch of sleep can help bears save much metabolic energy. Sleeping metabolic rates are known to be about 7 to 28% lower than basal rates (Heller 1988, Robbins 1993).

The proportion of whole day or proportion of various periods of day (except nights) sloth bears remained active decreased when the heat stress conditions increased and vice versa, within the range of activity observed. In contrast, the proportion of night spent active decreased when the nights grew colder. The period that the sloth bears could remain active is likely to be limited by the prevailing thermal conditions, although the proportion of a day spent active by bears should ideally be related to their daily energy and protein requirements, the need to accumulate fat reserves, and the availability of high quality food in the habitat. This limitation might be causing the observed relationship between activity and thermal conditions. However, the magnitude of changes in activity among months were not great (Fig. 5.7), and this indicates the probable absence of a strong seasonality of diet and energy related factors. Or, perhaps because the thermal conditions have constrained the bears to be strictly nocturnal and crepuscular and thus, in effect, limiting the number of hours available for them to be active. This proposition is somewhat supported by the lack of evidence for a relationship between activity and fruit productivity (see below).

Brown bear and American black bear are known to spend a large proportion of a day (up to 18 hours) feeding in the fall season (termed "hyperphagia"), when there are abundant acorns or pine seeds available, to prepare themselves for the approaching winter hibernation, and additionally, to meet the lactation demands in females (Garshelis and Pelton 1980, Nelson *et al.* 1983, Hellgren *et al.* 1989, Craighead *et al.* 1995). Considering the phylogenetic relatedness of the sloth bear with these other bears and the consequent possible physiological similarities, sloth bears too might have the ability to accumulate energy reserves. In addition, energy availability (see Chapter 7: Feeding Behaviour) and energy demand may vary seasonally. Therefore, the lack of substantial seasonal difference in activity levels observed in this study may be caused by the constraints posed by thermal conditions of the habitat not permitting activity to extend to daytime. The inverse relationship between activity and thermal conditions seen within the observed range of activity lends support to this interpretation. However, to draw any strong inferences, I am limited by the relatively coarse-scale hourly level of data that I used here. A finer scale data might reveal the patterns and relationships better.

Do food habits influence sloth bear activity?

Food-habit related variables did not show any relationship with bear activity characteristics. During fruiting season, bears were expected to be frequently active during daylight because it might be quicker for them to locate fruits within the foliage in daylight using vision than in darkness. American black bears became more diurnal in fruiting seasons perhaps because of the benefits of colour vision (Garshelis and Pelton 1980). However, the absence of such increased diurnal activity and the activity start times not being appreciably earlier in fruiting season could be because sloth bears foraged frequently on fruits fallen on the ground rather than in trees, and they depended more on their olfactory sense than vision for searching for fruits on the ground and on shrubs. Also, many food plants presented their fruits suitably for potential seed dispersers, or the bears selected fruits with such good presentation (see Chapter 7: Feeding Behaviour). Different kinds of constraints may be imposed on bears foraging primarily on fruits or insects, by digestive physiology and morphology through permissible consumption rates. Bears, while feeding predominantly on fruits, are expected to show a bimodal pattern of activity, because that might help increase the rate (per day) of digestible matter intake. Despite this potential for differences, the activity pattern was not observed to differ between fruiting and non-fruiting seasons, suggesting that these constraints may not be of primary influence on sloth bear activity patterns. Higher diversity of food items in the sloth bear diet may indicate more dispersed, small patches of food and hence more effort may be needed for foraging by bears in seasons of higher diet diversity. However, diet diversity too did not show any relationship with bear activity. It might be that bear activity length or the timings of activity are not necessarily related to number of types of food or evenness of consumption of different types. Also, activity length may not be different when feeding on a few types of food or even predominantly on a single type of food. The influence of diet diversity on bear activity perhaps could be better discerned, if activity length is segregated into time spent searching for food and actually feeding, and the relationships assessed for each.

Does the activity of tigers, humans, and adult male bears influence bear activity?

Tiger activity does not seem to influence bear activity timings. The hourly activities of both species (in dry and cold seasons) were strongly positively correlated, even after controlling for the effect of temperature. They both were mainly crepuscular and nocturnal in activity and were probably influenced by the same thermal factors or an endogenous rhythm. Tigers showed a more bimodal pattern of activity than sloth bears, which was because of more daytime activity and much less post-midnight activity. This kind of increased day activity could be caused by the more thermal-buffered microhabitats (shaded, riverine habitats, etc.) the tigers used, and by the different foraging behaviours and underlying physiologies of both species. I did not find any evidence to support the hypothesis that bears avoid encountering tigers (reduce predation risk) by choosing a different timing to be active. Joshi *et al.* (1999) believed that to have happened in Chitwan NP, Nepal, but did not present evidence to support it. American black bears are reported to avoid brown bears by being active at a different period (Aune 1994). Many prey species are known to avoid predation risk by temporal and spatial segregation from the predators (Clarke 1983, Caldwell 1986, Ferguson *et al.* 1988, Lima 1988, Lima and Dill 1990).

Tiger avoidance may not be a primary force in shaping the diel activity of sloth bear, because they do not seem to have a strictly prey-predator association. Tigers do prey on sloth bear (Laurie and Seidensticker 1977, Joshi *et al.* 1999, unpublished data), but the killings may happen primarily during close encounters between them, and not as a case of hunting. Sloth bears are aggressive, strong, with sharp claws and large canine teeth and they could inflict serious injuries on tigers. There have been instances when tigers have been injured or chased away by sloth bears or both withdrew during such close encounters (Joshi *et al.* 1999, *personal observations*). So, the tigers too may perceive a risk and therefore avoid encountering bears. For the bears, tigers may just be adversaries, with the outcome risky mainly when encountered suddenly. Therefore, it may not be critical for sloth bears to avoid the timings when tigers are active. Sloth bears in Panna NP did not seem to avoid tigers spatially either. They frequently use habitats such as escarpments (see Chapter 6: Space Use and Habitat Selection) that tigers also frequently used. Escarpment habitat offers suitable daytime resting sites for both species and they use this habitat frequently and simultaneously. However, it is possible that the bears may be avoiding certain microhabitats that tigers frequently use, or actively avoid tigers by avoiding places where they are present. I have found evidences of active avoidance of tigers by sloth bears and relatively frequent vigilance behaviour in bears (*personal observations*) in Panna NP.

I did not find evidence in this study for the supposition that the sloth bears were mainly nocturnal so as to avoid humans during daytime. The hourly activities of both bears and humans did not seem to have any relationship or at the most a weak one. There is a high overlap in activity timings of bears and humans during the crepuscular period, particularly in the evening hours. Humans were also probably influenced by the mid-day heat conditions to reduce their activity during mid-day, or conversely show peaks in activity in the mornings and evenings. In addition, a major reason for human presence in the forests in Panna NP is for tending domestic livestock while they graze in the forest, and the livestock probably prefer to, or are constrained by their physiology, to show peak grazing activity in the crepuscular period. Therefore, if the bears were to avoid encounters with humans, they should avoid the crepuscular period. But this was not observed. In fact, the high activity overlap in the crepuscular period probably led to frequent close encounters between them, some of which ended in bears causing serious injuries to humans (see Chapter 8: Bear – Human Conflict). Further, the bears in Panna NP do not seem to spatially avoid human-use areas. Many bears used peripheral areas of the Park and forest habitats near villages. At night, they even used places very close to villages.

In Panna NP, sloth bear – human encounters are apparently not very frequent as compared to some other areas, despite the high overlaps in activity peaks of both, and the frequency of bear caused injuries to humans is also low (about 4 incidents per year; see Chapter 8: Bear – Human Conflict). This could be because, many parts of Panna NP do not experience high usage by humans, and where there is high human usage, there is also dense shrub cover available. Bears use such dense cover, whereas humans actively avoid such localities of dense cover. Therefore, there probably was less scope for strong interference from humans, so as to influence the bears to change their activity timings in response to human disturbance. For the bears to develop a pattern of avoidance of human activity times, the human disturbance probably needs to affect acquisition of critical resources, have long-term effect on foraging efficiency, or directly decrease survival or reproduction. In another area in India, which is said to be severely degraded by humans, human activity was proposed to be the cause for sloth bear nocturnal activity (Chauhan *et al.* 2004). The results from the present study may not apply to such areas, but studies considering all the potential factors that may influence bear activity need to be done to confirm such propositions.

The American black bears that are habituated to human-generated food (“garbage feeding”) are supposed to have responded to human activity by having become nocturnal (Beckman and Berger 2003). In such cases the human interference may have been high during daytime or food abundance compensated for the energy expended for thermoregulation. Alternatively, energetic demands of bears were probably met by shorter periods of foraging, as compared to bears foraging on wild food (Beckman and Berger 2003). Also, hunted populations of bears may become nocturnal under diurnal human hunting pressure (Kaczensky *et al.* 2001). For the temperate bears, thermal conditions favour them being diurnal, while they become nocturnal due to human disturbance. In the case of sloth bear, both these factors may influence them to be nocturnal, and separating the effect of the two factors becomes necessary to assess the influence of each, independent of the other. When the effect of temperature with which bear activity was strongly correlated and with which human activity too might have been related was statistically controlled for, the relationship between bear and human activities in different periods of day showed inconsistency, in both magnitude and direction. These inconsistent relationships support the broad finding that there does not seem to be a relationship between bear and human activity. The seemingly inverse relationship seen in the crepuscular period is because the crepuscular activity peaks of both do not coincide exactly and the activity peak of one starts to drop at the time the other starts to rise (Fig. 5.35). Similarly, the seemingly positive relationship in the night time is because the activity peaks of both start to rise and fall simultaneously in the night time.

For an endothermic animal, regulating body temperature is a constant necessity, and any other factor influencing its behaviour may become secondary. So, it is possible that human activity exerted some influence on bear activity, in addition to thermal conditions, but is not evident because of the stronger influence of the thermal factor. This is probably hinted by the continued daytime resting behaviour of bears even in the cold season, when the thermal conditions do not seem to be a deterrent to activity (but see discussion in the later sections). It will be ideal if the relationship between sloth bear and human activities is investigated in areas where thermal conditions are not a great influencing factor, or still better if tested through experimental manipulation rather than observational studies.

Activity of adult bears is known to influence the activity patterns of female bears with dependent cubs (Klinka and Reimchen 2002), and this was proposed to be to avoid the risk of infanticide. Such temporal avoidance of adult sloth bears was proposed for Chitwan NP, Nepal, where females with cubs were reported to be diurnal and the adult males to be nocturnal (Joshi *et al.* 1999). Considering such a hypothesis, the limited evidence I have did not show such a pattern in Panna NP, where the radio collared adult males and females showed similar patterns of activity. Also, activity patterns were similar for the females that had dependent cubs and the ones that did not. The main differences observed were between the bears occupying core and peripheral areas of Panna NP. Although the activity patterns of more bears in Panna NP needs to be known to test this hypothesis, the activity of adult males may not be greatly influencing the activity of females in Panna NP for the following reasons: sloth bear occurs in low density there, there is limited scope for immigration of adult males, there is no concentrated and rich source of food available for many male bears to converge. Therefore, the factors that may promote cannibalism/infanticide seem to be absent in Panna NP. In addition, the female sloth bears in Panna NP have adopted a multiple mating strategy, similar to bears elsewhere (Craighead *et al.* 1995, Joshi *et al.* 1999). Such a strategy may result in uncertain paternity of cubs and thereby influence the males to have reduced infanticidal tendency.

Are there other factors influencing bear activity?

Changes in prey activity, prey availability, and prey capture efficiency over a day may influence the daily activity patterns of bears (White *et al.* 1998, 1999, Klinka and Reimchen 2002). Sloth bear feed predominantly on fruits and social insects (see Chapter 7: Feeding Behaviour). Availability of fruits for them is not likely to change over a day, except for *M. longifolia* flowers, which blossom and drop their fleshy petals in the early mornings. However, the foraging efficiency on fruits may change over a day because of vision limitations. Activity of main prey insect groups, ants and termites, changes over the day and their daily activity patterns further change with seasons (unpublished data), similar to patterns in ant activity elsewhere (e.g., Briese and Macaulay 1980). Many prey species of ants were mostly nocturnal in the dry (hot) season, but were more active in the daytime in the wet and cold seasons. However, the relatively constant sloth bear activity patterns over seasons suggest that they are probably not affected by seasonal changes in insect activity patterns. Further, sloth bears forage mainly on the insect nests/colonies and therefore the changes in insect activity is not likely to affect their ability to forage on the nests. Sloth bears forage on subterranean nests relying highly on their olfactory sense and so the darkness related vision constraints should not affect their foraging ability on insects. However, these insects, particularly ants, might move (or move their brood) vertically under ground depending on changes in temperature and humidity over a day, similar to the army cutworm moths in the alpine slopes of Rocky Mountains in North America (White *et al.* 1998, 1999), and thereby may cause changes in the foraging efficiency over the day. Ants and termites are known to move their nests according to seasons (Josens 1983, Levieux 1983), but whether they do it over a daily cycle is not known. Other than this possibility, it seems unlikely that the bear activity pattern would be influenced by insect activity, although further studies exploring this question are necessary.

Garshelis and Pelton (1980) suggested that the dichromatic vision of American black bears is probably an adaptation for feeding on fruits. Considering its phylogeny, the sloth bear too might be dichromatic and this kind of vision might be useful for foraging on fruits in daylight. Trichromatic colour vision is considered to be an adaptation for frugivory in diurnal primates (Surridge *et al.* 2003). Although bears are known to be only dichromatic, they might be able to see fruits by detecting blue-yellow signals reflected by many fruits (Dominy and Lucas 2001). The greater ability to locate fruits among foliage in the daylight and thus a greater foraging efficiency does not seem to have influenced the sloth bears to become more diurnal, at least in the fruiting seasons. The absence of a difference in daily activity pattern between fruiting and non-fruiting seasons, and the absence of a relationship between fruit proportion in diet and fruit productivity with bear activity in the different daylight periods probably indicates the secondary position of vision in determining sloth bear activity. This could be because sloth bears feed commonly on ripe fruits fallen on the ground, on fruits that have a good presentation (e.g., on branches without leaves, as clusters at branch tips; see Chapter 7: Feeding Behaviour), and on fruits that advertise by strong scent. Also, sloth bears might use rod-vision and 3-D vision to make out shapes and feed on fruits. They often feed on large fruits and the shapes of these could be seen better using night vision. Further, sloth bear could forage well in the night time with their highly developed olfactory sense and hence the vision constraint may not be an effective influence on activity.

Phylogenetic relatedness is known to explain many patterns in animal behaviour which otherwise would have been attributed to various other factors (Harvey and Pagel 1991, Gittleman 1993). The sloth bear is closely related to other bear species, has many morphological, genetic and physiological similarities with other bears. Some molecular phylogeneticists believe that the sloth bear should be grouped with most other bear species in the genus *Ursus* (Goldman *et al.* 1989). Other bears of the genus *Ursus* are mainly temperate in distribution (except Malayan sun bear) and are primarily diurnal and crepuscular in habits (Amstrup and Beecham 1976, Garshelis and Pelton 1980, Lariviere *et al.* 1994, Craighead *et al.* 1995, Machutchon *et al.* 1997, White *et al.* 1998, Gende *et al.* 2001, Beckmann and Berger 2003). So, considering the phylogenetic relatedness, sloth bear is expected to be diurnal, if no particular ecological influence exists. However, the sloth bear is reported to be primarily nocturnal in many parts its range, although scientific investigations are mostly lacking. It appears that the sloth bear has become nocturnal mainly under the influence of tropical thermal conditions. It will be important to study sloth bear activity patterns in areas where day temperatures are moderate, water availability (for hydroregulation) is dependable, nights are cold, or where the habitat is predominantly closed (by vegetation cover).

What factors influence the times of start and end of bear daily activity?

Sloth bears in Panna NP started their activity increasingly earlier than sunset when the range of daytime temperature was smaller and vice versa, although the temperature alone did not seem to be related to activity start time, particularly relative to sunset. In addition, bears started activity later when sunset times were later, even when the effects of temperature and range of day temperature were accounted for. Similarly, bears started their activity increasingly later in the evening when the frequency of their day-resting in escarpment increased, or correspondingly, the more they day-rested in *Lantana*, the earlier they started activity. However, the relationship between activity start time and day-resting in escarpment disappeared after controlling for the effects of both sunset time and range of day temperature. The bears ended their activity earlier when the temperature increased and vice versa (although with much variability), but the activity end time did not show a relationship with range of day temperature or sunrise time after controlling for temperature. This could be because sunrise times and temperature were highly correlated and temperature overshadows the effect of sunrise time.

In general, bears seem to be cuing to both sunset and sunrise times and heat conditions to start and end their diel activity. It is not clear as to which of the explanatory variables has primary effect because they are strongly correlated. Other characteristics of bear activity (hourly activity, etc.) are strongly influenced by thermal conditions, and so it is likely that the thermal conditions substantially influence times of start and end of bear activity. However, it is highly probable that the basic stimuli are sunset and sunrise times, and the thermal conditions only modify the basic pattern to some extent. Many animals are known to synchronise their activity with periodic environmental factors such as sunrise and sunset times (called “zeitgebers”; Aschoff 1966, Kavanau and Ramos 1972, Palomares and Delibes 1994, Chiarello 1998). It appears that it is possible to explain a major part of the pattern of sloth bear activity timings with a purely daylight related circadian rhythm (see further discussion on this in the later sections). Controlled experiments alone could separate out the effects of such interrelated factors better. Bear activity end times seem to have high variability in its synchrony with sunrise time, probably because the high heat conditions constrained the bears from being active for long after sunrise in the hot seasons. As for the lower limits of activity end time, individual bears might have become satiated or reached the limits of their gut capacity after different lengths of foraging each night. Similar pattern of high synchrony of activity start time with sunset time and variability in activity end time has been reported in small nocturnal carnivores (Kavanau and Ramos 1972).

What factors influence the bears to select certain microhabitats to rest?

Usage of the two main habitats (escarpment and *Lantana*) for day-resting by sloth bears was strongly related to range of daytime temperature. The bears day-rested more often in escarpment habitat (essentially, in dens) when the range of day temperature increased, and more often in *Lantana* cover when it decreased. These habitats, in general, offered suitable cover for resting, and protected the bears from daytime thermal stress. Dens had the lowest and least variable temperatures among all the different day-resting sites and thus provided the best refuge from high temperatures. In particular, during the dry season, when the heat stress conditions were high outside, dens offered much lower temperatures. The bears thus may not need to make frequent regulation of temperature by physiological or behavioural means while resting in dens. Also, heat gain would be minimal in dens, which remain cooler than body temperature, and heat loss through conduction and radiation would be higher in dens. *Lantana* cover or forest-shade habitat provided microenvironments with lower temperatures than forest-open habitat, but the temperature variability remained high compared to dens. Therefore, it seems that the dens are providing the best thermal environment for bears to day-rest in the dry (hot) season. In the wet season, in *Lantana* shrub cover habitat, temperature variability was low, vegetative cover was high, plants were fruiting, ants and termites were probably abundant, and therefore that habitat could be used by bears frequently. In the cold season, temperatures in the forest-shade habitat were comparable to dens, but were very variable (Fig.

5.22). Den temperatures were more or less constant and remained above 13 ^{o}C, the reported lower critical temperature for sloth bear (McNab 1992). Also, as the leaf fall progressed in the cold season, the forest opened up and protection from disturbances could have become a factor. Resting in dens probably provided the added advantage of protection from other disturbances (predators, humans, fire, etc.), so that the bears could conserve additional physiological energy. By resting inside dens, bears could maintain resting metabolic rate, or even have a lower sleeping metabolic rate, and thereby save energy. These additional advantages may have influenced the bears to rest in dens, even in the cold season when the outside temperatures were not high.

When the frequency of bear day-resting in escarpment habitat increased, the portion of day bears remained active decreased. In other words, the more the bears day-rested in escarpment, the longer they were resting, or conversely, the more they day-rested in *Lantana*, the shorter they were resting. This could be merely because the bears day-rested more often in *Lantana* during the wet season months and that was when the thermal conditions were favourable for higher day and crepuscular activity than the dry season months, when the bears day-rested more in escarpment. This suggests that there may not be a direct relationship between day-resting habitat and activity level. However, it could also be because of more human disturbances in the peripheral *Lantana* habitat causing the bears to be more active irrespective of other influences. Despite the disturbances, many bears used *Lantana* shrub cover for day-resting frequently in wet and post-wet seasons, because they shifted their seasonal home-ranges to peripheral areas (due to seasonal abundance of food in such areas, etc.; see Chapter 6: Space Use and Habitat Selection), where no better shelter are generally available. When the seasonal home-ranges of bears were far from escarpment, they did not travel to distant escarpment habitat to day-rest; instead the bears rested in thick *Lantana* cover that was available locally. In such instances, energy costs of travelling probably exceeded disturbance costs (distance from escarpment to centre of seasonal core ranges for 2 bears that shifted to peripheral areas ranged from 3 to 5 km, and this might involve 1 to 2 h of walking. This might cost a bear about 600 Kcal for a round trip, and a loss of 2 to 4 h of valuable foraging time). This indicates that the usage of different habitats for day-resting by bears is also according to their availability within their seasonal home ranges, in addition to being influenced by the seasonal thermal environment.

Differences in activity patterns among individual bears

Garshelis and Pelton (1980) attributed some of the variability in activities of a population of American black bear to individual peculiarities. Individual bears are known to alter their activity patterns to avoid conflicts (e.g., with humans; Roth 1983, Ayres *et al.* 1986), and particularly when associated with anthropogenic food (Beckman and Berger 2003). Kaczensky *et al.* (2001) reported that younger brown bears had a different pattern of activity than older bears, and the younger bears learned to avoid human disturbance by changing their activity timings as they grew. Individual radio collared sloth bears in Panna NP, in general, were quite similar in their activity patterns. The female bear F76 showed the most dissimilarity, followed by female F80 and male M50, but they still conformed to the general pattern of activity. The differences observed among the bears in the various activity characteristics had a pattern related to the location of home ranges of the bears and did not seem to have been caused by individual peculiarities, age, or life-time learning. The main differences were between the bears that occupied central or core areas of Panna NP and those that occupied peripheral areas. The ‘core bears’ had substantial escarpment habitat available to them, their habitat were of better quality (had higher food plant density and diversity, tree density and canopy cover), and were better protected from human disturbance. In contrast, the ‘peripheral bears’ had low escarpment and high *Lantana* cover available within their home ranges, and their habitat was degraded by human over-use and other disturbances.

Female F76 was almost exclusively a peripheral bear; F80 and M50 were partly peripheral, whereas F63 and M69 were almost exclusively core bears. The differences among bears in the usage of habitats for day-resting could be explained by the differences in availability of the 2 main resting habitats within their home ranges. The differences in timings of start and end of daily activity between core and peripheral bears were seen mainly in wet and cold seasons. This could be because of higher disturbance in peripheral areas, and more thirst or hunger among peripheral bears exposed to harsher thermal conditions or lower food availability. The factors influencing the reduced nocturnal and increased diurnal (more bimodal) activity pattern observed in peripheral bears, particularly in the wet season, are unclear. Perhaps they are related to higher disturbance during daytime, combined with meagrely sheltered day-resting sites causing the bears to rest more during the nights. The discordant activity characteristics of the bears occupying peripheral areas may indicate that they were living in sub-optimal conditions, but the consequences of such marginal living can only be assessed based on survival and reproduction parameters.

Is the bear activity largely a circadian rhythmic behaviour?

Thermal conditions probably influence most aspects of sloth bear activity in Panna NP. However, there are certain characteristics that could not be satisfactorily explained by the thermal factors and may even seem to contradict it. Some of those are considered below. During evening and morning hours, irrespective of whether temperatures were low or high, the bears showed peaks in activity (Fig. 5.28). Bears showed high levels of activity (over 60%) during midnights, even when temperatures were as low as 10 ^{o}C (Fig. 5.31). On the other hand, bear activity remained very low during midday, even when temperatures were not greater than 20 ^{o}C (Fig. 5.32). Midnight and midday activity varied highly regardless of temperature, and appeared to depend solely on the time of day (Figs. 5.31 & 5.32). The response of bear activity to temperature also varied among seasons. While activity was low at temperatures of about 25 ^{o}C in cold season, activity was very high at similar temperatures in wet and dry seasons (Fig. 5.29a). The time bears started activity was directly related to sunset time, independent of temperature (Table 5.6). Bear activity end times too were referenced to sunrise time. All these peculiarities seem to have a common underlying factor. That is, they appear strongly related to time of day per se rather than to thermal factors.

In other words, bear activity seems to have become broadly synchronised with time, rather than responding to everyday changes in the thermal environment. That is, it does not seem to be a simple stimulus-response system, but the synchronisation with thermal conditions developed over evolutionary time. Such determination of activity timings by endogenous circadian rhythm have been observed in many animals (Aschoff 1966, Mech *et al.* 1966, Enright 1970, Kavanau and Ramos 1972). Further, this pattern of activity is probably maintained as a routine in response to daytime adverse thermal conditions, and additionally perhaps as an adaptation to maximize intake of their low energy-density food. Sloth bears feed mostly on low energy-density food such as fruits and insects (McNab 1984) that are also distributed over a wide space and available in small patches (see Chapter 7: Feeding Behaviour). To meet their energy and protein requirements, the bears probably needed to forage for long periods in a day and repeat that long session of activity every day. As a consequence, this pattern of daily activity is probably maintained as a routine and this routine reinforces the persistence of circadian rhythmic behaviour.

Conclusions

Day time thermal conditions seem to have the greatest influence on bear activity, out of the explanatory ecological factors considered in this study. However, in addition to the thermal conditions, there could be a few other factors secondarily influencing bear activity. Importantly, bear activity timings, rather than responding to concurrent environmental stimuli, seem to have been synchronised with time of day, probably founded on an endogenous circadian rhythmicity. The primary influence of thermal conditions is probably in modifying the basic pattern of circadian activity, besides having been a probable major influence in the development of circadian rhythm over evolutionary time of the sloth bear. In other words, the endogenous circadian rhythm is probably the main proximate factor in determining sloth bear daily activity pattern and the thermal environment is rather an ultimate (i.e., evolutionary) factor.

Statistical caveats

This study is essentially observational. Even the fundamental descriptions of sloth bear activity patterns were inadequate prior to this study, and therefore describing the patterns became a key objective of this study. A significant limitation of this study has been that the observations of specific activities of sloth bear could not be made directly, due to their primarily nocturnal activities, and their closed-cover habitats. Some of the inferences from this study are exploratory and would serve as hypotheses for future confirmatory studies. Also, the relationships found in this study do not necessarily indicate causal relationships and so the relationships should be subjected to further studies. Since many factors may be influencing sloth bear activity patterns at the same time or in a hierarchical manner, it would be best to use experimental studies to separate out the effects of individual factors and to reflect on causation. Although a multiple regression or partial correlation type of analyses (similar to the one I have done) could be used to identify the minimal number of factors influencing activity, problems related to multi-collinearity becomes a serious concern (MacNally 2000). However, I selected the explanatory variables (research hypotheses) *a priori* based on existing knowledge and it should mitigate the concern about spurious relationships (see Anderson *et al.* 2001).

Management implications

- Dens or such secure shelters are essential to sloth bear for resting during midday and for successful cubbing. Localities with natural dens should be protected and artificial dens could be provided in places where they are scarce. Availability of dens may also contribute to reduced conflict with humans, by way of reducing sudden encounters.
- Escarpment and knoll habitats with their natural sloping topography and abundance of boulders offer caves and crevices that serve as excellent shelters for bears to rest during the day. In addition, these habitats provide secure dens for cubbing. Daytime resting is an important factor in the lives of sloth bear, at least in the areas of adverse thermal conditions, and good shelters are critical for their survival. Much of the escarpment

and knoll habitats that offer such shelters should be included in the protected reserves, either during the initial formation or by later extension of boundaries to include such habitats.

- Areas with dense shrub cover should be maintained, particularly in the peripheral areas, even if it consists purely of *Lantana* shrub. This habitat, in addition to dens, is important for bears for day resting. Such dense shrub cover patches also serve as shelters for many other species of animals, including tiger.
- Water availability during dry season could be crucial for hydroregulation and therefore for effective thermoregulation. Water sources in the localities of day-resting sites should be protected or if lacking, should be provided.
- Human usage of escarpment and knoll habitats should be restricted to reduce disturbance to bears and also to avoid human encounters with them.
- Maintenance of patches of dense shrub cover in high human usage areas would serve as secure resting sites for bears. Further, in such areas, wide passages should be made available for humans, so that they avoid travelling on narrow trails in such dense-cover patches. This may help reduce sudden encounters with bears.

5.5. SUMMARY

- The patterns in daily and seasonal activity of sloth bears in Panna NP were studied and the factors that influenced the patterns were assessed.
- Activity states were recorded by manually monitoring radio-tagged, motion-sensor fitted bears, and by deploying automated receiver-recording units that logged the strengths and pulse rates of signals from the bears. Daily and seasonal changes in temperature, relative humidity and other heat indices of the microhabitats used by bears were recorded using temperature and RH loggers. Tiger and human activities were also monitored to assess the influence of these on bear activity patterns.
- Bears were found to be essentially nocturnal and crepuscular in activity and they rested during midday. This pattern of activity was similar among all radio collared bears, but with some variability. The differences in diel activity patterns among climatic and fruiting seasons were rather small. In the wet and cold seasons, bears extended their activity into the day hours and reduced their activity in post-midnight, pre-morning hours, as compared to the dry season.
- Bears (except the cubbing females) were active almost every day of the year, and for several hours (> 10 hours) each day. Overall, bears were active for 48% to 54% of the whole day (out of 24 h) in all seasons. There were no large differences seen among months in percent of whole day, day time, night time, and morning time the bears were active, but evening time showed large differences.
- The differences in activity start and end times among individual bears within seasons were large in certain seasons, and the differences among seasons of a bear were large for certain bears. Bears such as F63, F78 and M69 did not show much difference among seasons, while others such as F76, F80 and M50 showed large differences. Also many bears showed higher variability in cold and wet seasons than in dry season, particularly in activity start times.
- Bears started their activity later and ended it earlier in the dry season than the other two climatic seasons. The earliest activity start and latest activity end was in the cold season. The differences among climatic seasons in both timings were statistically significant (ANOVA, $\alpha = 0.05$). However, when activity start and end times were adjusted for seasonal sunset and sunrise times, the patterns in seasonal differences changed remarkably.

Wet season activity start times with reference to sunset were much earlier than the other two seasons, whereas the difference between cold and dry seasons became small. Differences in activity end times after sunrise between cold and the other two seasons too became small.

- Escarpment habitat was most frequently used (50% to 85%) for day-resting by bears in all months, followed by *Lantana* shrub thickets (15% to 50%). The use of escarpment was predominant in dry season months and decreased in monsoon and post-monsoon months, with a converse increase in the use of *Lantana* habitat as day-bed.
- The ‘core’ bears, which had substantial escarpment habitat available within their home ranges, used escarpments for day-resting predominantly in all seasons, and the ‘peripheral’ bears, which had low escarpment and high *Lantana* cover available, used these habitats for day-resting variably.
- The radio-tagged female bears gave birth during the cold season. They entered secluded and protected dens (termed “maternity dens”) before parturition and stayed inside those dens caring for the cubs for several weeks. The cubbing period started towards end of November and continued until February, ranging from 9 to 12 weeks.
- Monthly mean day time temperatures in forest-open habitat rose to about 40 ^{o}C in some months and were over 30 ^{o}C in most months. The monthly maximum temperatures were over 30 ^{o}C in all months and were close to 50 ^{o}C in April and May. The monthly minimum night temperatures dropped lower than 5 ^{o}C in cold season months. In the forest-shade habitat, night temperatures were similar to forest-open habitat, and day temperatures were lower by up to several degrees.
- The pattern of change over months in the heat index, Wet Bulb Globe Temperature (WBGT), was similar in forest-open and forest-shade habitats during the day, with forest-shade values consistently lower than forest-open. While the temperature declined after May and remained lower in wet season months, WBGT increased as dry season progressed and stayed the highest in wet season months.
- In the forest-open habitat, temperatures were the highest in dry season, followed by wet and cold seasons, while the temperature ranges were the smallest in wet season and the largest in dry season. RH values were the highest in wet season and the lowest in dry season. Relative changes in RH over the day were similar to temperature, but in the opposite direction.

- Den temperatures (means) were about 27 °C in dry season, 25 °C in wet season and 18 °C in cold season. Temperature variability was the lowest in dens, among the different microhabitats, in both day and night in all months. Temperature range during day was over 20 °C in forest-open habitat in many months, whereas it was less than 5 °C in dens.
- Tigers were generally nocturnal and crepuscular in activity during the dry and cold seasons. The activity of tigers peaked during crepuscular times; they predominantly rested during mid-day, and had a reduced level of activity during post-midnight, pre-morning hours.
- Diel activity patterns of bears and tigers were similar to a large extent, in the two seasons tigers were monitored. The activity peaks of both species more or less coincided in the mornings and evenings, and high levels of activity of both occurred in night and crepuscular times.
- Tiger activity does not seem to influence bear activity timings. The hourly activities of both were strongly positively correlated, even after controlling for temperature, with which bear activity was strongly correlated.
- Humans using the forest habitats showed a high level of activity in the morning and evening times, moderate level of activity in the mid-day, early morning and late-evenings, and a low level of activity in the immediate pre-morning and early night hours.
- Human activity overlapped highly with that of bear activity during early morning and evening hours. Overlap period was longer and the activity peaks of both coincided in the evenings of wet and cold seasons. No relationship could be seen between their hourly activities.
- After controlling for the effect of temperature, activity start time was positively correlated to sunset time, while activity end time showed no relationship with sunrise time. When controlled for the effect of sunset time, activity start time did not show a relationship with temperature, but showed a strong positive correlation with range in daytime temperature in forest-open habitat.
- Bears seem to be cuing to both sunset and sunrise times and heat conditions to start and end their diel activity. It is probable that the basic stimuli are sunset and sunrise times, and the thermal conditions only modify the basic pattern to some extent.
- Bear activity seemed to have an inverse relationship with temperature in forest-open habitat for day time, but that relationship did not hold for night.

Bear activity was minimal during the period of high temperature. At night, when bear activity was high, temperatures were commonly <25 ^{o}C. However, even at low temperatures such as 10 ^{o}C or at relatively high temperatures such as 30 ^{o}C, if the period was crepuscular, bear activity nevertheless peaked. These peaks seem to have been synchronised with dawn and dusk, probably by an endogenous circadian rhythm.

- High temperatures (>30 ^{o}C) combined with or without high RH during the day caused high thermal stress conditions. These stress conditions probably have influenced bears to rest during the day and to choose to rest in sites where they could reduce heat gain and increase heat loss.
- Bears day-rested more often in escarpment habitat (essentially, in dens) when the range of day temperature increased, and more often in *Lantana* cover when it decreased. Dens had the lowest and least variable temperatures among all the different day-resting sites, and thus provided the best shelter from heat conditions. The differences among bears in the usage of habitats for day-resting could be explained by the differences in availability of these habitats within their home ranges.
- Day time thermal conditions seem to have the greatest influence on bear activity and selection of habitat for day-resting. However, bear activity timings, rather than responding to concurrent environmental stimuli, seem to have become synchronised with time of day, probably founded on an endogenous circadian rhythmicity. That is, it does not seem to be a simple stimulus-response system, but the synchronisation with thermal conditions developed over evolutionary time.
- **Conservation implications**. Dens or such secure shelters are essential to sloth bear for resting during midday and for successful cubbing. Localities with natural dens should be protected and artificial dens could be provided in places where they are scarce. Escarpment and knoll habitats that offer such shelters should be included in the protected reserves. Areas with dense shrub cover should be maintained, particularly in the peripheral areas, even if it consists purely of *Lantana* shrub. Human usage of escarpment and knoll habitats should be restricted to reduce disturbance to bears and also to reduce encounters between them.

CHAPTER 6. SLOTH BEAR SPACE USE AND HABITAT SELECTION

6.1. INTRODUCTION

Where do animals live, and why, are interesting questions for behavioural ecologists to seek answers for. Also, these are important questions to answer, in order to plan for their conservation. Burt (1943) provided a conceptual definition for ‘home range’ as, “the area traversed by an animal in its normal activities of food gathering, mating, and caring for young”. This definition succinctly expresses the need to study home ranges of animal species, since an assessment of home range space would provide the information necessary for ensuring that an animal continues to gather food, reproduce and care for young. Identifying and mapping the space used by an animal is a prerequisite for assessing the habitat features associated with that space. Information on the habitat features used by an animal, and the ones that are preferred or avoided are needed to understand many ecological aspects of the animal and to plan for its conservation.

Estimating home range size has been a major focus of animal behavioural ecology studies. Home range size and its spatial location would reflect the energy needs and social behaviour of an animal, and thus provide information on many aspects of animal ecology. Home range sizes have been found to be related to sex, body mass, diet and abundance of food and other resources (McNab 1963, 1983, Harestad and Bunnell 1979, Gittleman and Harvey 1982, MacDonald 1983, Gomper and Gittleman 1991). Of these factors, abundance of food and other resources, which determine the quality of a habitat, have fundamental influences on home range size. Assessing these influences and identifying the key resources are of great importance for conservation.

Home ranges vary in size and location in relation to changing resources over time and space. In particular, bears are known to shift their seasonal ranges according to changes in the distribution of food and other resources (Garshelis and Pelton 1981, Rogers 1987, Reid *et al.* 1991, Schwartz and Franzmann 1991). Omnivores such as bears may also change their food habits to reflect what is locally available. Sloth bears live in tropical habitats where the resources are not as seasonal as the temperate regions, and may adopt this behaviour rather than making long range movements. On the other hand, monsoonal climate of the Indian subcontinent results in considerable seasonality of resources. Consequently, bears may exhibit at least seasonal shifts in core ranges within their annual ranges. Further, in places where the forest habitats occur in rather small fragmented patches, such as in India, there may not be a scope for bears to make long range movements among seasonal resource patches, and it would be interesting to see how they adapt to that.

Seasonal changes in locations of use have been well recognised and most space use studies incorporate this aspect. However, the subject of changes in space use within a day, depending on activities performed at different times of day has not been given its due importance (Harris *et al.* 1990). Most studies pool data from different times of day and this may obscure certain important patterns in use of space within a day. Earlier authors have pointed out that animals select particular habitats to perform particular activities at particular times of day (Palomares and Delibes 1992, Beyer and Haufler 1994). Animals such as sloth bears have distinct patterns in daily activity (Joshi *et al.* 1999, this study) and this may result in changes in habitats used by them among different periods.

Habitat selection by an animal has been proposed to occur in a hierarchical order (Johnson 1980). Selection of a geographical range by a species is considered a first-order selection, placement of home ranges within that is second-order selection, usage of various resource components within the home range is third-order selection, and the actual procurements of resources is considered fourth-order selection. Selection of habitat at the scale of vegetation and terrain types (third-order) may reflect a selection for resources within those habitat types (fourth-order). Since the abundance of many resources is known to be associated with broad vegetation types, an assessment of habitat selection by a species at this broad level would be useful for management of its habitat and for its landscape-level conservation.

In addition to abundance of resources, habitat quality is also determined by the level of disturbance and degradation by humans. Human activities in forests impact animal habitats at two levels: structure of the habitat, and resources within habitat. Structure is changed by actions such as modification of plant density and canopy cover. Changes in habitat structure may affect the thermal environment and is of particular significance to sloth bears. Food resources that are important for animals may be extracted by humans and this would impact their availability to animals. In sloth bear habitats, such impacts are frequent. Therefore, it becomes important to study the impacts of such habitat degradation on habitat quality for sloth bears.

In the only other comparable study on sloth bears, conducted in the highly productive alluvial grassland - moist deciduous forest habitats of Chitwan National Park, Nepal, home range sizes were estimated and the habitats used by the bears were briefly discussed (Joshi *et al.* 1995). Little information is available on home range sizes or habitat use of sloth bears elsewhere, particularly in the dry deciduous forests, which forms the majority of the range where sloth bears now occur (Yoganand *et al.* in press). Given the changes in vegetation community, habitat structure and other habitat features due to several anthropogenic factors, it is important to identify the habitat features that are essential for the continued survival of sloth bears. From another perspective, considering the focus of wildlife management in India on flagship species such as the tiger, and the attempts at habitat management to meet conservation needs accordingly, the requirements of other species get sidelined or even ignored. It is even simply assumed that conserving habitat for a flagship species would conserve every other species. Few of us know how valid this assumption is! Considering these aspects, I chose to study space use and habitat selection of sloth bears in a dry deciduous forest habitat, and attempted to identify the resources that are important for their survival and reproduction.

The objectives of this study were to:

- Identify and map the space used by sloth bears and estimate their home range sizes.
- Study habitat use and assess habitat selection by sloth bears.
- Examine the seasonal and diel period changes in space and habitats used by bears and assess habitat selection jointly with the time factor.
- Study the habitat characteristics of space used by bears, and assess if bears selected for particular characteristics.
- Assess how habitat degradation by humans impacts habitat quality for sloth bears, and how sloth bear space use and habitat selection is influenced by it.

6.2. METHODS

Radio tracking

I radio-tracked the tagged bears on foot to make direct observations (Plate 8), and used a jeep or a motorbike to estimate locations by triangulation. Occasionally, I used riding elephants to home-in on the bears. The locations of homed-in bears were obtained with a handheld GPS (Garmin 40) unit, and the locations of tracking stations that were regularly used for triangulations were obtained and differential corrected using GPS base station and roving units (Trimble Pathfinder). I attempted to locate each radio-collared bear every day, ensuring that sampling covered the different periods of the 24-hour cycle. In monsoon rainy seasons, when daily locations were not possible to obtain, they were located at least three days in a week. In addition, their diurnal activity and daily movements were tracked by locating them every 1 or 2 hours throughout the time they were active (up to 24 hours of continuous tracking). These continuous tracking sessions were conducted for each tagged bear on randomly chosen 2 or 3 days every 10 days. However, during monsoon seasons, or when I was trapping, continuous monitoring was done less frequently.

Triangulation

Bears could not be homed-in frequently, such as at night times, when they were far off from roads, or when I needed to locate many bears in a day. Therefore, their locations were often estimated by method of “triangulation”. Compass bearings of the direction of the monitored bear were recorded from three to five known locations (called “tracking stations”). These were done using mobile receivers, within an interval of 15 minutes, to minimise error due to bear movement. These bearings were plotted using a computer program “Locate II” (Nams 1989) and the locations were estimated using Lenth’s Maximum Likelihood Estimator (MLE; Lenth 1981). Before triangulating to estimate locations, all bearings were plotted and the bearings that seemed to have been bounced off or refracted or otherwise unreliable were identified and discarded. The standard deviations of bearing angles were used to estimate 95% error ellipses.

Home range estimation

The location estimates with >10 ha of associated 95% error ellipses were discarded from all analyses. The locations with an interval of <2 hours were also removed from home range estimation and habitat use analyses, while being retained for assessing bear movements. During the first 2 years of the study, locations for measuring movement rates were obtained at 1-hour interval and in the subsequent years, 2-hours interval was used. Testing based on first year's data indicated that the sloth bears could travel half their home range lengths in an interval of 2 hours, and this interval could be considered to yield statistically independent location estimates. However, these locations may not be biologically independent. The bears in PNP generally rested in a day-bed site during daytime (see Chapter 5: Activity Patterns), and during such time only one location was recorded for day time. If a subsequent location of a bear was logged, a minimum of 2-hours interval was kept, after the bears started their activity cycle in the evening.

I used 95% fixed kernel method (Worton 1989, Seaman and Powell 1996) to estimate home ranges of radio-tagged bears. The bandwidth 'h' selection was made by least-squares cross-validation (LSCV; Seaman and Powell 1996). However, I often encountered a problem in estimating 'h' this way. The LSCV estimated a very small 'h', approaching 0, because many locations for each bear had the same or very close by coordinates. This happened because the bears used many of the day-bed sites repeatedly for resting. To deal with this problem, a subset containing unique locations was selected from the location sets (seasonal, annual location sets) for each bear and 'h' was estimated from the subsets. These 'h' were entered as user-prescribed values for estimating home ranges from the full sets. For many of the tagged bears, the tracking period extended over a year. For those bears, an annual subset of locations was selected, spanning a biological year (comprising three consecutive seasons) and were used in annual home range estimation and habitat use analysis. This was because pooling data from >1 year, without considering annual variations, has the potential of resulting in misleading inferences (Schooley 1994). The seasonal home ranges too were estimated from the 'selected' year's data. Although I believe, in conformity with earlier workers (Seaman and Powell 1996, Powell *et al.* 1997), that the fixed kernel estimate is the best available estimate of home range, I estimated 100% MCP and 95% restricted polygon areas, for comparing with other studies that have reported only those estimates.

Some parts of an animal's home range would be used more intensively than others, and they are called 'core ranges' (Samuel *et al.* 1985). The core ranges are presumably more important for the animal's survival and reproduction than other parts, and I attempted to identify them. I defined core range as the area delimited by 50% fixed kernel contour (= area having 50% probability of use). Although 50% is an ad hoc level, it should be acceptable for comparative purposes.

The coordinates of locations of homed-in bears obtained using GPS units, and the locations estimated by triangulation method were exported to GIS software for estimating home ranges, movement rates, and for analysing habitat selection. I used "ArcView" (v3.2, ESRI 1996) GIS software, "Animal Movements" extension for Arcview (Hooge *et al.* 1999) and "Home Range Extension" for Arcview (Rodgers and Carr 2002) to estimate home ranges and to analyse habitat selection.

Analysis of habitat selection

Habitat map of the study area classified from satellite imagery (see Chapter 4: General Methods) was used to assess habitat use by radio-tagged bears. While 95% fixed kernel estimates was used as representative of home ranges, 99% adaptive kernel estimates were used to delineate the area to be considered 'available' for bears (and not as 'used' by bears). A composite of 99% adaptive kernel home ranges of all bears was considered as the total study area. Since the location estimates were associated with two types of errors, the precision of the estimate (as quantified by 95% confidence ellipse), and the accuracy of the location (distance of the estimated location to the actual location), the habitat type where the point estimate of the location fell could not be considered to reliably represent the habitat used. Therefore, I drew 150 m buffer around each location estimate to account for both the errors, and measured the habitat composition within the buffer area and considered that as 'used habitat' in analysing Johnson's (1980) 3rd-order selection (= selection of habitat types within home ranges). For analysing Johnson's (1980) 2nd-order selection (= placement of home ranges within the available study area), I compared habitat composition within 95% fixed kernel home ranges (as 'used' habitat) with habitat composition of study area (as 'available' habitat). Such a 2-stage approach to analysis of habitat selection is considered biologically realistic, because it recognises the hierarchical nature of habitat selection by animals (Johnson 1980, Aebischer *et al.* 1993). Habitat selection analysis was conducted using the program "Resource Selection for Windows" (Leban, 1999). Since the sample size of six radio-tagged bears (with year-round data) was not large enough, advanced analyses of habitat selection, such as compositional analysis (Aebischer *et al.* 1993) and Johnson's (1980) method, which take into account the compositional nature of habitat use and availability data, could not be not conducted. Habitat selection analysis was therefore limited to chi-square analysis (Neu *et al.* 1974, White and Garrott 1990) and graphical description of data.

Assessment of habitat quality for sloth bears

Habitat quality, in terms of resources required for survival and reproduction of sloth bears, was assessed by measuring associated characteristics such as food plant densities, prey insect colony densities, canopy, shrub cover, etc., in uniformly spaced locations spread over the study area (see Chapter 4: General Methods). Number of plots sampled in each habitat type was roughly in proportion to habitat composition of the study area, except that the dense forest habitat was probably under-sampled. To obtain the combined density of 4 main food plants in each bear's home range area, estimated densities of each food plant in each habitat type was weighted by the proportion of different habitats in each home range area and were summed.

Habitat degradation by humans and its impact on habitat quality for sloth bears

Based on habitat composition in a 1-km buffer around plot locations, proximity to Park boundary and villages, each of the 48 vegetation sampling plot locations was classified into one of five ordinal degradation levels: 1 – least degraded, to 5 – most degraded. Vegetation and insect colony characteristics in the plots in each of the degradation level were summarised to judge the impact of degradation of habitat on sloth bear food plant and prey insect colony densities. In addition to these food-related parameters, other variables that depict the degradation of habitat by humans and its impact on habitat quality for sloth bears such as, shrub cover, litter cover, availability of dead stump, level of grazing, etc., were assessed and ranked (from 1 - low, to 6 - high) at each sampling location.

The usage/selection of different habitat types, in particular, open shrub and degraded scrubland (the two habitat types degraded by humans) by tagged bears allowed me to make inference on the selection status of degraded habitats by bears. Vegetation and insect colony characteristics in the habitat types informed me of the factors probably influencing usage/selection of habitats by bears. The habitat characteristics of preferred and avoided habitats by individual bears were compared using paired samples t-Test. An *a priori* Type-I error rate of 5% was fixed for the statistical significance tests. For significance testing, emphasis was placed on estimates of effect sizes, confidence intervals of effect sizes and biological significance, rather than making decisions merely based on statistical significance.

Plate 8. Radio tagged bears were tracked year-round and their movements, space use, and habitat selection were assessed. Additionally, intensively monitoring bears such as this female 'F78' provided us detailed information on hitherto little known 'cubbing' behaviour of sloth bears, and on their requirement for critical habitats such as maternity dens.

6.3. RESULTS

Twelve sloth bears were fitted with radio-collars during the study (the maximum number permitted by the State and Central Governments for this study). Three of them provided data for <3 weeks and so were not used in analysis. Nine bears (5 females and 4 males) were monitored for varying periods, ranging from 3 to 32 months (a median of 18 months), and over 4,000 radio relocations were logged in total. From these, about 300 relocations (about 7%) were deleted because the estimated 95% error ellipses were >10 ha in area. Another about 400 relocations were discarded because they were logged <2 hours apart from the locations that were used in analysis. 3219 relocations of 9 bears were used in home range estimation and habitat use analysis (Fig. 6.1). The number of relocations for each bear ranged from 57 to 728, with a median of 382 relocations. Out of the total, 1,232 were collected in the night time and the rest during day. The bear identities, sex, tracking period for each bear, causes for ending radio-tracking, total number of relocations for each bear, number of active, resting, day and night relocations are summarised (Table 6.1).

Home range estimates

Six bears (4 females and 2 males) had year-round tracking data covering all seasons; one bear (M90) was tracked for two seasons; and 2 bears (M37 and F26) were tracked for one season each. The former six bears also had more than a year of relocation data. Therefore, total home ranges were estimated using all relocations for those bears, annual home ranges were estimated using subsets containing only one biological year of data, and seasonal home ranges were estimated for all three seasons in that year. For the latter three bears, only seasonal home ranges could be estimated (which were also used to estimate total home ranges). 95% fixed kernel estimates of total home ranges ranged from 12.41 km^2 for a female (F78) to 84.97 km^2 for a male (M69), both bears having been tracked for >1 year (Table 6.2). The annual home range sizes too showed a similar range and the relative positions of bears remained the same, except for one change (in the position of female F63). The 100% MCP estimates were much larger than 95% fixed kernel estimates for a majority of bears, and were larger by over 100% for two bears.

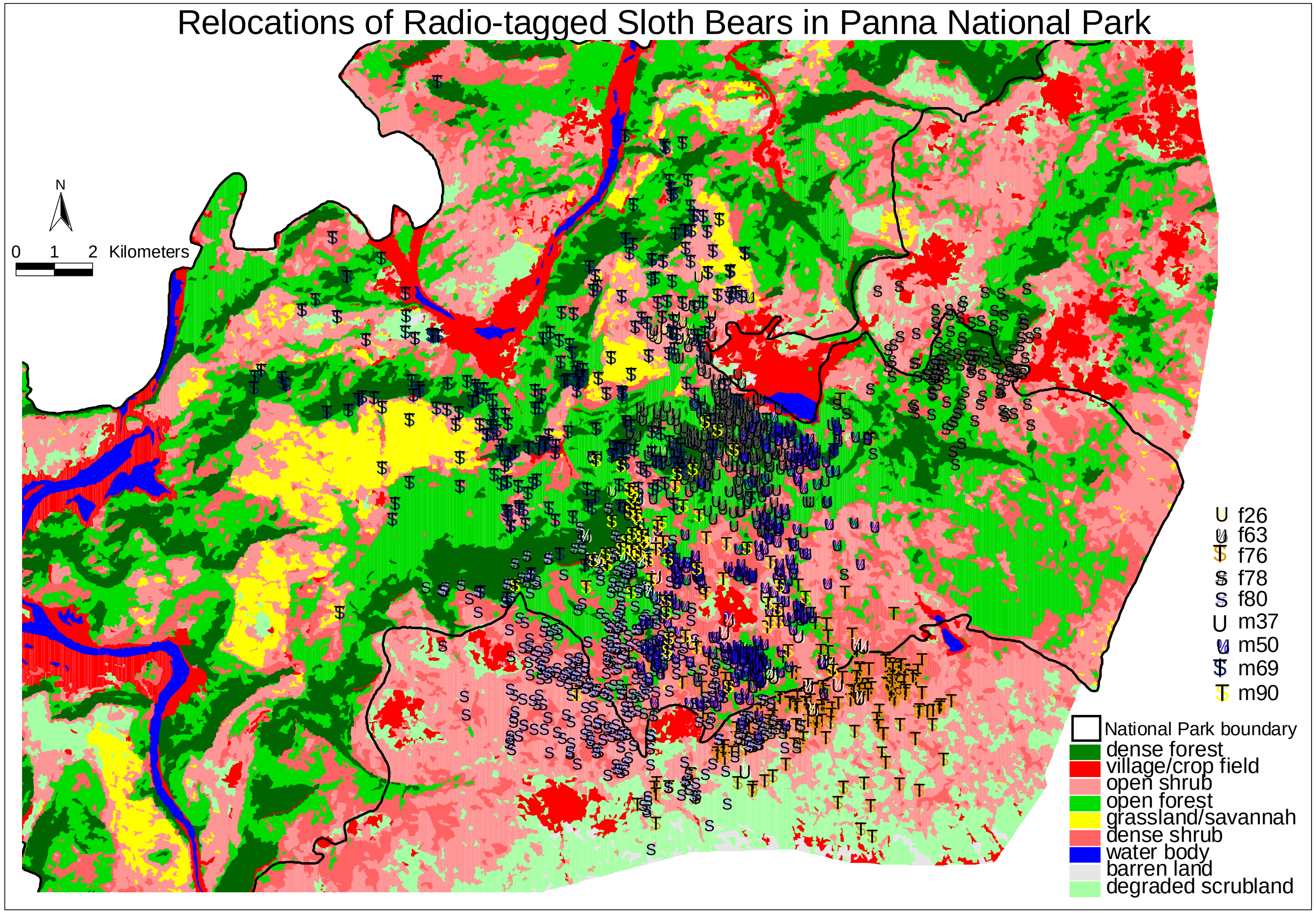


Fig. 6.1. Relocations of 9 radio-tagged sloth bears (5 females and 4 males) that were tracked between 1996 and 2000, overlaid on a habitat map of Panna National Park and adjoining areas.

In comparison, the 95% restricted polygon estimates were comparable to 95% fixed kernel estimates for most bears (Table 6.2).

Total home range sizes were similar to annual home range sizes for all bears, which indicated that the extent of space used by (adult) bears probably did not change much among years. All the bears for which annual home ranges were estimated have large sample sizes (median: 333, range: 198 to 401 relocations) and hence were probably accurate estimates (Garton *et al.* (2001) reported that error in adaptive kernel home range sizes in relation to true sizes was <15% when >200 locations were used for estimation, and therefore the estimates in this study are likely to have even smaller error). However, an exception could be that the space used by females in the cold season may not have been representative of actual cold season ranges, because all females were cubbing (denning) during most part of cold season in the monitored years. Annual, total, and seasonal home range sizes of male bears were, on an average, larger than females (although home range sizes of two females were greater than or comparable to one male, M50). However, from this rather small sample of radio-tagged bears, no strong inference on sex difference in home range sizes could be made. A male (M69) was in the higher end of the scale of home range sizes and 2 females were in the lower end, with a great difference in home range sizes (6 times) between the two ends (Table 6.2).

Table 6.1: Summary of tracking period, number of relocations, and other information on sloth bears that were (VHF) radio-tracked in Panna National Park and adjoining forest areas in central India during 1996 – 2000. Twelve bears were fitted with radio-collars and over 4000 radio relocations were logged in total. 3219 relocations of 9 bears were used in home range estimation and habitat use analysis.

Bear No.	Sex	Monitoring period		Tracking period (months)	Causes for ending radio-tracking	Total relocations	Active relocations	Resting relocations	Day relocations	Night relocations
		From	To							
M90	Male	April 1996	July 1996	4	collar found dropped; probably removed by the bear during aggressive interactions with other bears	96	55	41	47	49
M37	Male	April 1996	June 1996	3	stopped giving signals; cause not known	57	31	26	26	31
F63	Female	May 1996	March 1998	23	collar found dropped; leather worn out and broke	539	311	228	171	368
F80	Female	April 1997	November 1999	32	stopped giving signals; transmitter life probably ended	728	211	517	507	221
M50	Male	April 1998	May 1999	14	stopped giving signals; cause not known	475	152	323	311	164
F26	Female	December 1998	February 1999	3	Bear found dead in a den; cause not known	81	8	73	71	10
M69	Male	January 1999	October 2000	22	Transmitting when field work was wound up	567	186	381	361	206
F78	Female	April 1999	October 2000	19	transmitting when field work was wound up	382	90	292	256	126
F76	Female	May 1999	October 2000	18	transmitting when field work was wound up	294	72	222	237	57
9 bears – 5 females and 4 males		April 1996 to October 2000		138 bear-months	**<=Summary=>**	3219	1116	2103	1987	1232

Table 6.2. Estimated home ranges of radio-tagged bears in Panna National Park, central India. 100% minimum convex polygons (MCP), 95% restricted polygons, and 95% fixed kernel (Kernel 95%) estimates of total, annual and seasonal home ranges, and the number of locations used for each estimation are summarised here. Area estimates are given in km^2.

Bear ID and Sex[a]	Total 100% MCP Area	Total 95% MCP Area	Total Kernel 95% Area	Annual (Kernel 95%) All		Annual (Kernel 95%) Active		Annual (Kernel 95%) Rest		Cold (Kernel 95%)		Dry (Kernel 95%)		Wet (Kernel 95%)	
				N	area	*N*	Area	*N*	area	*N*	area	*N*	area	*N*	area
F26	15.99	14.91	14.31	--	--	--	--	--	--	81	14.31	--	--	--	--
F63	22.53	15.90	14.82	344	12.01	202	12.71	142	3.89	86	10.51	134	14.37	124	12.09
F76	82.04	47.36	33.95	198	34.57	60	31.97	138	30.19	23	21.85	69	25.11	106	24.18
F78	25.96	11.66	12.41	245	12.54	71	13.16	174	5.12	44	10.83	76	11.14	125	11.85
F80	51.72	44.74	43.59	322	36.68	100	34.83	222	30.25	45	23.23	104	19.12	173	29.7
M37	24.13	17.72	15.81	--	--	--	--	--	--	--	--	57	15.81	--	--
M50	41.22	35.56	29.90	401	30.25	132	25.13	269	25.48	133	23.93	78	17.44	190	27.53
M69	128.53	66.23	84.97	380	81.32	148	79.54	232	39.28	166	65.14	106	51.14	108	45.72
M90	38.35	26.22	35.84	--	--	--	--	--	--	--	--	50	15.03	46	33.73

[a] the IDs starting with F are females and M are males

The annual home ranges estimated using only the relocations when bears were ‘active’ were similar in size to home ranges estimated using all relocations (Table 6.2). Whereas, when only the ‘resting’ relocations were used, the estimated home range sizes were up to two or three times smaller than ‘active’ home range sizes for three bears, while having remained similar in size for others. The seasonal home range sizes were, expectedly, smaller than annual home range sizes (Table 6.2). The range sizes were not much different among seasons for females (except F80; mean of differences = 1.8 (1S.E. = 0.4), range = 0.31 – 3.86), while they were considerably different for males (mean of differences = 11.1 (1S.E. = 2.42), range = 3.6 – 19.42). Two males had smaller dry season home ranges, and their wet season ranges were much larger than dry season ranges.

Overlap in home ranges

Home ranges of male bears showed extensive spatial overlap (the pairs of males M37 & M90, and M50 & M69 were tracked at the same period within-pairs, but the pairs, between them were tracked at different periods), whereas, home ranges of females were spatially separated to a considerable extent (except F26, which showed a high overlap with F63; Fig. 6.2). The female F26 was tagged as a dependent yearling when it was accompanied by its mother, which I believe (based on its size, use of space and resting locations) is F63, which dropped its radio-collar 8 months before and it had a cub of about 4 months age then. Note that the pairs F63 & F80 and F76 & F78 were tracked at the same period within-pairs, but the two pairs were tracked in different years. There was high overlap in home ranges between sexes (Fig. 6.2), with each male’s home range at least partly overlapping the ranges of two or more females, and each female’s range partly overlapping more than one male’s range. Again, the small sample of tagged bears, and the likelihood of untagged bears having used the same space and having overlapped with tagged bears, limit me from discerning patterns in and making strong inferences about overlap in home ranges of bears.

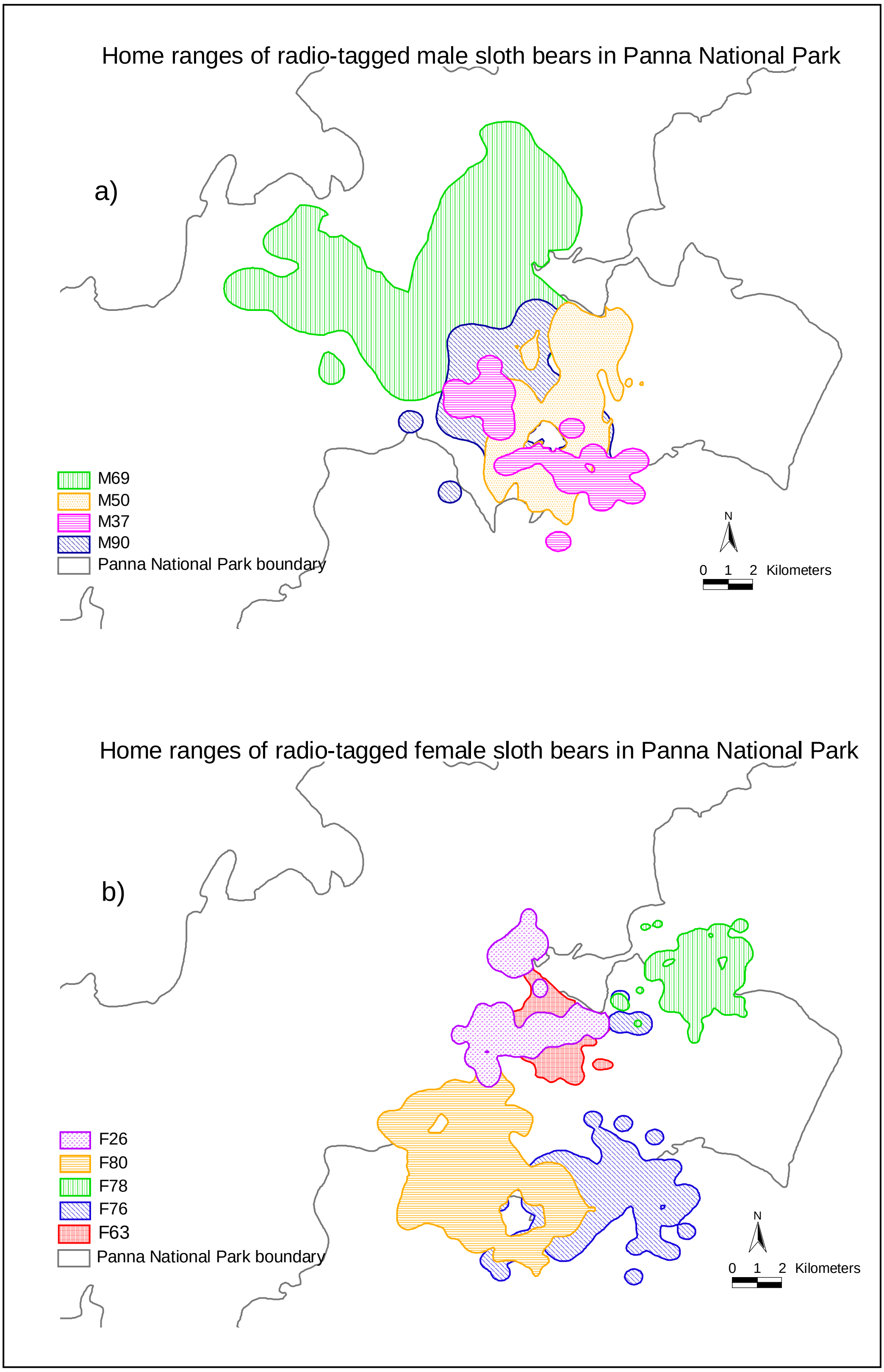


Fig 6.2: Estimated home ranges (95% fixed kernel estimates) of (a) male, and (b) female radio collared sloth bears in Panna National Park.

Seasonal changes in space and habitats used

Space used by some of the radio-tagged bears changed in size and shifted in location when seasons changed, while it remained about the same for others. Intensively used areas within seasonal home ranges (= ‘core ranges’) shifted in location among seasons (Fig. 6.3) for bears F80, M50 and M69, while remained the same for bears F63, F78 and F76. The core ranges of F63 and F78, in all the seasons, were located in escarpment and adjoining areas. F76 had its core ranges in the peripheral areas in all seasons, except for a disjunct patch of cold season core range far away from the rest of its range. This was due to the usage of an escarpment location by that female bear for ‘cubbing’. F80 located its dry season core range along the escarpment habitat, whereas it shifted its wet and cold season core ranges to peripheral areas. Similarly, male bears M50 and M69 had their dry season core ranges around the escarpment habitat, but shifted to other peripheral or core locations of varied habitat composition in the wet and cold seasons.

Habitat composition (considering only the 4 main habitats that together constitute >90%) of locations actually used by bears (as opposed to estimated home ranges) in the three seasons were similar for bears F63, F76 and F78, but changed considerably for the other 3 bears (Fig. 6.4). This indicated that the changes in spatial location of seasonal core ranges of the latter three bears also had underlying changes in habitats used by them. Bears F80, M50, and M69 used dense forest habitat more in dry season as compared to the other seasons, and conversely, used open shrub and dense shrub habitats less in the dry season. Further, the bear F80 used open shrub and dense shrub habitats more often than other habitats in the wet and cold seasons. Usage of open forest habitat did not change much among seasons for all bears. Bears F63 and F78 used dense forest and open forest habitats for >75% of the time, and that did not change among seasons; as was usage of dense shrub and open shrub habitats by the bear F76.

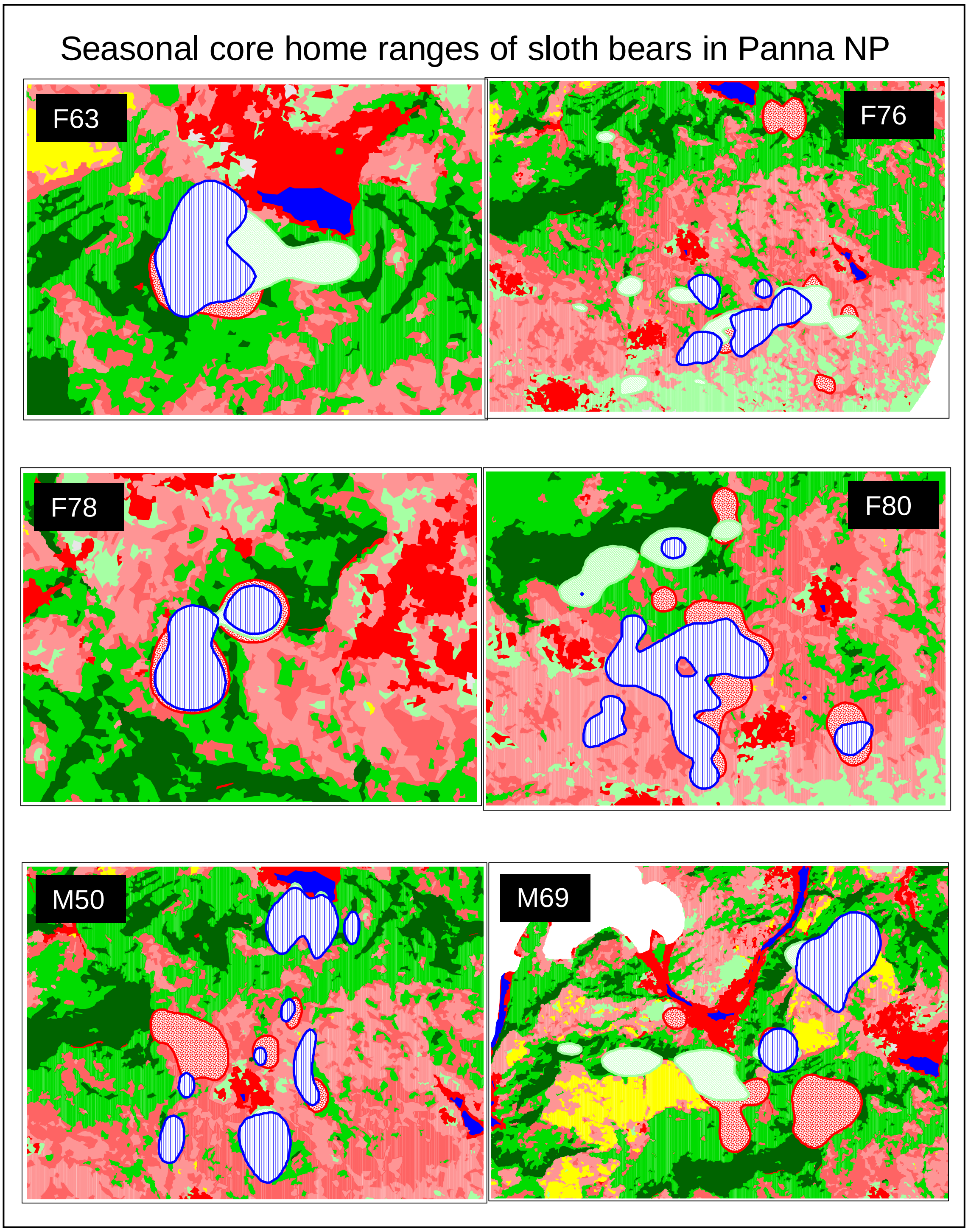

Seasonal core home ranges of sloth bears in Panna NP

Fig. 6.3. Seasonal core home ranges (intensively used areas; 50% fixed kernel density) – cold (red stippled), dry (green cross-hatched), and wet season (blue striped), of radio-tagged bears, overlaid on habitat map of the study area. Bears such as F80 and M69 clearly shifted core ranges among seasons, while F63 and F78 intensively used the same spaces in all three seasons of a year. Bear names that start with ‘F’ are females and ‘M’ are males.

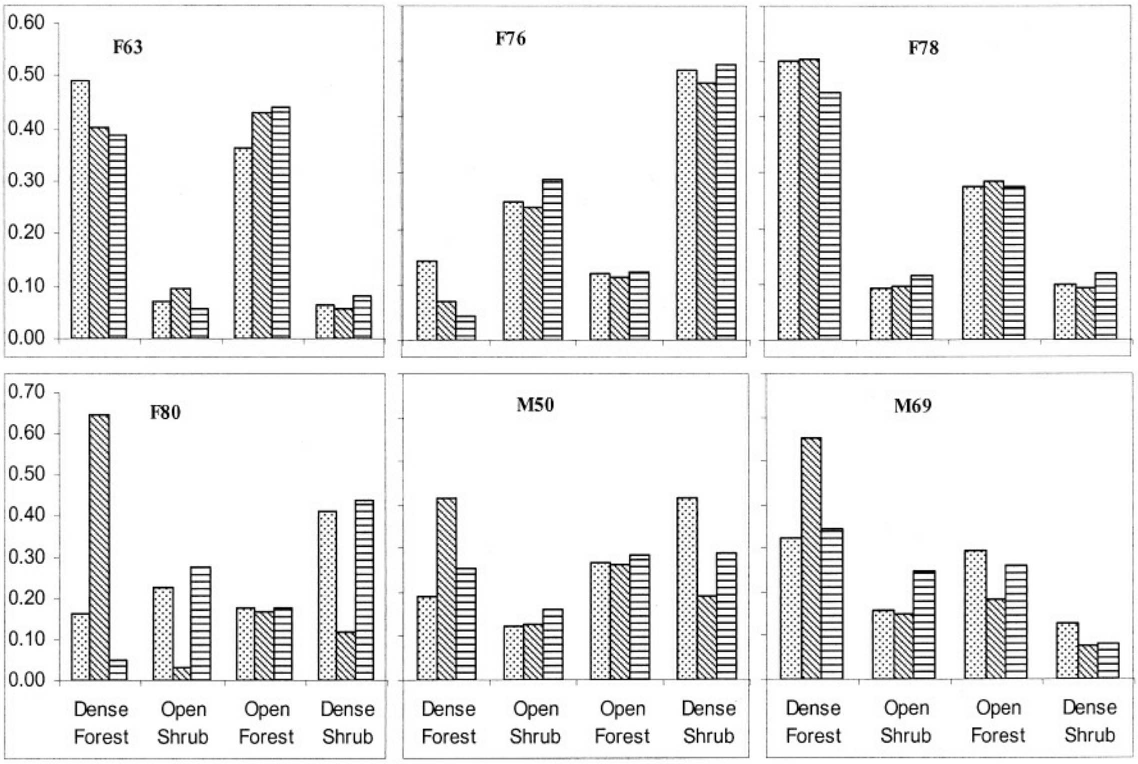


Fig. 6.4. Habitat composition (proportions of 4 main habitats) of all relocations (150-m buffer around location estimates) used by six radio-tagged bears in cold (dotted), dry (cross-hatched), and wet (striped) seasons.

Diel period changes in space and habitats used

Home ranges estimated (95% fixed-kernel estimates) by using day, crepuscular, and night period locations separately were different in size, location, or often both, for most radio-tagged bears. Day ranges were the smallest (1.5 to 4 times smaller than night ranges and 1 to 2 times smaller than crepuscular ranges for all bears, except F76) and were generally confined to day-bed locations (Fig. 6.5). For the bears F63, F78 and M69, day ranges were mostly around escarpments; for the bear F76 it was in peripheral areas; and for the bears F80 and M50, these were in discrete patches located in escarpment, knolls, and peripheral areas. The seemingly isolated patches of day ranges seen for F80, M50 and M69 (Fig. 6.5) were the result of seasonal shifts in space used by those bears (Fig. 6.3). Crepuscular ranges expanded outwards over day ranges, as bears became more active in the crepuscular period as compared to the day time, when they predominantly rested. Night ranges, which reflected foraging ranges, were the largest and covered spaces farther away from day-bed habitats. For the ‘peripheral’ (habitat) bears such as F76 and F80, the night time home range expansion was not as distinct as it was for ‘core’ (habitat) bears such as F63 and F78. Further, for the bear F76, ranges in all three diel periods were similar in size and location.

Expectedly, for most bears, along with range size and location, habitat composition of ranges too was different among the three diel periods. Habitat composition (4 main habitats) of locations used by bears in the day and crepuscular periods showed only small differences, whereas the differences between night and the other two periods were substantial (Fig. 6.6). For the ‘peripheral’ bear F76, although the habitat composition of day and night locations looked somewhat similar, a considerable difference was seen in the less frequent usage of dense shrub and dense forest habitats, and conversely, more frequent usage of open shrub habitat in the night. Also, this was in agreement with the changes in habitat use of the other bears. The bears used open shrub habitat more often, and conversely, used dense forest habitat less often in the night than in day and crepuscular periods. Further, the ‘core’ (habitat) bears F63 and M69 used open forest habitat more often, and the bears F78, F80, and M50 used dense shrub habitat more often in the night, as compared to day. Overall, bears used dense forest less and open forest, open shrub, or both, at times in combination with dense shrub habitat more often in the night. In the day and crepuscular periods, dense forest or dense shrub habitat was used more frequently than the other habitats, depending on whether a bear had escarpment areas available within its home range, and also depending on the season. This was expected because the bears generally rested in the day and they chose to rest in sites provided by these two habitats (see Chapter 5: Activity Patterns).

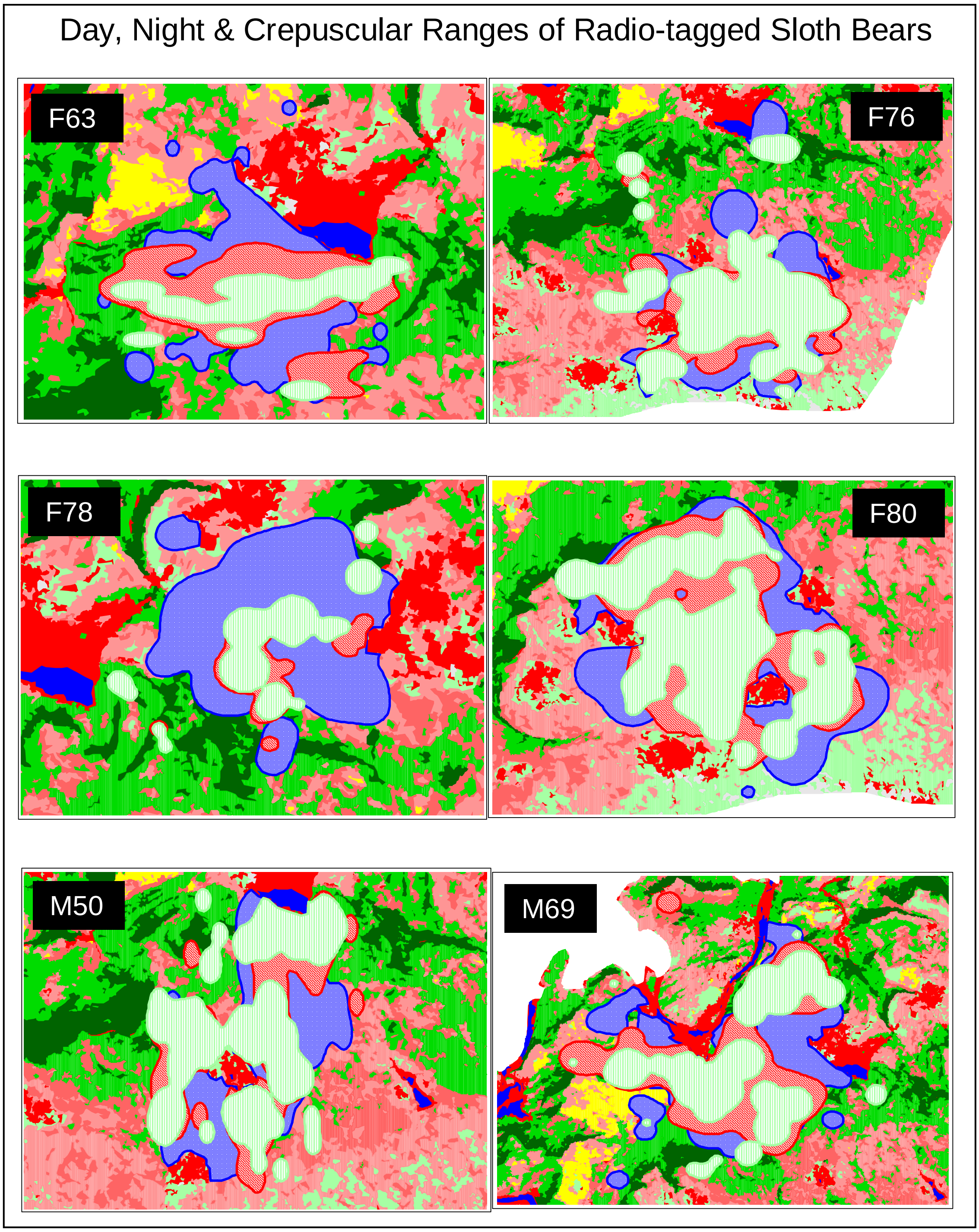


Fig. 6.5. Day (green striped), crepuscular (red cross-hatched), and night (blue dotted) ranges of radio-tagged sloth bears. Day ranges were the smallest and generally confined to day-bed habitats; crepuscular ranges expanded outwards over day ranges, as bears became more active; and night ranges were the largest, and covered spaces farther away from day-bed habitats. For ‘peripheral’ (habitat) bears such as F76 and F80, the night time home range expansion was not as distinct as it was for ‘core’ (habitat) bears such as F63 and F78.

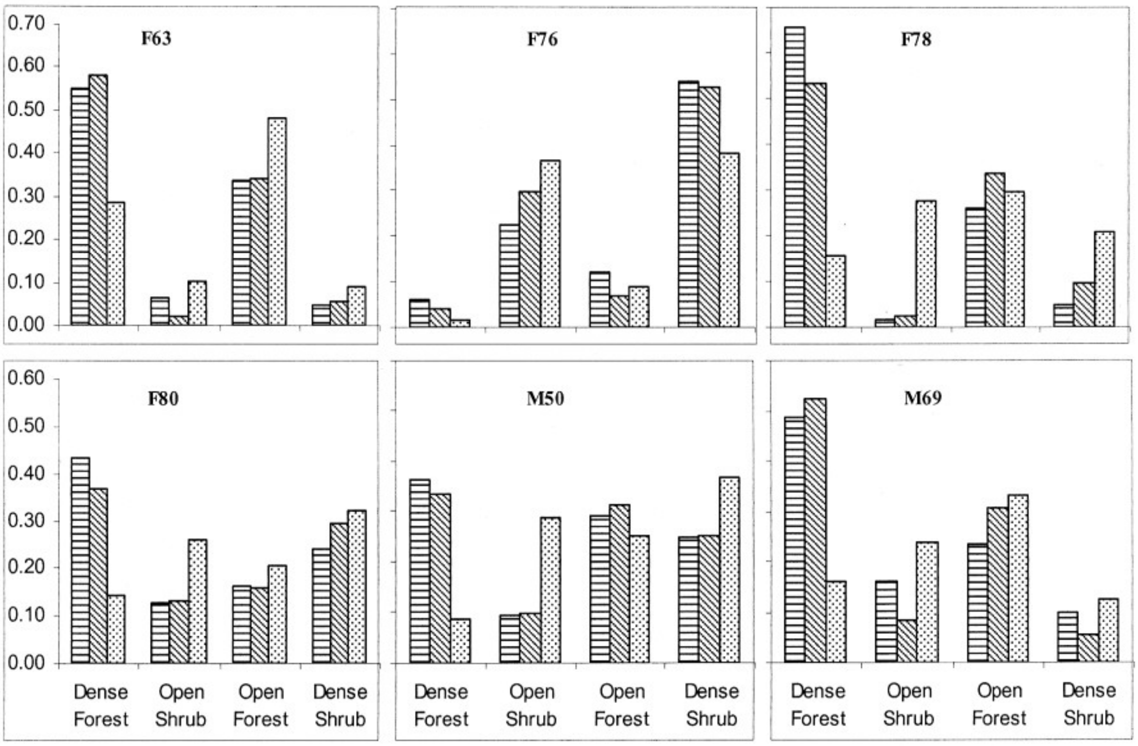
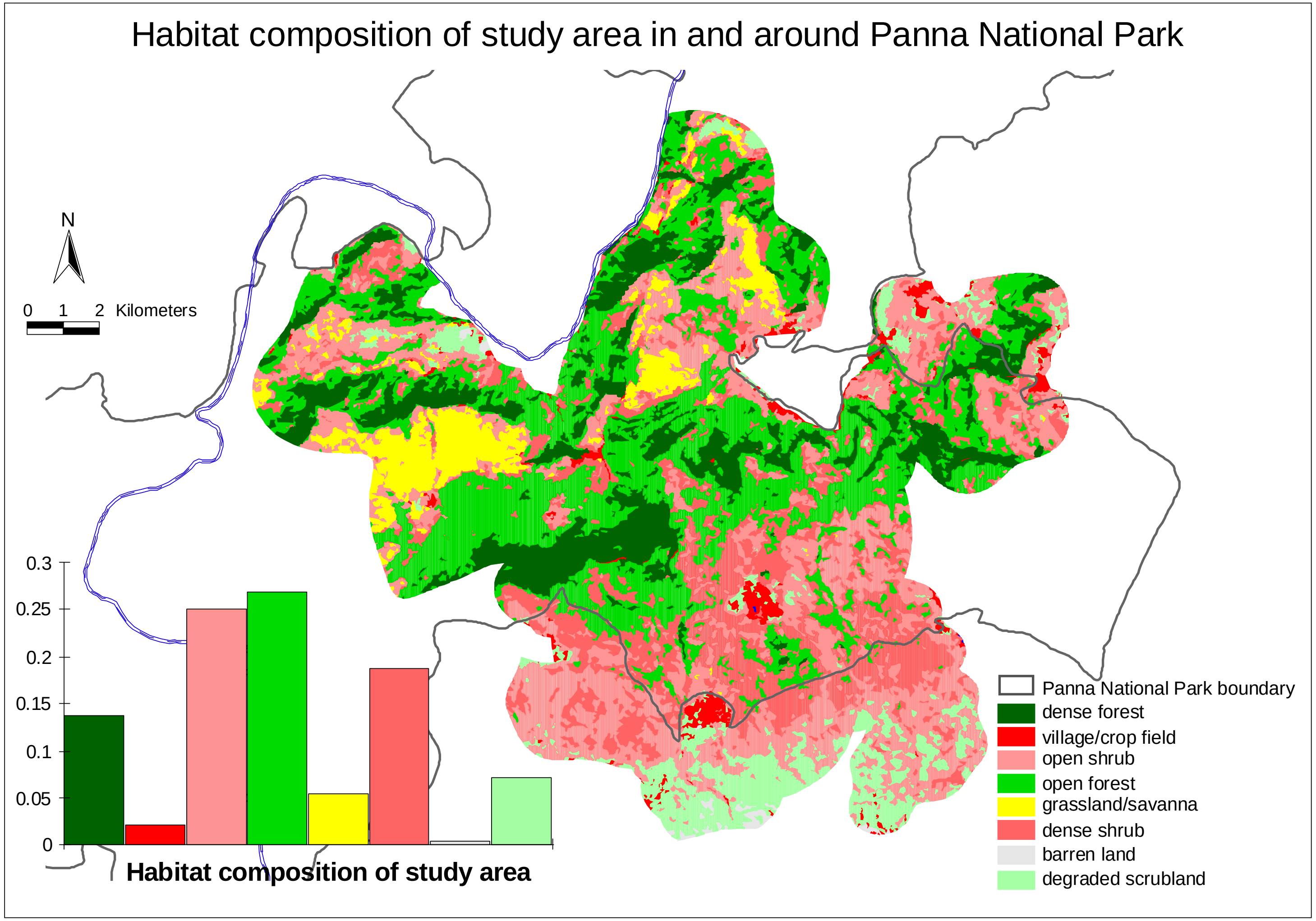


Fig. 6.6. Habitat composition (proportions of 4 main habitats) of all relocations (150-m buffer around location estimates) used by six radio-tagged bears in day (striped), crepuscular (cross-hatched), and night (dotted) periods.

Habitat use and selection

The study area of 239 km^2 was composed of 27% open forest, 25% open shrub, 19% dense shrub, 14% dense forest, 7% degraded scrub land, and 6% short-grassland / open-savannah habitats (Fig. 6.7). The different habitat types were characterised by various dominant plant species (trees and shrubs) and common sloth bear food plants (Table 6.3).



Habitat composition of study area in and around Panna National Park

Fig. 6.7. Habitat composition of study area (composite of 99% adaptive kernel home range estimates of all bears) in Panna National Park and adjoining areas. The inset chart gives proportions of each habitat type out of total study area of about 240 km^2.

Table 6.3: Dominant plant species, sloth bear food plant species, and % of total study area (= 239 km^2), of each of the broad habitat types identified in the study area and mapped using satellite imagery data.

Habitat Type	Dominant plants	Food plants	% of study area
Dense forest	*Terminalia tomentosa, Anogeissus latifolia, Tectona grandis, Diospyros melanoxylon, Schleichera oleosa*	*D. melanoxylon, Cassia fistula, Madhuca longifolia*	14
Open forest	*T. grandis, Acacia catechu, Lannea coromandalica, D. melanoxylon, A. latifolia, Aegle marmelos, Zizyphus mauritiana*	*D. melanoxylon, A. marmelos, Z. mauritiana, Lantana camara, C. fistula, Buchanania lanzan*	27
Dense Shrub	*L. camara, L. coromandalica, T. grandis, D. melanoxylon, Acacia sp.* Shrub	*L. camara, D. melanoxylon, A. marmelos, Z. mauritiana*	19
Open shrub	*L. camara, T. grandis, L. coromandalica, D. melanoxylon, Butea monosperma, Acacia sp.* Shrub	*L. camara, D. melanoxylon*	25
Short-grassland / open-savannah	*L. coromandalica, Z. xylopyros, Laegestromia parviflora*	*D. melanoxylon, A. marmelos*	6
Degraded scrubland	*L. camara, B. monosperma*	*L. camara, D. melanoxylon, M. longifolia* (near villages)	7
Village / Crop-field	*M. longifolia*, cultivated crops (Wheat, Mustard, Chickpea)	*M. longifolia*	2

The home ranges of radio-tagged bears had varied habitat composition, and some home ranges seemed randomly placed within the study area (habitat composition of home range was in proportion to availability within study area), while others showed selection for (= ‘preference’) particular habitat types (Fig. 6.8). Female ‘F63’ appeared to have selected for open and dense forest habitats, while avoiding open shrub habitat to place its home range. Female ‘F76’ seemed to have selected a space in the study area to place its home range that had less dense and open forest habitats, and more dense and open shrub habitats than was available in the study area. Female ‘F80’ and male ‘M50’ appeared to have selected for dense shrub habitat while placing their home ranges; female ‘F78’ and male ‘M69’ appeared to have placed their home ranges randomly. All bears seemed to have consistently selected against (= ‘avoided’) degraded scrubland while placing their home ranges. Chi-square analysis of testing for preference showed that the usage was not in proportion to availability (G_{adj} = 38.4733; $P<0.0001$), and an evaluation of Bonferroni simultaneous confidence intervals suggested that the dense shrub habitat was preferred and short-grassland / open-savannah, and degraded scrubland were avoided in placement of home ranges.

When Johnson’s (1980) 3rd-order selection was assessed using habitat composition of space considered available for each bear to use (99% adaptive kernel estimate), and the habitat composition of actual locations (buffers around locations) of usage, habitat selection became more apparent (Fig. 6.9). All bears except female ‘F76’ used dense forest habitat more often than was available to them. Female ‘F76’ seemed to have selected for dense shrub habitat; females ‘F63’ and ‘F78’ have used open shrub habitat less than was available; and all bears have used degraded scrubland much less than was available to them. Also, the proportion of dense forest and dense shrub habitats used by bears put together, out of all area used by bears, exceeded 0.5 for all bears. Again, usage was not in proportion to availability (G_{adj} = 159.3389; $P<0.0001$), and an evaluation of Bonferroni simultaneous confidence intervals suggested that dense forest and dense shrub habitats were preferred, and open forest and short-grassland / open-savannah habitats were avoided by bears.

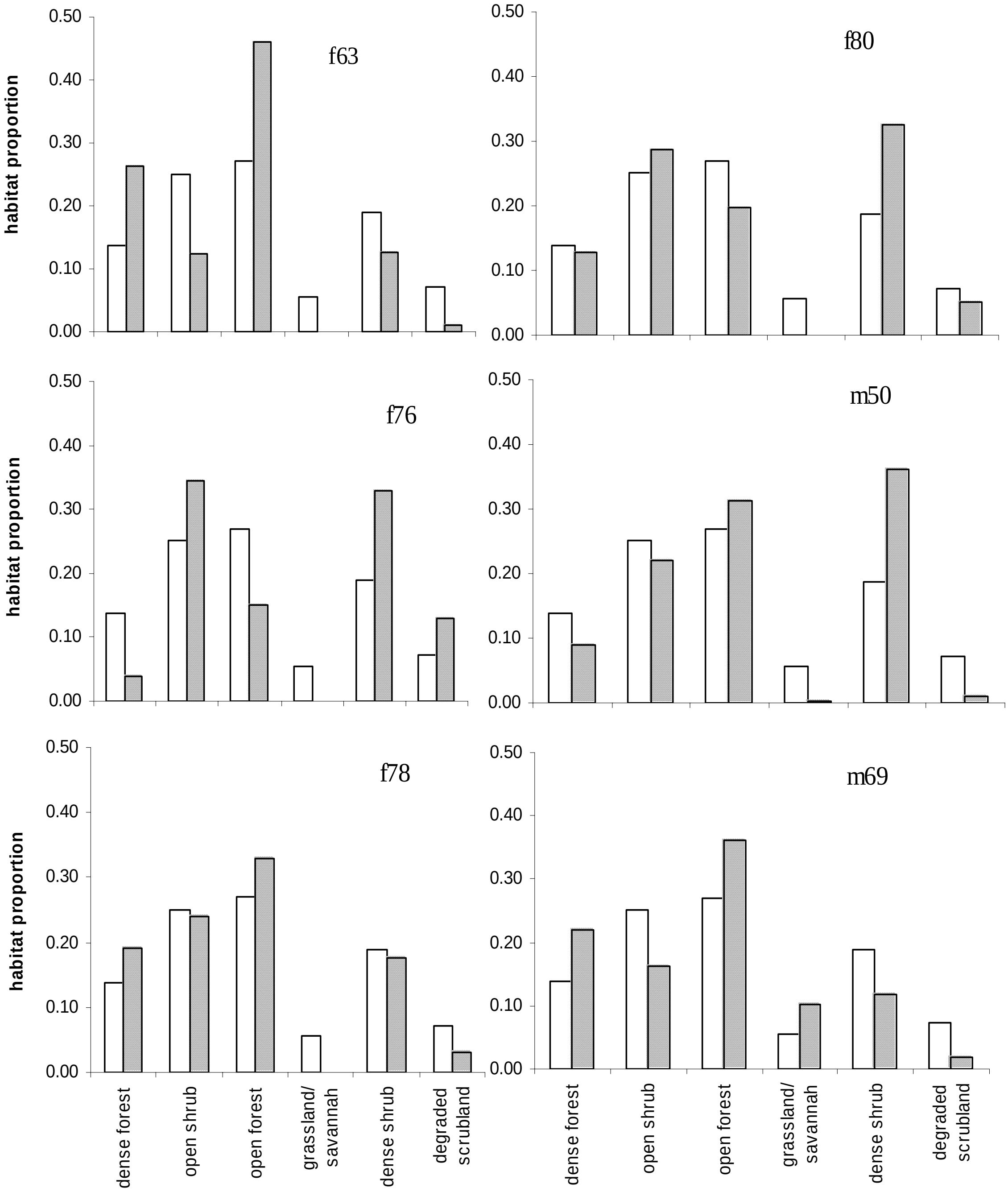


Fig. 6.8. Comparisons of habitat composition of study area (clear bar; area delineated by composite of 99% adaptive kernel home ranges of 9 radio-tagged bears), with habitat composition within 95% fixed kernel home ranges of each radio-tagged bear (cross-hatched bar).

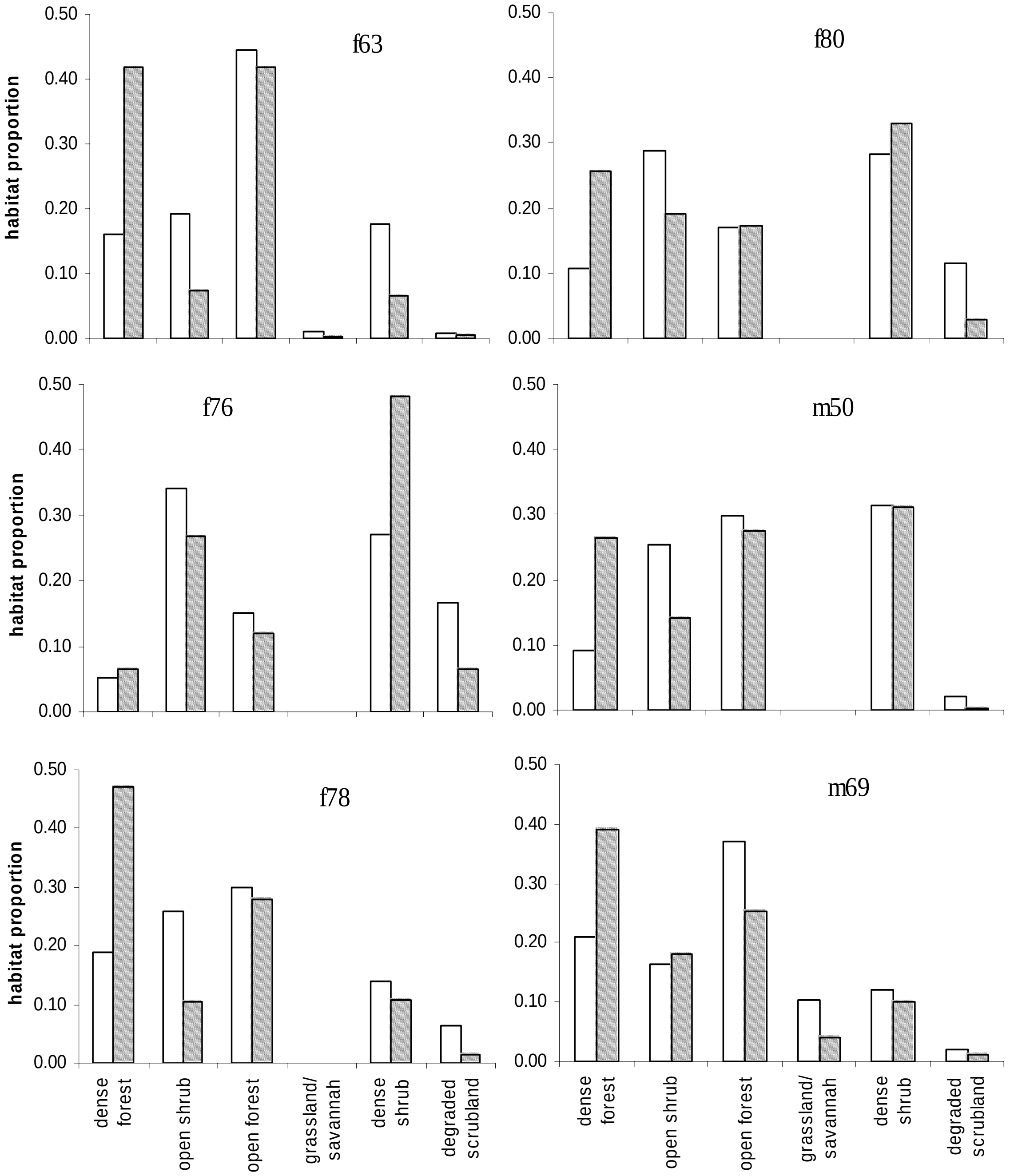


Fig. 6.9. Comparisons of habitat composition of space considered ‘available’ for each radio-tagged bear (clear bar; area delineated by 99% adaptive kernel home ranges), with habitat composition of area within 150 m radius buffer around all location estimates (considered ‘used’) for each radio-tagged bear (cross-hatched bar).

Food plant and prey insect characteristics of habitat types

Density of trees (sum of all tree species) was the highest in dense forest habitat, followed by open forest, dense shrub and others (Table 6.4). A key food plant for sloth bears, *D. melanoxylon* occurred at highest density in dense forest habitat, followed by dense shrub, open forest, and others. Another key food plant, *Z. mauritiana*, occurred at highest density in open forest and was sparse in other habitats. *L. camara* was most abundant in dense shrub habitat, followed by open shrub and others. Open forest habitat type had all the main food plants occurring at moderately high densities, and it was followed by dense shrub habitat. Open shrub habitat had lower density of trees and food plants, and higher density of *L. camara* shrub, reflecting the degraded condition of that habitat, but a moderately high density of *D. melanoxylon* was found in that habitat. Short-grassland / open-savannah habitat generally had low density of trees, and particularly low densities of sloth bear food plants. Degraded scrubland type was the poorest in terms of diversity and densities of food plants and other trees.

Table 6.4. Densities of sloth bear food plants, and all tree species, in different habitat types in Panna National Park. Means (±1 standard error of mean) are given.

Habitat type	No. of Plots	Density (No. / ha)					
		Diospyros melanoxylon	*Aegle marmelos*	*Cassia fistula*	*Zizyphus mauritiana*	*Lantana camara*	Total trees
Dense forest	3	92.0 (±50.0)	2.6 (±2.6)	5.3 (±2.6)	0.0	0.0	966.7 (±94.9)
Open forest	16	32.0 (±7.5)	19.0 (±10.2)	3.0 (±1.03)	29.5 (±22.3)	91.0 (±43.4)	577.8 (±57.8)
Short-grassland/ open-savannah	5	14.4 (±4.41)	2.4 (±1.46)	0.0	0.8 (±0.73)	0.0	215.2 (±35.2)
Dense shrub	9	39.6 (±11.36)	13.8 (±6.18)	2.2 (±1.17)	3.1 (±2.64)	382.2 (±110.5)	440.4 (±75.7)
Open shrub	13	23.4 (±6.17)	1.5 (±0.96)	2.2 (±0.86)	2.5 (±1.39)	256.9 (±87.4)	277.8 (±38.2)
Degraded scrubland	2	14.0 (±2.0)	0.0	0.0	0.0	80.0 (±52.0)	150.0 (±46.0)

Important prey insect taxa, *Camponotus* spp. of ants and ground-living termites occurred at highest colony densities in dense forest habitat (Table 6.5). Open forest habitat had all the important prey insect taxa and they occurred at moderate densities in that habitat, followed closely by open shrub habitat. All other habitat types, including degraded scrubland had comparable colony densities of ants and termites among them. In general, sloth bear prey insect colony densities were not substantially different among the different habitat types, during the wet season when I conducted the study. Densities of a key prey ant species, *Dorylus labiatus*, and subterranean termites with no mounds could not be estimated in this study, but the difference in whose densities among different habitats may influence differential usage of habitats by sloth bears.

Table 6.5. Colony densities of sloth bear prey species of insects, in different habitat types in Panna National Park. Means (±1 standard error of mean) are given.

Habitat type	No. of Plots	Density (No. / 100 m^2)				
		Camponotus spp.	*Pheidole* spp.	*Leptogenys* spp.	Ground-living Termites	Other *Myrmicinae* ants
Dense forest	2	8.5 (±4.5)	3.5 (±0.5)	0.0	4.5 (±1.5)	2.0 (±2.0)
Open forest	14	2.7 (±0.52)	1.2 (±0.39)	0.36 (±0.17)	1.7 (±0.69)	1.4 (±0.48)
Short-grassland/ open-savannah	5	2.6 (±0.93)	1.6 (±0.24)	0.0	3.0 (±0.95)	1.8 (±0.97)
Dense shrub	6	2.8 (±1.11)	2 (±0.52)	0.0	1.2 (±0.6)	2.2 (±1.04)
Open shrub	9	4.7 (±1.11)	1.9 (±1.16)	0.0	2.9 (±1.01)	2.3 (±0.85)
Degraded scrubland	2	2.0 (±1.0)	0.5 (±0.5)	0.0	2.5 (±1.5)	2.5 (±0.5)

Home range sizes and habitat characteristics

Home range sizes of six radio-tagged bears, whose annual home ranges were estimated, do not seem to be strongly related to sex or body mass. Given the limited sample I have, it seems that the home range sizes might be related to abundance of resources within home ranges. These data suggest that home range size might be negatively related to proportion of dense and open forest (the 2 resource-rich) habitats in home range, positively related to proportion of open shrub and degraded scrubland (the 2 degraded) habitats in home range, and negatively related to combined density of 4 main food plants (species as in Table 6.4, excluding *L. camara*) in home range (Fig. 6.10). Note that the three explanatory variables are not independent, but highly correlated. A male, M69, with a large home range size (81.3 km^2) does not conform to the patterns that the other bears seem to show, and its home range size could be related to other unknown (perhaps social) factors. When that outlier was excluded, the correlations between home range size and the two above mentioned negatively related factors were strong and statistically significant (Spearman's r_s = -0.9, $P<0.05$, N=5, for both), whereas the correlation between home range size and proportion of open shrub and degraded scrubland habitats in home range was not statistically significant (Spearman's r_s =0.8, P=0.1, N=5), a result that was possibly due to small sample size, and the consequent low power.

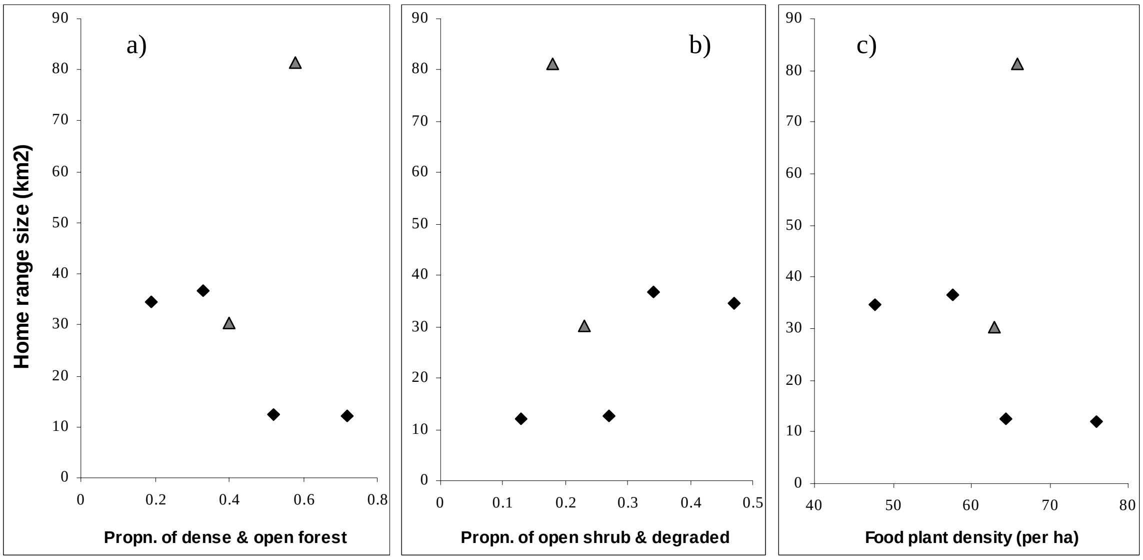


Fig. 6.10. Relationship between home range size and 3 explanatory variables: a) proportion of dense and open forest habitats in home range, b) proportion of open shrub and degraded scrubland habitats in home range, c) combined estimated density of 4 main sloth bear food plants in home range, of six radio-tagged bears (males are marked as triangles) whose annual home ranges were estimated.

Habitat degradation by humans and its impact on habitat quality for sloth bears

Total tree density decreased (although not monotonically) with increasing level of degradation of habitat, within the levels of degradation that was found in the study area (Table 6.6). Two main food plant species of sloth bears, *A. marmelos* and *Z. mauritiana* densities declined sharply with increasing degradation, while the density of *L. camara*, a shrubby weed associated with degraded habitats, increased with degradation level. Density of a key food plant, *D. melanoxylon*, showed no monotonical decline with increasing degradation level. It occurred at higher densities at intermediate levels of degradation (Table 6.6).

Table 6.6. Densities of sloth bear food plants and all tree species, at different levels of degradation of habitat in Panna National Park. Means (±1 S.E.) are given.

Degradation level	No. of plots	Density (No. / ha)					
		Diospyros melanoxylon	*Aegle marmelos*	*Cassia fistula*	*Zizyphus mauritiana*	*Lantana camara*	Total trees
1	8	19.5 (±5.2)	20.5 (±17.7)	2.0 (±1.3)	49.0 (±46.2)	--	539.0 (±134.0)
2	15	39.2 (±12.3)	15.7 (±7.2)	2.4 (±0.76)	2.9 (±2.38)	34.1 (±17.8)	389.6 (±63.3)
3	15	37.6 (±8.9)	3.7 (±2.39)	3.2 (±0.66)	4.0 (±2.68)	295.2 (±77.4)	552.3 (±60.2)
4	8	23.0 (±9.9)	1.5 (±1.5)	1.5 (±1.05)	5.0 (±3.36)	340.5 (±128.3)	279.0 (±57.9)
5	2	28.0 (±16.0)	--	--	--	366.0 (±234.0)	212.0 (±68.0)

Two important prey insect taxa, *Camponotus* spp. of ants and ground-living termites were at highest density in the least degraded habitats, and at lowest density in the most degraded habitats. However, there does not seem to be a steady decline in density with increasing degradation (Table 6.7). Three other prey insect taxa, *Pheidole* spp., *Leptogenys* spp. and *Myrmicinaea* sub-family of ants, did not show any discernible trend along the degradation gradient. Densities of key prey, an entirely subterranean ant *D. labiatus*, and subterranean termites with no mound, could not be estimated with the sampling method that I followed, and therefore, the effect of degradation on their colony densities could not be assessed. *Apis* spp. of bees too could not be assessed reliably with the method that I employed. Also, the commonest prey species of bee, *A. dorsata*, located its colonies primarily on cliff faces in Panna, and their densities were found negligible in the insect sampling plots.

Table 6.7. Colony densities of sloth bear prey insects, at different levels of degradation of habitat in Panna National Park. Means (±1 S. E. of mean) are given.

Degradation level	No. of plots	Density (No. / 100 m^2)				
		Camponotus spp.	*Pheidole* spp.	*Leptogenys* spp.	Ground-living Termites	Other *Myrmicinae* ants
1	7	6.14 (±1.6)	2.0 (±0.7)	0.29 (±0.2)	3.57 (±0.95)	2.0 (±0.75)
2	13	2.08 (±0.52)	1.62 (±0.37)	0.15 (±0.15)	2.38 (±0.74)	1.38 (±0.63)
3	10	3.6 (±0.81)	2.1 (±1.03)	0.1 (±0.1)	1.8 (±0.88)	2.0 (±0.74)
4	6	3.67 (±0.92)	0.67 (±0.33)	0.0	1.67 (±0.67)	2.7 (±0.67)
5	2	1.5 (±0.5)	1.0 (±0.0)	0.0	1.0 (±0.0)	2.0 (±1.0)

Canopy cover and grass cover seem to decline with increasing degradation level, while shrub cover did not show any such trend (Table 6.8). Weed abundance, livestock grazing intensity, and overall human presence and use of forest habitat increased with degradation level (Plate 9). Three micro-habitat characteristics that provide nesting substrates for social insects, and thus may be associated with sloth bear prey insect abundance – litter cover, abundance of fallen wood, and dead stumps, decreased with increasing degradation level of habitat.

Table 6.8. Ranks of habitat characteristics, which are associated with habitat quality for sloth bears, at different levels of degradation of habitat in Panna National Park. Median values are given.

Degradation Level	No. Of Plots	Canopy Cover	Grass Cover	Shrub Cover	Weed Abundance	Grazing Intensity	Human Use	Litter Cover	Fallen Wood	Dead Stump
1	8	4	6	3.5	1	2	2	4	3	4
2	15	4	5	4	3	3	4	4	3	3
3	15	4	5	5	4	5	5	3	3	3
4	8	3	5	4.5	4.5	6	6	3	2	2.5
5	2	3	4.5	4	4.5	6	6	2	2	2.5

Habitat selection in relation to habitat degradation by humans

Overall, degraded scrubland and short-grassland / open-savannah habitats were avoided, and dense forest and dense shrub habitats were preferred by tagged bears. Further, at the individual level, most tagged bears seem to have avoided degraded scrubland while placing their home ranges, and in terms of usage within the space available to them (99% adaptive kernel estimate), all bears seem to have avoided degraded scrubland habitat and some have avoided open shrub habitat. On the whole, bears seem to have avoided habitats degraded by humans, and these degraded habitats were lower in quality in terms of resources for sloth bears. Food plant, total tree, and insect colony densities were higher in the preferred habitats, overall (Tables 6.4 & 6.5), and for each bear, as compared to avoided habitats (Fig. 6.11; paired samples t-Test, N=6; for food plants, t = 10.29, P<0.001, 95% CI of difference in means = 50.8 to 84.7; for all trees, t = 8.38, P<0.001, 95% CI of difference in means = 447.4 to 843.2; for insect colonies, t = 5.42, P=0.003, 95% CI of difference in means = 4.1 to 11.4).

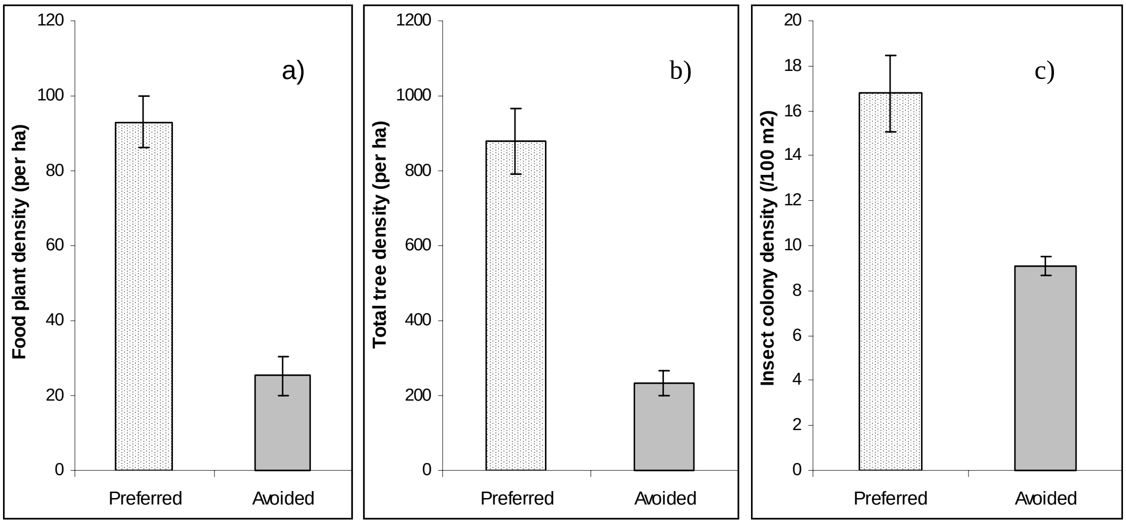


Fig. 6.11. Mean (± 1 S.E. of mean) densities of (a) 4 main food plants, (b) all trees, and (c) prey insect colonies in habitats preferred and avoided by tagged bears, at the individual level.

Plate 9. Lopping of trees such as *Diospyros melanoxylon* (left picture), which provides fruits for bears, by humans for collecting fruits and young leaves degrades habitat quality for bears. Degradation influences habitat selection by bears and consequently may affect their reproduction and survival in such degraded habitats. Over-grazing by cattle and associated human presence in forests also degrade habitat quality for bears, by affecting regeneration of plants, facilitating weed invasion, and perhaps by impacting abundance of social insects.

6.4. DISCUSSION

Home range sizes of sloth bears in Panna National Park were much larger as compared to the home range sizes of sloth bears in Chitwan National Park, Nepal, the only other population for which an estimate has been made and published. In Chitwan, mean annual home range sizes (Minimum Convex Polygon (MCP) estimates) were 9.4 and 14.4 km^2 for females and males, respectively (Joshi *et al.* 1995). Another home range size estimate that is available for sloth bear, a lone male bear that was radio-tracked (the first one ever to be done so), again in Chitwan (Sunquist 1982), had a MCP estimated annual home range size of 10 km^2.

Mean annual home range size (95% fixed kernel estimate) of female bears in Panna was about 2.5 times larger, and that of males was 4 times larger than Chitwan bears. When I compared MCP estimates of home range sizes of Panna bears with Chitwan bears, only for comparisons sake (see below for a discussion on this), mean home range size of Panna females was over 4 times the size of Chitwan females' and that of Panna males was 6 times the size of Chitwan males'. MCP estimates are highly sensitive to extreme data points and can include large areas that have hardly been used by an animal, so, I concur with other researchers (Worton 1987, Horner and Powell 1990, Powell *et al.* 1997) that MCP estimates are not reliable representation of home ranges of animals. Therefore, I do not wish to infer much from this comparison, because even a comparison between MCP estimates could be highly misleading, when the internal structure of home ranges was not considered, and when the estimates were made with small number of locations (say, < 100 relocations), which was frequently the case for Chitwan bears. A caveat that needs to be added here is the small sample of radio-tagged bears in this study. Nevertheless, I believe that these bears have reflected the general pattern, because the sample of bears was likely to be representative of the (small population of about 15 bears) population that occurred in the study area. On the whole, it seems likely that Panna bears had larger home ranges than Chitwan bears.

A main factor that caused the Panna bear home ranges to be larger than Chitwan could be the probable lower abundance of resources in Panna. However, an estimate of abundance of resources such as food plant, or prey insect densities is not available from Chitwan for comparisons with Panna. Given the generally higher primary productivity of alluvial grassland / moist deciduous forest habitat than dry deciduous forest habitat, it is likely that the food resources for sloth bears too are higher in abundance in alluvial grassland interspersed habitats. For instance, abundance of a main sloth bear food, termites, is likely to be directly linked to primary productivity of a habitat. Similarly, food plant densities too could be correlated to the climatic and edaphic factors influencing primary productivity of a habitat. An indication to the effect of abundance of resources, and the proportion of preferred habitat in home range on home range sizes was seen in the limited data from Panna. Sloth bear home range size appears to increase with decreasing proportion of preferred habitats (dense and open forest habitats), increasing proportion of degraded habitats, and decreasing density of main food plants contained in the home range space. If this apparent relationship holds true for larger samples and across study sites, it would have important implications for sloth bear science and conservation.

Within populations, home range sizes have been found to be related to sex, body mass, diet, and abundance of food and other resources (McNab 1963, 1983, Harestad and Bunnell 1979, Gittleman and Harvey 1982, MacDonald 1983, Gomper and Gittleman 1991), and across populations, to vegetation and climatic attributes (Koehler and Pierce 2003), food abundance (McLoughlin *et al.* 2000), and population density (Dahle and Swenson 2003). The intuitive relationship with body mass is expected to be observed (or to be strong) when comparisons are made among many species (large biological-scales), or across many study sites (large spatial-scales), or within a species, when habitat (resource abundance) is homogenous. When habitat is heterogeneous, the varying abundance of resources may confound the effect of body mass on home range size.

Difference in home range sizes (in sexually dimorphic species) between sexes is thought to be due to social factors, in addition to mass-related differences. While home range sizes of females were likely to be influenced purely by resource (food and cover) requirements, male home range sizes would be additionally influenced by availability and accessibility to females (Sandell 1989, Powell *et al.* 1997). Behavioural differences between the two sexes (often due to social factors) too might lead to differential usage of habitats, and consequently different home range sizes (Garshelis and Pelton 1981, Wielgus and Bunnell 1994). In Panna, male home ranges seem to be, on an average, larger than females. A male's (M69) home range was up to six times larger than the smallest home ranges of females'. But the difference in size between sexes is not clear-cut and has probably been obscured by the effect of habitat quality on home range sizes. Two females that had their home ranges in peripheral areas had large home ranges and were comparable to a male's home range size. If I consider MCP estimates, one female, F76, had a very large home range, because it used a den site in escarpment habitat, far from its regular home range, as a maternity den (for cubbing). At other times it hardly ever used that area. It used that site for cubbing probably because it provided far better security than any place in her regular home range, which is located in the peripheral area.

Annual home range sizes of animals may be related to seasonality of habitat, seasonal movement of animals among resource patches, and juxtaposition of habitats. The annual home range sizes of animals that show seasonal shifts in space use would be larger than the range sizes of animals that do not show shifts, all other influential factors being equal. In Panna, seasonal changes in home range size and shifts in range locations were observed for some bears. Three female bears did not shift their core ranges seasonally, while one female and two males did. The shifts in range location were accompanied by shifts in habitat use, suggesting that the changes in habitat use may have caused the changes in range location. Further, these changes were probably related to seasonally changing food abundance and distribution in the study area. Sloth bear diet changed prominently among seasons and it was related to changing abundance (biomass productivity) of different diet constituents (see Chapter 7: Feeding Behaviour). The distribution of food plants was patchy in the study area, and distribution of insect colonies too was likely to be so. Further, the food plant and insect colonies were associated with habitat types, and the habitat types were patchily distributed in the study area (Fig. 6.7). If areas with seasonal food abundance also had suitable resting cover, the bears shifted their core ranges (areas of concentrated use) to such localities. The result of this association was seen in the discrete patches of day ranges of the bears that seasonally shifted their cores (Fig. 6.5).

The factors influencing some of the bears to not shift ranges seasonally remain unclear, for want of detailed information on seasonal changes in abundance and distribution of food and other resources within individual bear home ranges. However, it seems that those bears with more homogenous habitat composition of their home ranges did not seasonally shift their ranges, while the ones with more heterogeneous habitat composition shifted. This was perhaps because the bears with heterogeneous habitat did not have access to enough resources from one habitat type around the year and therefore had to use seasonally available resources in multiple habitats. Or, due to the availability of multiple habitats, those bears could maximise rate of energy gain by exploiting seasonally abundant resources by shifting their ranges, rather than remaining in the same range location. The bears that used more homogenous habitat probably had enough resources available within their ranges and therefore did not have to shift. However, in the case of bear F76, which had a homogenous habitat, the resources within its home range were probably poorer and hence had a much larger home range, as compared to the bears F63 and F78.

The male bears and a female F80 had smaller dry season home ranges and larger wet season ranges. Also, these bears used dense forest habitat more in dry season than other seasons. These features may be related to the abundance of fruiting plants, and suitable resting sites in dense forest habitat (and associated escarpment terrain) in the dry season. In the wet season, vegetation became denser and cover was widespread. There was less fruit and more insect available for bears during wet season, and consequently the food distribution became more widespread, as opposed to fruit plants that generally occurred in patches, and at higher densities in forest habitats. Bear F80 shifted to dense shrub and open shrub habitats in wet and cold seasons, even though there was much of dense forest habitat available within its home range. This was perhaps to exploit the seasonally abundant insect resources in those habitats. In contrast, the bear F76 did not shift to dense forest habitat in dry season, and continued to use dense shrub and open shrub habitats in all seasons. This was despite its knowledge of the existence of such habitats and localities. It even had used the escarpment habitat occasionally for resting and foraging, and used an escarpment site for several weeks for cubbing. The factors that influenced this behaviour could include competition for the resource-rich habitats and the consequent lower rate of energy returns, exclusion due to the possible inferior social status of that bear, and territoriality among female bears. However, these suppositions could not be examined in this study.

In Chitwan, male sloth bears occupied larger annual home ranges than females (Joshi *et al.* 1995), which was primarily due to their larger wet season ranges. Wet season ranges of both males and females were larger (by 1.9 times) than dry season ranges, and this difference was probably related to food distribution and abundance (Joshi *et al.* 1995). Seasonal range shifts in correspondence with changes in resource abundance have been known in other bear species (Garshelis and Pelton 1981, Rogers 1987, Reid *et al.* 1991, Schwartz and Franzmann 1991). It is probably a common feature of all large-bodied, omnivorous animals that live in seasonal habitats.

In addition to seasonal changes, changes among day, crepuscular and night periods in size, location, and habitat composition of home ranges were observed in this study. Day ranges were generally smaller and were composed largely of resting spaces and habitats; and night ranges were much larger and reflected foraging spaces and habitats. Bears used dense forest habitat less often, and open forest and shrub habitats more often in night than day. Bears travelled in the nights to locations and habitats often away from resting spaces, particularly in wet and cold seasons. Bears in Panna had distinct periods of activity and this was reflected in the spaces and habitats used in different diel periods. Bears foraged in the nights and rested in the day, a behaviour that probably had evolved to avoid being active in adverse thermal conditions (see Chapter 5: Activity Patterns). Bears started and ended their diel activity cycles in the crepuscular period. The spaces used in that period were near resting habitats, and therefore were similar in habitat composition to day ranges. It was in these habitats and in this diel period that there were higher possibilities for humans to encounter bears, which sometimes led to bear-caused injuries to humans (see Chapter 8: Bear – Human Conflict).

Resting sites of the peripheral bears, which had less escarpment habitat available within their home ranges, were in dense shrub habitats and knolls, and so were not as restricted in spatial distribution as escarpment sites. Therefore, their day ranges were often as large as night ranges. The core habitat bears moved back and forth between their resting sites (confined, but secure escarpment sites) and foraging areas, and hence the night time range expansion was prominent, in contrast to the peripheral bears. The tagged bears, in general, were using open (canopy) habitats more frequently in the night time. Open habitats probably provided the bears with important nutrients (protein), seasonally abundant food (energy), or both. Open habitats may have been crucial sources of food, particularly when fruits were scarce, and further aided the bears to meet their essential protein requirements in all seasons (see Chapter 7: Feeding Behaviour). This suggests that along with the more closed-cover resting habitats, open habitats too are important for sloth bears. However, it appeared (in a pooled data, individual-level, Johnson's 3rd order habitat selection analysis) that the open shrub habitat was avoided by some bears (see discussion in later sections). It may mean that the open shrub habitat by itself was not preferred by all bears, but was preferred when interspersed with dense shrub habitat. A mosaic of open and closed-cover habitats probably provided optimal resources for sloth bears, over a day, and round the year. This finding, when supported with more evidence, would have important conservation implications. When a large sample of bears are studied, a more general pattern might emerge, which would provide unambiguous results.

The preceding discussion also highlights the importance of studying habitat selection of animals covering all time periods of day, and seasons of year. Studying habitat selection at one time period would have misrepresented the importance of habitats that were used at other periods. For example, in a radio-tracking study, if most fixes were on resting animals, foraging habitat would be underestimated, and this would lead to erroneous management practices. Also, pooling data from different time periods and assessing habitat selection again might have the potential of misrepresentation, and this dimension should be considered while interpreting the results. Similarly, seasonal variability in habitat selection too should be assessed and considered in studies of habitat selection. Previous studies have emphasized the importance of studying habitat selection jointly with the time factor (Harris *et al.* 1990, Palomares and Delibes 1992, Beyer and Haufler 1994). However, not many later studies seem to have considered this crucial point. Assessing space use and habitat selection by including the time factor gives important insights on animal behavioural ecology and further, has great implications for conservation. Critical management decisions concerning even endangered species could become flawed if the time factor is not included. The recent controversy surrounding Florida panther habitat selection (Gross 2005) underscores this dimension in habitat selection studies.

Home ranges of male bears in Panna showed extensive spatial overlap, while that of females appeared more spatially separated. There seemed to be high overlap in home ranges between sexes. However, no strong inferences could be made from this small sample of bears and due to the fact that not all bears in the study area were tagged. My field observations of tracks and sightings of untagged bears indicate that there were a few other untagged bears, in particular, 2 males that overlapped the ranges of tagged male bears. Untagged females were observed, but they seem to be primarily occupying the gaps in home ranges of tagged female bears. However, it could only be hypothesized at this stage that the females have less range overlap than the males have among them. In contrast to this supposition, Joshi *et al.* (1999) observed in Chitwan sloth bears that home ranges overlapped extensively among adults of the same sex (>50%) and between adults and sub-adults of both sexes (>70%), and that the zones of overlap were used in proportion to their area. Joshi *et al.* (1999) also observed that the extent of overlap varied among localities, perhaps depending on the resource abundance in an area. In all studies on sloth bears, it had been observed that they were solitary, but not territorial (Laurie and Seidensticker 1977, Joshi *et al.* 1999, this study). However, more studies and studies specifically designed for investigating this aspect are needed, before a conclusion could be made on this behavioural aspect of sloth bears.

Sloth bears in Panna showed preference for dense shrub habitat and seem to have avoided open-savannah and degraded scrubland habitats while placing their home ranges. Some bears seem to have selected against dense and open forest habitats in placement of home ranges, and this could be because factors such as social hierarchy might have influenced the placement of home ranges. Young bears or subdominant bears might not have a choice of placing their home ranges in the best of the habitats, but place them in seemingly suboptimal habitats. They might, however, compensate for this by having larger home ranges, and use more often the habitats within home ranges that are of higher quality, as was seen in the limited sample of tagged bears in Panna. Further, the benefits of using the large home range area probably exceeded the cost of having a large area.

Assessment of habitat use (based on actual locations of usage) within the area that was available for each bear to use showed that dense forest and dense shrub habitats were preferred and open forest and open-savannah habitats were avoided. It might seem ironical that the open forest habitat, which was of relatively high quality, were avoided. But this could be because of, 1) small sample size, 2) pooling data from different time periods, and 3) the fact that the dense forest and dense shrub habitats were preferred might have caused open forest habitat to show up as avoided, when actually it may not have been avoided. Such a problem of non-independence of proportional data have been discussed by Aebischer *et al.* (1993), who suggested that the proportion data be log-ratio transformed and compositional analysis (Aitchison 1986) applied to that. But the small sample of radio-tagged bears in this study did not permit me to conduct such an analysis. Dense forest and dense shrub habitats together composed over 50% of habitats used by all bears. A factor influencing this pattern of frequent usage of these habitats of dense cover could be the behaviour of bears preferring to day-rest in these habitats.

The different habitat types that I classified using satellite imagery data were identified and classified in the field primarily based on vegetation density, understorey and canopy cover. I thought that these characteristics would be related to sloth bear habitat selection because these may reflect variability in cover conditions and food plant densities, the two factors important for sloth bear survival. The different habitat types indeed had different levels of food plant densities and cover conditions, although insect colony densities did not seem to be related to these habitat classes. Therefore, my habitat selection analysis was definitely at a biologically relevant scale. However, a multivariate type of habitat model including the various other variables along with vegetation physiognomy, such as terrain, insect biomass availability, human disturbance levels, etc., (e.g., using the approach of Manly *et al.* 1993) would have been better for assessing habitat selection.

Bears in Panna seem to have avoided habitats degraded by humans, and these degraded habitats were lower in quality in terms of resources for sloth bears. Habitat degradation by humans affected the components of habitat quality for sloth bears detrimentally, but in varied degrees. While total tree density and some food plant densities decreased with increasing degradation level, a key food plant, *D. melanoxylon,* showed a humped pattern. It occurred at higher densities at intermediate levels of degradation. This could have been caused by several factors. Young leaves of *D. melanoxylon* are harvested every year for making country cigarettes, and so are of high economic value for local people. This probably induces them not to fell this species, while they fell most others, causing degradation. Even when this tree is cut, it coppices well and provides leaves for people. This species is also resistant to fire and so probably survives the regular forest fires well, while many other plants die out. This plant also sends out root suckers and so might occur at higher stem densities. However, because of regular lopping of branches for extraction of leaves (and often fruits), the fruit production of this species may be adversely affected (although I did not measure this). Therefore, even though the species may occur at higher stem densities in moderately degraded habitats, it may be of less value for sloth bears. Further, habitat type related differences in density of this species could be partly confounding the degradation level related differences in density (e.g., the short-grassland / open-savannah habitat in Panna has low density of *D. melanoxylon*, but is also less degraded by humans). Therefore, the effect of degradation on density of this species may not have stood out in this analysis.

Social insect colony densities in Panna were probably influenced by ecological factors (such as soil humidity, primary productivity in the rainy season) that were not strongly impacted by degradation by humans, and therefore, did not show a steady decline with increasing degradation levels. However, two key prey insect taxa occurred at highest densities in the least degraded habitats and at lowest densities in the most degraded habitats, suggesting that they too are definitely impacted by severe degradation of habitat by humans. Further, the micro-habitats that provide nesting substrates for social insects declined with increasing degradation, and this may be impacting insect colony densities. Also, I grouped insect species at genus or sub-family level, and this might obscure certain patterns. For example, *Camponotus* spp. was pooled at the genus level, and its density did not seem to steadily decline with degradation, whereas the main prey species among *Camponotus* genus, *C. compressus* appear to get replaced by *C. sericious* and *C. parius*, in more degraded habitats. Therefore, a decline in *C. compressus* colony density might have been obscured due to the pooling of these conspecifics. Further, the comparison of insect colony densities, rather than insect biomasses too could be a concern here, because, while colony densities remain similar, colony biomasses might well change with degradation level (through changes in colony sizes). Importantly, I estimated insect colony density only in the monsoon season, when the seasonal spurt in primary productivity probably supported colony densities in moderately degraded habitats comparable to less degraded habitats. Estimates from other seasons could show an entirely different picture. Also, the method that I followed to estimate insect colony densities was probably not the best method, and so it would serve to be a little unconvinced about these estimates.

Conservation implications

About 21% of Panna National Park area is composed of open shrub habitat and another 6% is of degraded scrubland and barren land. These habitats are mainly distributed in the southern, northern and north-western parts, peripheral areas, and near villages. An additional 7% of the National Park area is village / crop-field land. Restoration of the degraded habitats, which were of lower quality for sloth bears and which were avoided by them, could improve sloth bear reproductive success and survival in the National Park. Restoration measures could involve checking the causes that lead to degradation, facilitating regeneration of plants, and planting tree species, including key food plants to augment cover and food for bears in those habitats. Dense shrub habitat, even though dominated by *Lantana* sp. shrub, should be maintained at least in patches, due to their value as cover for sloth bears and many other animals. Dense shrub patches should particularly be restored or even created in vast open habitats. Since the dense shrub habitat also has high density of trees, the dense shrub cover may have been facilitating regeneration and recruitment of trees. This habitat eventually can get restored as higher quality habitat for bears. Human use in areas surrounding the National Park should be regulated so that the habitats do not become severely degraded and completely devoid of patches of dense cover.

Dense forest habitat, which is found mainly along escarpment, seems crucial for sloth bears and so should be kept out of possible degradation by humans. Human use of this habitat, e.g., for grazing, or for collection of forest products, should be limited. If additional dense forest habitat along escarpment is available in the vicinity of the National Park, it should be brought under the jurisdiction of the National Park, as this would greatly benefit sloth bears and many other animals. This habitat would serve as secure core habitat where sloth bears could rest during daytime and use as cubbing sites, while being able to use the surrounding lower quality habitats for foraging in the night time. Along with the more closed-cover habitats, open forest and open shrub habitats too are important for sloth bears, as these provide important nutrients and seasonally abundant food. A mosaic of open and closed-cover habitats interspersed with patches of varying sizes of each other is probably the optimal habitat for sloth bears to meet their daily and annual requirements of food and cover, in places such as Panna National Park. Habitat management plans and actions in such areas should keep this guideline in purview.

6.5. SUMMARY

- Sloth bear space use, home range sizes, and habitat selection were studied in Panna NP, by fitting radio-collars to 12 bears. Nine bears (5 females and 4 males) were monitored for varying periods, ranging from 3 to 32 months (a median of 18 months), and over 4,000 radio relocations were logged in total.
- Habitat quality, in terms of resources for sloth bears was assessed by measuring associated characteristics such as food plant densities, prey insect colony densities, shrub cover, etc. Sloth bear selection for such habitat characteristics was examined. Additionally, the impact of habitat degradation by humans on habitat quality for sloth bears, and its influence on sloth bear space and habitat use was assessed.
- 3219 relocations of 9 bears were used in home range estimation and habitat selection analysis. The number of relocations for each bear ranged from 57 to 728, with a median of 382 relocations. Six bears (4 females and 2 males) had year-round tracking data covering all seasons.
- 95% fixed kernel estimates of total home ranges ranged from 12.4 km^2 for a female to 85 km^2 for a male, both bears having been tracked for >1 year. The annual home range sizes were similar to total home range sizes, which indicated that the extent of space used by (adult) bears probably did not change much among years.
- Annual, total, and seasonal home range sizes of male bears were, on an average, larger than females. However, from this rather small sample of radio-tagged bears, no strong inference on sex difference in home range size could be made. The range sizes were not much different among seasons for females, while they were considerably different for males.
- Seasonal shifts in location of core ranges and changes in habitat use were observed for some bears. Two core (habitat) bears used dense and open forest habitats, and a peripheral bear used dense and open shrub habitats, in all seasons. The bears that had substantial area of dense forest (and associated escarpment) habitat within their home ranges used that habitat frequently in dry season, and three of those bears shifted to more open habitats in wet and cold seasons.

- Home ranges in day, crepuscular, and night periods were often different in size, location and habitat composition. Day ranges were generally smaller and were composed largely of resting spaces and habitats (dense forest and dense shrub habitats); and night ranges were much larger and reflected foraging spaces and habitats. Bears used open forest and open shrub habitats more often at night than during the day.
- It appears that along with the more closed-cover habitats, open habitats too are important for sloth bears. A mosaic of open and closed-cover habitats is probably the optimal habitat for sloth bears to meet their daily and annual requirements of food and cover.
- Home ranges of male bears showed extensive spatial overlap, whereas, the ranges of females seemed spatially separated to a considerable extent. There was high overlap in home ranges between sexes. Again, discerning patterns and making strong inferences about home range overlap was limited by the small sample of tagged bears in this study.
- The annual home ranges of bears had varied habitat composition, and some ranges seemed randomly placed within the study area (habitat composition of home range was in proportion to availability within study area), while others showed selection for particular habitat types. All bears seemed to have consistently selected against degraded scrubland while placing their home ranges. Overall, dense shrub habitat was preferred, and short-grassland / open-savannah and degraded scrubland habitats were avoided in placement of home ranges.
- When habitat composition of actual locations of usage was compared against habitat composition of space considered available for each bear to use (Johnson's 3rd-order selection), dense forest and dense shrub habitats were preferred, and open forest and short-grassland / open-savannah habitats were avoided by bears.
- Density of trees was the highest in dense forest habitat, followed by open forest, dense shrub and others. A key food plant for sloth bears, *D. melanoxylon* occurred at highest density in dense forest habitat, followed by dense shrub, and another key food plant, *Z. mauritiana*, occurred at highest density in open forest and was sparse in other habitats. Open

forest habitat type had all the main food plants occurring at moderately high densities, and it was followed by dense shrub habitat. Degraded scrubland type was the poorest in terms of diversity and densities of food plants and other trees.

- Important prey insect taxa, *Camponotus* spp. of ants and ground-living termites occurred at highest colony densities in dense forest habitat. Open forest habitat had all the important prey insect taxa and they occurred at moderate densities, followed closely by open shrub habitat. All other habitat types, including degraded scrubland had comparable colony densities of ants and termites.
- It appears that the bear home range sizes are related to abundance of resources within home ranges. The limited data suggest that home range size may be negatively correlated to proportion of dense and open forest (the 2 resource-rich) habitats, positively correlated to proportion of open shrub and degraded scrubland (the 2 degraded) habitats, and negatively correlated to combined density of 4 main food plants, in the home range.
- Bears seem to have avoided habitats degraded by humans, and these degraded habitats were lower in quality, in terms of resources for sloth bears. Food plant, total tree, and insect colony densities were higher in the preferred habitats as compared to avoided habitats.
- **Conservation implications**. Degraded habitats, which compose a significant proportion of Panna National Park should be restored; patches of both dense shrub habitat and open habitats in the Park should be maintained; the crucial dense forest habitat found along escarpment should be kept away from possible degradation by humans; security of escarpment (with dense forest) habitat found in the vicinity of the Park should be assured; and human use of forest land surrounding the Park should be regulated.

CHAPTER 7. ECOLOGY OF SLOTH BEAR FEEDING BEHAVIOUR

7.1. INTRODUCTION

Bears, in general, are omnivorous except for the giant panda (*Ailuropoda melanoleuca*) and the polar bear (*Ursus maritimus*), which are folivores and carnivores, respectively (Schaller 1970, Landers *et al.* 1979, Peyton 1980, Eagle and Pelton 1983, Schaller *et al.* 1989, Hellgren *et al.* 1989, Mattson *et al.* 1991, Reid *et al.* 1991, Mattson 1998, Jacoby *et al.* 1999). The omnivorous bears feed on fruits, nuts, roots and tubers, foliage, small and large mammals, fish and invertebrates. The American black bear (*U. americanus*) and the brown bears (*U. arctos*) of North America and Europe include considerable amounts of ants in their diet (Mattson *et al.* 1991, Schwartz and Franzmann 1991, Clevenger *et al.* 1992, Craighead *et al.* 1995, Noyce *et al.* 1997, Swenson *et al.* 1999a, Mattson 2001).

In keeping with its *Ursid* lineage, the sloth bear is expected to be an omnivore. However, certain morphological features, such as the long front claws, short hind legs, long and near naked muzzle, long and raised palate, the loss of first maxillary incisors in adults, indicate adaptation to the myrmecophagous (ant and termite feeding) niche (Laurie and Seidensticker 1977). However, earlier studies have reported that the sloth bears feed on a large amount of fruits along with insects (Schaller 1967, Laurie and Seidensticker 1977, Johnsingh 1981, Baskaran 1990, Gokula *et al.* 1995, Baskaran *et al.* 1997, Desai *et al.* 1997, Joshi *et al.* 1997, Bargali *et al.* 2002). The relative proportions of fruits and insects in sloth bear diet vary among study areas and also vary seasonally within study areas. In Chitwan National Park, Nepal, insects formed a dominant portion of the annual diet (Joshi *et al.* 1997). In some other studies, the proportion of fruits was much higher than insects (Baskaran *et al.* 1997, Bargali *et al.* 2002). This leads to the question as to whether the sloth bear is an obligate myrmecophage or just an omnivore, with a diet including insects.

The variability in food habits of sloth bears among study areas may be due to an adaptation to local availability of various fruit and insect resources. The diversity and abundance of fruiting plants, and consequently the fruit biomass productivity varies geographically and with vegetation types (Leigh and Windsor 1982, Howe and Westley 1986, Ganesh and Davidar 1999), as does the diversity and abundance of insects (Lee and Wood 1971, Josens 1983, Aubensberg-Traun and De Boer 1990, Holldobler and Wilson 1990, Belshaw and Bolton 1993, Eggleton *et al.* 1996, Basu 1997). For example, ant diversity varied with size, abundance and condition of woody debris (Johnson 1996). The level of degradation of habitat also may affect the abundance of fruit and insect resources (Holloway *et al.* 1992, Belshaw and Bolton 1993, Eggleton *et al.* 1996). In degraded habitats, if the food abundance is low, sloth bears may even get habituated to feeding on agricultural crops (Iswariah 1984, Garshelis *et al.* 1999, Bargali *et al.* 2002). This leads to conflict between bear and people (Rajpurohit and Krausman 2000, Bargali *et al.* 2002). Improving the habitat quality in terms of food resources is essential to reduce such conflicts. Exactly how such habitats might be improved can be deduced, in part, from studies on food habits.

Even within a study area, food habits vary from year to year, over seasons and across space. Annual variability in the availability of various food resources in an area would affect the relative consumption of various resources over years (Mattson *et al.* 1991, Baskaran *et al.* 1997, Desai *et al.* 1997, Iverson *et al.* 2001). Within a year, fruits are available only in certain periods of the year and the same may be true for insects (Wolda 1988, Basu 1997). Bears may feed on insects when reproductives or pre-adult stages (which are nutritionally richer) are present (Noyce *et al.* 1997, Swenson *et al.* 1999a, Mattson 2001, 2002), and the presence and abundance of these life stages may vary seasonally (Ueckert *et al.* 1976, Levings 1983, Wolda 1988, Noyce *et al.* 1997).

Fruit plants and insects may also be patchily distributed over space and their abundance is related to habitat types. Bears have large home ranges and they shift their core home ranges in correspondence with food distribution or may move to distant fruit patches during fruiting seasons (Garshelis and Pelton 1981, Rogers 1987, Peek *et al.* 1987, Garner *et al.* 1990, Reid *et al.* 1991, Schwartz and Franzmann 1991, Craighead *et al.* 1995, this study – see Chapter 6: Space Use and Habitat Selection). Bear ranging patterns, home range sizes, seasonal range shifts and movement rates may depend on what they feed on and how much is available. Sloth bears in Chitwan NP, Nepal have been observed to move between two habitat types seasonally and this may be related to differences in food availability between the habitat types (Joshi *et al.* 1995, 1997). In the present study, some radio collared sloth bears shifted their core ranges (Chapter 6: Space Use and Habitat Selection) and showed changes in relative use of different habitats seasonally. This may have been related to seasonal changes in food distribution and availability.

The habitat and seasonal factors will have a bearing on the relative consumption of plant and insect food by sloth bears. To compare the food habits among study areas and determine what is causing the variability, data on food biomass availability is needed. Although there have been efforts to relate the fruit consumption to fruit plant diversity and density (Baskaran *et al.* 1997, Gokula *et al.* 1995, Desai *et al.* 1997), no study in the sloth bear range has attempted to relate food consumption and biomass productivity. Food abundance in an area and consequent nutritional status of animals directly influences reproductive success and population productivity (Jonkel and Cowan 1971, Bunnell and Tait 1981, Rogers 1987, Elowe and Dodge 1989, Schwartz and Franzmann 1991, Samson and Huot 1995, Hilderbrand *et al.* 1999). Thus, information on food habits and food resource abundance has considerable conservation implications.

Apparent differences in food habits among study areas may also be a result of erroneous or non-comparable methods to some extent. Earlier studies on sloth bear diet have used a variety of methods ranging from visual estimation to quantitative sampling procedures. They have also represented their results in various forms such as, frequency of occurrence in faeces, relative composition, volume, or dry weight of faecal remains. For the results to be comparable, there needs to be one standard method of analysis and the form of representation should also be meaningful, such as the relative biomass consumed, rather than what was excreted. Developing such a standard method, which could be followed in future studies is a priority. Joshi *et al.* (1997) attempted to develop an efficient method of analysis and I have assessed the biases inherent in this method and improved on it.

Whether the sloth bear food habits follow spatial and seasonal pattern of availability of food resources and if they chose one food over the other are questions to investigate. Animals are expected to choose food resources as governed by the rules of foraging energetics – reduction in search time, handling time, and enhancement in nutritional benefits (Krebs and Davies 1993). Food abundance, distribution pattern of resources, ease of foraging, prey defence, and nutritional value would determine the optimal food choice. Nutritional benefits could be in terms of energy or essential nutrients, e.g., protein, minerals. Among food groups (fruits, ants, termites), choice may be related to abundance and nutritive value of a food group or related to the relative availability and relative quality of other food groups. For example, consumption of ants by American black bears increased with an increase in nutrient quality of ant colonies (by the availability of pupa) and a decrease in quality of plant food. They shifted from ants to fruits when fruits became abundant, despite the continued presence of quality ant colonies (Noyce *et al.* 1997). However, they did not consume only fruits even when they were seasonally abundant, but frequently mixed it with insects for nutritional reasons (Rode and Robbins 2000). Whether some species/taxa within food-groups were selected over the others and the factors that lead to such a selection is a further question to investigate. Larger ants may or may not be preferentially selected (Johnson 1996, Noyce *et al.* 1997, Swenson *et al.* 1999a), and fruits that are presented well may be preferred by bears as they offer higher bite rates and thus a higher energy gain per unit time (Welch *et al.* 1997).

My objectives were to describe sloth bear foraging behaviour and food habits, examine what factors influence these, and further investigate why some resources are chosen over others.

The questions that I attempt to answer here are:

i. How do sloth bears in Panna forage on various resources?

ii. What kinds of food do they feed on and what food-type characteristics do they select, in general?

iii. Are food habits uniform throughout the year, or is there a large seasonal variation? If so, do food habits follow seasonal patterns of food availability?

iv. Do sloth bears feed randomly on all types of available food or do they show preference for some? Is the preference related to abundance or other factors such as nutritional quality?

v. Is there selection or preference for some species/taxa within food-groups (ant, termite, or fruit)? What traits do the bears select for in plants and insects?

vi. Are sloth bears in Panna obligate myrmecophages or omnivores with a diet including insects?

In addition, I developed a method of faecal analysis for studying food habits of sloth bears that could be adopted as a potential standard method.

7.2. METHODS

I studied sloth bear feeding behaviour by direct observation of bears foraging and by estimating diet composition from faeces (scats). Information on various characteristics of food and other common plant species (phenology, fruit abundance, fruit size), prey and other insect species (colony abundance, colony size, activity), biomass productivity, etc. were collected by field sampling, the methods for which are described elsewhere (Chapter 4: General Methods) in this dissertation. Sampling and analytical methods for other data used in this chapter are described below.

Foraging observations

I homed in on the radio collared sloth bears periodically, observed them and collected information on their foraging behaviour. I also observed other bears that were not fitted with radio collars, while tracking the radio collared ones or while I was on observational towers or vantage points. I observed the bears mainly from vantage points such as ledges over-looking bear resting dens, from a distance of 30 to 100 m, through binoculars. I occasionally used riding elephants to follow and observe bears. I sometimes followed the bears also on foot to observe their activities often after they emerged from day-resting dens. Observation was usually possible until I was detected, the bear was lost, the vegetation or terrain was unfavourable or until there was daylight. Most of the observational data was collected in the evenings and mornings when the bears usually started and ended their activity, respectively. Night observations were relatively infrequent and were done from jeeps or from tree platforms occasionally using a night-vision scope. Extended observations were not possible, as the period the bears were active during daylight hours was short and at night, the bears shied away once they detected me. The length of observations ranged from a few minutes to a few hours. In total, about 200 hours of visual observations were made on active bears.

When bears were sighted, the location, habitat, and type of activity were recorded. The activity of bears was categorised as travelling, feeding, vigilance, interaction with other bears, other animals, or humans, mother-cub interaction, marking activity, etc. When the bears were seen feeding, the foraging method (digging, picking, climbing, etc.), type of food (plant, insect, other), and length of feeding on one patch of food were recorded. The species of food, parts (for plants) or life stages (for insects) eaten were recorded at close quarters, after the bears moved away (Plate 10). During nights, at times, I listened to the feeding sounds of bears from a distance and examined the site after the bears had moved away. Insect specimens were collected for later identification if necessary. The characteristic signs that were left at the feeding site by bears foraging on various food items were also recorded. A feeding event at one patch of food (e.g., a fruiting bush, fallen fruits under a tree, or an insect nest) was considered a sample unit. A similar measure was used by Joshi *et al.* (1997) to study foraging behaviour of sloth bears in Chitwan NP, Nepal.

Diet composition from faeces

Food habits of animals and the importance of various food items to diet have often been estimated by analysing faeces. Faecal analyses have been widely used (e.g., Peyton 1980, Putman 1984, Hellgren *et al.* 1989, Craighead *et al.* 1995) and is perhaps the best available method for studying the food habits of species such as the sloth bear, which are difficult to observe closely or for extended periods. However, the results from scat analyses need to be corrected for the biases in variable digestibility. Since the end result of faecal analyses is usually the contribution of various food items to diet in relation to each other (relative values), the biased under-representation of one item falsely inflates the importance of others.

In omnivores like bears with a varied diet, the estimation of food habits without correcting for variable digestibility will often give highly misleading results. Pritchard and Robbins (1990) found that the digestibility of various food items by grizzly and American black bears varied much among different food types. Hewitt and Robbins (1996) developed correction factors to convert faecal residues to biomass consumed for the various food categories consumed by omnivorous grizzly bears. So far, correction factors have not been derived for the kinds of fruits, ants and termites that constitute sloth bear diet. Developing such correction factors is necessary for correctly estimating the importance of various food items to sloth bear diet. I developed correction factors for various food items and converted the composition of scat residuals into composition in terms of ingested biomass. The methods I used for faecal analysis are described below.

Scat collection and randomisation

Sloth bear scats were collected fortnightly from about 100 km of trails and jungle roads that were uniformly spaced over the study area (Plate 10). Thus, the scat collection effort was kept uniform over space and time. Scats were also collected regularly from a few bear resting sites. Location of each scat was recorded and each scat was given a specific code for later reference and randomisation.

I estimated monthly diet composition as opposed to seasonal composition, so that it could be related to patterns of monthly space and habitat use of bears and food availability. For analyses, 30 scats from each month were randomly selected, out of the total collected for that month. Out these 30 scats, initially 10 scats were analysed. Then, sets of five scats were added incrementally until the diet composition reached an asymptote for a month (data from additional scats made trivial changes to the estimated composition). The number of scats required to reach an asymptote varied with diet – more in the months of varied diet and less during the months of homogenous diet. Ten to 25 scats were found to be sufficient to estimate the composition of diet per month.

Five to 10 additional randomly selected scats were analysed for months during the dry seasons of 1998 and 1999 and the cold season of 1998-99. Scat incidence rates were much higher during these periods (Table 7.1), presumably because the bears fed more during these seasons. American black and grizzly bears fed more during the seasons when they fed on fruits (Rogers 1987, Mattson *et al.* 1991, Welch *et al.* 1997, Rode and Robbins 2000). This phenomenon of increased feeding in the North American bears is thought to compensate for the high dietary fibre content of fruits and the consequent low digestibility and faster gut passage rate (Pritchard and Robbins 1990), or to meet the higher maintenance energy requirement that occurs during periods of fruit-only diet (Rode and Robbins 2000). It may also serve to accumulate fat tissues and gain body mass prior to winter hibernation (Welch *et al.* 1997).

The food habits in the months when bears fed more needed to be given a proportionate weight in the calculations of annual diet composition. Keeping the sample sizes of scats uniform for different seasons would underestimate (in annual diet) the importance of seasonal food items that were eaten more and vice versa. To correct for this bias, a fixed proportion of scats that were deposited by animals should be analysed for every season. Since my scat collection effort was uniform and scat incidence rates were monitored, I could correct for this bias. Twenty to 25% of the collected scats were analysed for each season, except for 1999 wet season, when, although the incidence rate was low, I analysed disproportionately more scats to maintain a minimum number of scats analysed for each season. Also, during the wet season, scats were washed away by rains or disintegrated before they could be collected. Hence, the incidence rates could have been underestimated. Altogether, about 60 to 80 scats were analysed for a season in a year, and 410 scats were analysed in total in two years (Table 7.1). Only two months each were included in the cold seasons of 1997-98 and 1999-2000, and hence it totalled to fewer scats collected and analysed.

Table 7.1. Number of sloth bear scats collected and randomly selected for analysis to estimate sloth bear diet during various seasons.

Year & Season	Scats collected	Scats analysed
1997-98 – Cold	107	25
1998 – Dry	379	76
1998 – Wet	288	64
1998-99 – Cold	648	73
1999 – Dry	324	82
1999 – Wet	113	56
1999-2000 – Cold	119	34
TOTAL	1978	410

Scat analysis

I followed a frequency sampling method to quantify composition of food remains in sloth bear scats. This point sampling procedure originally used in ungulate diet studies (Chamrad and Box 1964) was adapted and used for sloth bear scat analyses by Joshi *et al.* (1997). Using this method does not require separation of innumerable fragments of residuals. Also, the composition can be quantified to any taxonomic level (e.g., species level for ants) that is desired. With this method, the relative number of items and further, the relative consumption in terms of ingested biomass can be estimated. In earlier bear diet studies, faeces composition has been quantified by estimation of relative volume of various items either visually (Hellgren *et al.* 1989, Mattson *et al.* 1991, Noyce *et al.* 1997, Swenson *et al.* 1999a) or by displacement of water (Landers *et al.* 1979, Peyton 1980, Desai *et al.* 1997), or by estimating relative dry weights (Ohdachi and Aoi 1987, Baskaran 1990, Gokula *et al.* 1995, Baskaran *et al.*, 1997). There are two advantages in following the method of Joshi *et al.* (1997). First is to compare the results of this study with the only other intensive study that had been conducted on sloth bears and the second is to develop a standard scat analyses method. I assessed the biases in this method, improved on it and attempted to develop a standard method, which if followed in future studies would make the data comparable.

To assess the bias in this method, I counted all the fragments in 15 scats (5 from each season, so as to represent the various combinations of food items) and calculated relative composition. Relative composition of the same scats was then calculated with Joshi *et al.* (1997) method and compared with the results of the total count. Joshi *et al.* (1997) method was not biased with respect to the fragment size of the residues, but was biased with respect to the number of fragments a food item produces (or the relative area it covers). For example, a fruit that breaks into ten fragments had a higher probability of falling on a sampling point (on Petri-dish), than a termite that left only one residue fragment (a head). It grossly overestimated big fruits that broke into numerous fragments, such as *D. melanoxylon* and underestimated small items like termites. In the same way, many-seeded fruits were over estimated as compared to a similar sized one-seeded fruit.

To correct for this bias with regard to the number of fragments, I counted only the seeds for fruits and heads for insects, and disregarded other fragments (insect body, fruit shell, etc). This method was again calibrated with total counts. The results showed that the modified method only marginally overestimated big items such as *D. melanoxylon* and *Z. mauritiana* seeds (for the sampling grid size that I used), but correctly estimated small items. With the modified method, it was also possible to estimate relative abundance of whole units of food items (number of fruits/insects) consumed, rather than relative abundance of fragments of food items present in the scat. The relative abundance values could be used further to estimate diet composition in terms of relative consumed biomass or relative energy contributed by various food items. This modified method was used to analyse all scats in this study.

Scats were soaked in water, washed through 0.7 mm sieves and dried in the sun. A sample of dried material was sprinkled on a Petri-dish marked with nine sample points (grid intersections). All the seeds of fruits, heads of insects that fell on or closest to a sampling point were counted. A dissection microscope (20X to 60X) was used to identify the fragments. The items were identified to the species level where possible (for fruits and most ants) and to the genus or higher level otherwise. The counted sample was discarded and another pinch from the scat was taken out and nine more fragments were counted. This was continued until 100 fragments were counted. In case if the scat was entirely gone before counting 100 fragments, the number of fragments were standardised to 100. Each scat was considered as a sample unit for statistical analysis.

The relative composition values obtained as described above represent diet in terms of composition of residuals in the scat. This does not correctly represent the contribution of each food item to the diet, but rather represents which item was excreted more. The amount excreted for a unit amount consumed varies, depending on how much indigestible material is present in an item (e.g., shell, seed of fruits, exoskeleton of insect). In order to correct this error, the relative composition values need to be converted in terms of fleshy biomass ingested. I calculated ingested biomass using the following equation:

$b_a = c_a*(i_a/s_a)$

where;

b_a – ingested biomass (in g) of taxon 'a';
c_a – relative composition of item 'a' in a scat;
i_a – average ingestible biomass (in g) for each fruit/insect of taxon 'a';
s_a – average number of seeds each fruit of taxon 'a' contains (for insects, s_a=1).

The ingested biomass (in grams) was calculated for each taxon, values from all the taxa were summed for each scat, and "relative ingested biomass (%)" was calculated for each taxon for each scat. These values were then averaged (weighted average) for a month, season, year, etc. and were summed for each group of food (as fruits, ants, termites, etc). When bears fed on honey, only the wax from hives was excreted as a residual. Hence, for the scats that contained wax, relative volume was visually estimated and used in the place of relative composition, in ingested biomass calculation.

As a further extension in representing importance of a food item to the diet of sloth bears, the total energy (in calories) contributed by each food item (taxon/group) was estimated. The ingestible parts of each food item were analysed in a bomb calorimeter to estimate total energy content. The ingested biomass values were multiplied by the energy content (in Kcal) of each gram of a food item to get the energy contribution of each food item. Percent energy contributions of various food items to sloth bear diet were further calculated, as it was done for ingested biomass.

Energy content

Total caloric values have been used to estimate importance of food items to bear diet (Criaghead *et al.* 1995, Powell and Seaman 1990). Total energy content of various food items was estimated by using a ballistic bomb calorimeter (Prus 1975). Fresh ripe fruits were oven dried at 60^{o} C, the ingestible pulp from fruits was scrapped out, powdered and weighed for calorimetric analyses. Since ingestible material could not be separated in insects (ants and termites), whole insect adults and broods were collected from their nests, oven dried and powdered for analyses. Remains of each insect taxon were extracted from sloth bear scats and energy content measured. The caloric value of excreta remains was subtracted from the values of whole insects, and multiplied by the proportion of ingestible material in a taxon. This was assumed to give the energy content of the material ingested from insect food.

Samples of about 0.5 g each were fed into the calorimeter, ignited electrically and burned in excess of oxygen (20 to 25 atmospheric pressure) in the bomb and the heat produced was recorded. The maximum temperature rise of the bomb was measured with a thermocouple and galvanometer system (the peak galvanometer deflection 40 seconds after firing was recorded). By comparing this rise with that obtained from burning a sample of benzoic acid of known caloric value (6,318 kcal/g or 26,453 J/g), the caloric value of each sample material was determined. Three to ten replicate samples were analysed for each taxon.

Calorimetric analysis could not be done for a few food items like *Camponotus spp*. pupa and *Carabid* beetles. For these items, caloric values were taken from literature. For *Camponotus spp*. Pupa, 6 KCal/g was used (Noyce *et al.* 1997, Swenson *et al.* 1999a) and for a few other ant species 5 KCal/g was assumed. For *F. indica* fruits, 4 KCal/g; *Apis spp*. Bees, 6 KCal/g; honey, 4 KCal/g; *Carabid* beetles, 5 KCal/g; and *Varanus* lizard eggs 5 KCal/g was assumed, judged by whether the dominant constituent of these items was carbohydrate, protein or fat.

Selectivity and preference measures

I used ‘selection’ in the sense of a food item being used disproportionately more than its availability and ‘preference’ as the likelihood of an item being chosen if all food items were available in equal quantities (Johnson 1980, Garshelis 2000). Conversely, a food item that is being consumed less than its availability is termed ‘avoided’. Use that is proportional to availability indicates lack of selection (or random usage).

I used a linear index of food selection proposed by Strauss (1979), which was shown to be better than the commonly used Ivlev’s Electivity Index and Forage Ratio Index. This index is also perhaps better than the Manly-Chesson Index, which is an extension of the Forage Ratio Index (Manly *et al.* 1972, Chesson 1983).

Linear Selectivity Index, $L_i = C_i - P_i$
where;
C_i = relative consumption of a food item i by bears; and
P_i = relative productivity/biomass of a food item i in the habitat.

The index value ranges from –1 to +1, with positive values indicating selection and negative values indicating avoidance or inaccessibility. Values close to zero (within ±0.1) indicate random usage.

I ranked the relative (within food-group) biomass contribution of food species/taxa to sloth bear diet in a descending order and called it Importance Rank, and ranked the relative (within group) productivity of a food taxa in the study area and called it Productivity Rank. I then subtracted importance rank from productivity rank and ranked (within food-groups) the values in a descending order to get the order of preference. The order of preference ranks the food species/taxa from most to least preferred. This measure would not be influenced by inclusion or exclusion of any food item and the preference is explicitly stated as relative to other items, similar to the method suggested by Johnson (1980) for ranking habitats.

Frequency of occurrence of food items and heterogeneity of scat remains

Frequency of occurrence was calculated as the percentage of total number of scats a food item occurred. The gut retention times of grizzly and American black bears fed with different kinds of diet were from 6 to 16 hrs, and this is likely to be similar among the various species of bears (Pritchard and Robbins 1990). Sloth bears that feed on fruits (high dietary fibre) and insects (containing large amounts of indigestible exoskeleton and mud from dug-up insect nests) would have retention times close to the lower end of the range, probably less than 12 hours. Therefore, I assumed that any one scat would be composed of food that was eaten within one day of activity. Thus, heterogeneity of remains in a scat would indicate diversity of daily diet of bears. Heterogeneity of scat remains was assessed by calculating frequency distribution of number of food items or food-groups (fruit, ant, termite, etc.) the individual scats contained. This measure was used to make inferences on bear foraging behaviour.

Results from other studies

Joshi *et al.* (1997) converted the results of earlier studies on sloth bear diet (Schaller 1967, Laurie & Seidensticker 1977, Johnsingh 1981, Baskaran 1990, Gokula *et al.* 1995) in terms of relative composition of scat remains. I used their converted figures and added the results of other sloth bear diet studies (Baskaran *et al.* 1997, Desai *et al.* 1997, Joshi *et al.* 1997, Bargali *et al.* 2002) for comparison purposes. However, the comparison between populations/studies was hampered by the varied methods used. To make coarse comparisons possible, I converted the existing data from each population, to indicate which food-group (fruit vs. insect) contributed more or less to diet. For this, I used data (unpublished data) on bear-eaten fruit and insect weights and volumes and made some assumptions as described below. When the data on relative composition were converted to relative ingestible biomass, the relative value of fruits increased and that of insects decreased correspondingly. Similarly, when data on relative dry weight were converted, the relative value of fruits increased, because uningestible matter excreted per unit weight (wet) ingested was less heavy for fruits (assuming the bears fed on large, pulpy fruits in all populations) than insect adults. If consumption of large amounts of insect brood (which produced less heavy uningestible matter as compared to fruits) in all populations is assumed, then the data on relative dry weight was more or less similar to relative ingested biomass. Data on relative volume, when converted, greatly increased the relative value of fruits, because insects produced much more uningestible matter (in volume) than fruits per unit weight ingested.

Statistical tests

I used contingency table analysis for frequency data – Fisher's exact test for 2x2 tables with lower than permissible expected cell frequencies, and chi-square test of independence for others and for RxC tables (Siegel and Castellan 1988, Sokal and Rohlf 1995). If needed, classes of RxC tables were combined (where it is biologically appropriate) to form 2x2 tables, to comply with assumption requirements. I tested for associations using rank-order correlation and test for concordance (Siegel and Castellan 1988, Sokal and Rohlf 1995). An *a priori* type-I error rate of 5% was fixed for all statistical significance tests, unless indicated otherwise.

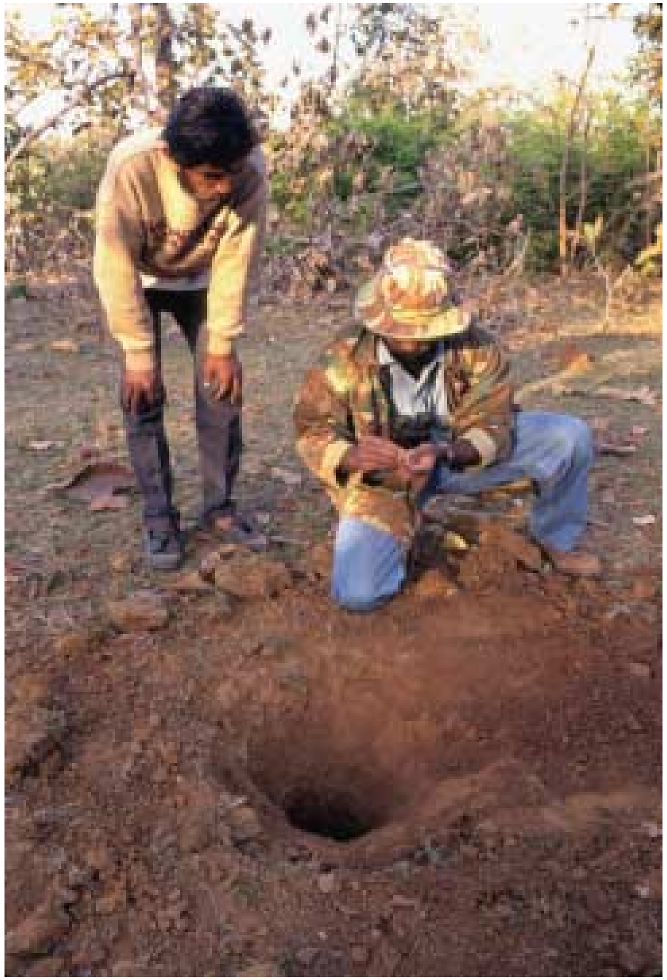


Plate 10. Bear food habits were studied by collecting bear scats, identifying the remains in them, and estimating their composition. Insect species were collected from holes dug out by sloth bears and were identified. Presence of fresh holes such as the one in the picture (right) were indicative of feeding by bears. Bears some times spent hours together for digging holes like this to access insect colonies. (Right Photo Courtesy: Gary Koehler).

7.3. RESULTS

Foraging observations

Bears were observed foraging primarily during crepuscular periods and at night. About 63% of observed feeding events were on fruits, 30% on ants and 6% on termites. The relative frequencies of these three main food groups, however, changed with seasons (chi-square = 61.3, *df*=4, *P*<0.001). During the dry season, most feeding was on fruits, and in the wet and cold seasons, it was about equally divided between fruits and ants. Observations of feeding on termites and other foods (i.e. not fruits, ants, or termites) were few in number generally (Table 7.2).

Table 7.2. Percent observations of radio-collared and other sloth bears feeding on various food resources, during different seasons and times of day (*N* = 254 feeding events).

Season	Time of day	*N*	Fruit %	Ant %	Termite %	Other %
Dry	Day	0	0.0	0.0	0.0	0.0
	Night	18	77.8	0.0	22.2	0.0
	Crepuscular	75	92.0	2.7	5.3	0.0
	Total	93	89.2	2.1	8.6	0.0
Wet	Day	7	71.4	28.6	0.0	0.0
	Night	47	29.8	63.8	2.1	4.3
	Crepuscular	12	50.0	33.3	8.3	8.3
	Total	66	37.9	54.5	3.0	4.5
Cold	Day	7	28.6	57.1	14.3	0.0
	Night	48	64.6	33.3	2.1	0.0
	Crepuscular	40	50.0	45.0	5.0	0.0
	Total	95	55.8	40.0	4.2	0.0
Annual	Day	14	50.0	42.9	7.1	0.0
	Night	113	52.2	40.7	5.3	1.8
	Crepuscular	127	74.8	18.9	5.5	0.8
	Total	254	63.4	29.9	5.5	1.2

During fruiting periods, when sloth bears fed mostly on fruits, they moved to food-plant patches soon after they started their daily activity. Once in a food-plant patch, they moved slowly feeding on fallen fruits under trees or browsing on fruits that were on shrubs. During the non-fruiting periods, they walked at moderate speeds, often stopping, scratching and sniffing the ground to locate insect nests. They searched for insect nests more intensively, following visual cues, in certain microhabitats such as mounds, in dead wood or under rocks where insect nests were likely to be found. They also foraged on large colonies as that of *D. labiatus* ants in some locations repeatedly, at periodic intervals. When insect nests were detected, they were dug out and fed when underground or sucked up when the nests were located under rocks or logs. The time spent at each food patch ranged from a few to several minutes. While feeding on large colonies like that of the *D. labiatus* ants, which involved extensive digging, up to a few hours were spent at a patch. The bears moved away from a food patch to another much before the resource was completely exhausted.

Bears foraged on fallen ripe fruits off the ground, but also fed on fruits of small tree or shrub species such as *Z. mauritiana* and *L. camara* directly from the plant, by browsing or sometimes after breaking off branches. They also occasionally climbed trees to feed on fruits. However, they climbed trees mostly to feed on honeybee (*A. dorsata*) hives. They fed on the hives while on trees or knocked down the hives and then fed on them on the ground. Most adult bees flew out of the hives, or swarmed around and stung the bears, while the bears fed on honey and larva that remained in the hives.

The bears fed frequently on ground nesting termite and ant colonies. On locating a ground nest probably by scent, they dug scoops of earth at several places, combined with sniffing, perhaps to determine where exactly to continue digging into the nest. They broke into termite mounds or into the ground with their front claws and moved the dirt away with their fore and hind legs. They frequently sucked the termites out from inside the nests, but mostly they located the chambers, which held the termite brood and concentrations of adults and fed on them. They often ate up the (fungus-growing) cartons along with termites or broke the cartons, sucked up the termites and blew away the debris. In the ant nests, adult ants, and pre-adult stages (pupa and larva), if present, were sucked up along with some debris. The bears also turned over rocks and logs to feed on ant and termite colonies that nested underneath (often during wet and cold seasons, Plate 11). They also scraped the shallow ground nests of small ants and when the ants emerged, they fed on them for a few seconds and moved away. They dug as deep as 1.5 m into ground to feed on large underground colonies of *D. labiatus* ants. The bears also sucked up foraging columns or groups of ants when encountered on ground surface. They also searched for and fed on termite reproductives when they emerged (during pre and post-wet seasons) from underground and became available on the surface.

The bears also fed on *Carabid* beetles that were found in groups sheltered under rocks, dug out *Scarabaeidae* (dung beetle) larva, and in the early wet period, dug up buried monitor lizard, *Varanus bengalensis* eggs. I did not observe them feeding on roots or tubers or grazing. Although small holes dug to feed on roots or tubers were found, mostly they were dug by wild pigs, *Sus scrofa,* or Indian porcupines, *Hystrix indica*, and sometimes the signs were indistinguishable. I also did not observe bears scavenging on meat nor found any evidence of this. However, six out of about 1800 scats collected contained unidentified hair, probably that of small mammals.

Food habits

Consumption periods of main food items

Fruits of *D. melanoxylon, Z. mauritiana, B. lanzan, C. fistula, A. marmelos, Z. oenoplia, G. latifolia, L. camara* and flowers of *M. longifolia* were eaten frequently by sloth bears in Panna (Plates 12, 13). Among insects, ant species such as *Camponotus compressus, C. irritans, D. labiatus, Leptogenys processionalis* and *Pheidole spp.*, termites (mostly *Odontotermes spp.*), honey bees (*A. dorsata* and *A. cerana*) and *Carabid* beetles were eaten frequently (Fig. 7.1). These foods were consumed during various periods of the year and for various lengths (as known from scat remains). Five species of fruits were consumed during the dry season, one species during dry and wet seasons, two species during cold season and one species during cold and wet seasons. *Camponotus spp.* ants and termites were consumed throughout the year, whereas other insects were seasonally consumed for varying lengths. Overall, fruit species were consumed seasonally and insects more or less throughout the year, except for the pre-adult stages, reproductives and *Carabid* beetles (Fig. 7.1). In addition, some ant species were not eaten during major part of the dry season and honey was not consumed during the cold season.

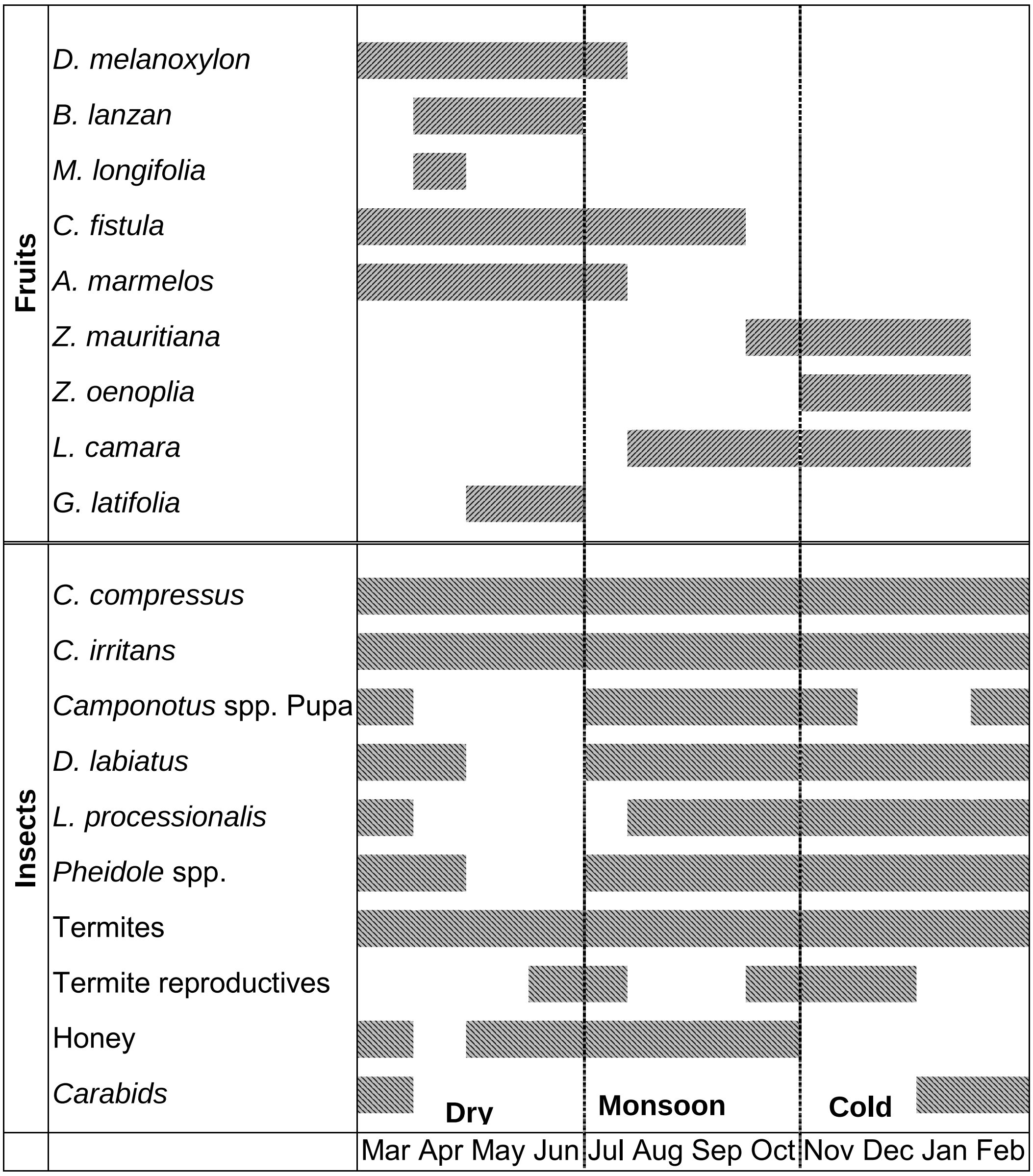


Fig. 7.1. Periods when main food plants and prey insects were consumed by sloth bears in Panna NP, as known from scat remains.

Heterogeneity of scat remains

Some scats were composed entirely of a single food-group (fruit, ant, termite, honey and other) while others were a mixture of more than one food-group.

About 44% of all scats contained only one food-group and another 37% were made up of two food-groups. About 35% of scats contained only fruits. Of the scats with two food-groups, about three-fourths were composed of ants and termites. The frequency distributions of number of food-groups in scats were related to season (chi-square =24.5, *df*=6, *P*<0.001; Table 7.3). About 59% of the scats from the dry season had only one group of food, of which 54% were of fruits. About 32% of the scats from the wet season were composed of one food-group, of which, about 17% were of fruits and 15% were of ants. During the cold season, about 38% of scats were of one food-group, 30% of which were composed of fruits and the rest made of ants. During both the wet and cold seasons, over 40% of the scats contained two food-groups, mostly a combination of ants and termites.

Table 7.3. Frequency distribution of number of food-groups (fruit, ant, termite, other) in scats (*N*=410).

Season (*N* of scats)	1				2	3	4
	Fruit%	Ant%	Termite%	Total%	%	%	%
Dry (158)	53.8	0.0	4.4	58.9	26.6	13.9	0.6
Wet (120)	16.7	15.0	0.0	31.7	44.2[a]	24.2	0.0
Cold (132)	29.5	8.3	0.0	37.9	43.9[a]	16.7	1.5
Year-round	35.1	7.1	1.7	44.2	37.3[a]	17.8	0.7

[a]– mostly composed of combinations of ants and termites

The frequency distributions of number of food-taxa (various fruit and insect species or taxon) in scats were also related to season (chi-square =42.95, *df*=12, *P*<0.001; Table 7.4). About 25% of year-round scats were composed wholly of one food-taxon, mostly of one of four species of fruits. Among the dry season scats, 30% scats were of one taxon, of which 23% is of *D. melanoxylon* fruits. Another 27% of dry season scats contained two food-taxa, most of which were combinations of fruit species. Among the wet season scats, only 14% of scats contained one food-taxon, with *C. fistula* or *L. camara* fruits composing most. Among the cold season scats, 27% contained one food-taxon, with either *Z. mauritiana* or *L. camara* fruits composing most of it. Only 9% of the scats had two food-taxa in the cold season. The scats that contained more than two food-taxa were mostly composed of fruits and termites in the dry season and of ants and termites in both wet and cold seasons.

Table 7.4. Frequency distribution of number of food-taxa (various fruit and insect species/taxon) items in scats (*N*=410).

Season (*N* of scats)	1 %	2 %	3 %	4 %	5 %	6 %	7 %	8 %
Dry (158)	30.4[a]	27.2[d]	14.6[e]	12.7	6.3	5.1	3.8	0.0
Wet (120)	14.2[b]	13.3	15.8[f]	20.8[g]	20.8[i]	10.8	4.2	0.0
Cold (132)	27.3[c]	9.1	12.9	18.2[h]	15.9[j]	9.1	6.1	1.5
Year-round	24.6	17.3	14.4	16.8	13.7	8.1	4.6	0.5

[a] –22.8% is *D. melanoxylon*; [b] – 7.5% is *C. fistula*, 5% is *L. camara*; [c] – 16.7% is *Z. mauritiana*, 9.9% *L. camara*; [d] – mostly fruit species combinations, a few fruit and termite combinations; [e] – mostly fruits and termites; [f, g, h, i, j] – mostly ants and termites

Diet composition

Overall, fruits contributed 56%, ants 29%, termites 10% and other food 4% to the annual diet (in terms of ingested biomass) of sloth bears. The relative contributions of the three major food groups to diet differed considerably among the seasons (Fig. 7.2). Fruits contributed about 75% of the diet during dry season, and ants and termites about 11% each. However, during the wet season, ants contributed 47% of the diet, fruits 37%, termites 7% and other food, mainly honey, about 9%. During the cold season, the diet was composed of 52% fruits, 35% ants and 11% termites.

Caloric values were between 3.8 KCal/g and 4.98 KCal/g for fruits, and between 5.12 and 7.32 KCal/g for insects (Table 7.5). Conversion of relative ingested biomass to relative energy contribution increased the importance of insects to sloth bear diet and decreased that of fruits only marginally (Fig. 7.3). Therefore, the relative contributions of the different food groups to annual or seasonal diet in terms of either measure were similar.

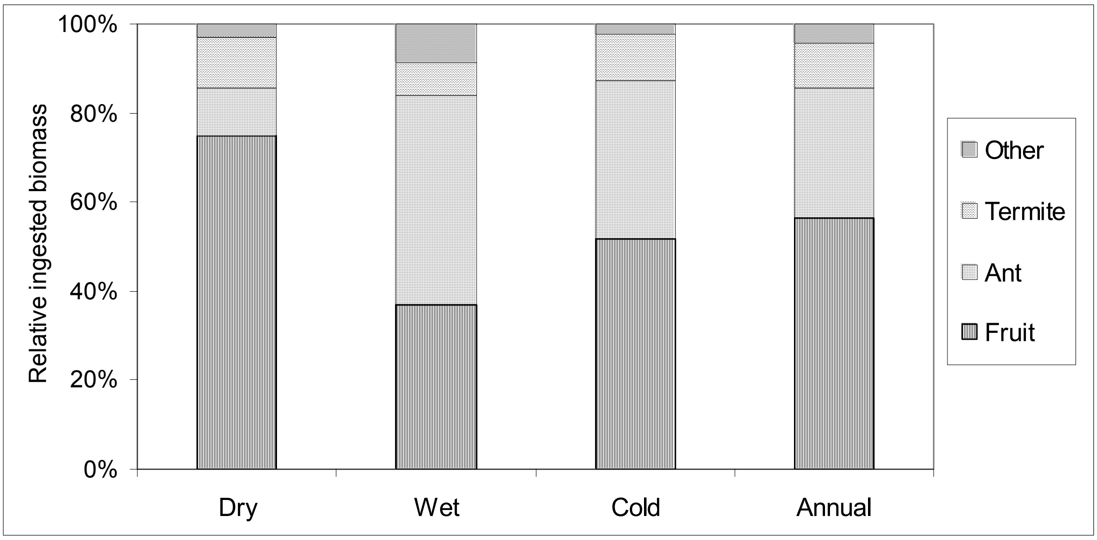


Fig. 7.2. Relative contribution (in terms of ingested biomass) of various food groups to sloth bear diet in different seasons and annually (*N* = 410).

Table 7.5. Caloric value (Mean ± 1 Standard Error of Mean) of common food items of sloth bear in Panna NP.

Food item	Form	Caloric value (KCal/g)
Diospyros melanoxylon	Ripe fruit	4.67 ± 0.06
Buchanania lanzan	Ripe fruit	4.44 ± 0.07
Cassia fistula	Ripe fruit	4.45 ± 0.08
Madhuca longifolia	Flower petals	4.20 ± 0.08
Aegle marmelos	Ripe fruit	4.53 ± 0.07
Zizyphus mauritiana	Ripe fruit	4.98 ± 0.04
Lantana camara	Ripe fruit	3.80 ± 0.01
Camponotus compressus	Adult ant (worker & soldier)	5.60 ± 0.06
Odontotermes spp.	Adult (worker & soldier)	5.37 ± 0.40
Termite	Reproductives	7.32 ± 0.13
Termite	Nymphs	5.12 ± 0.11

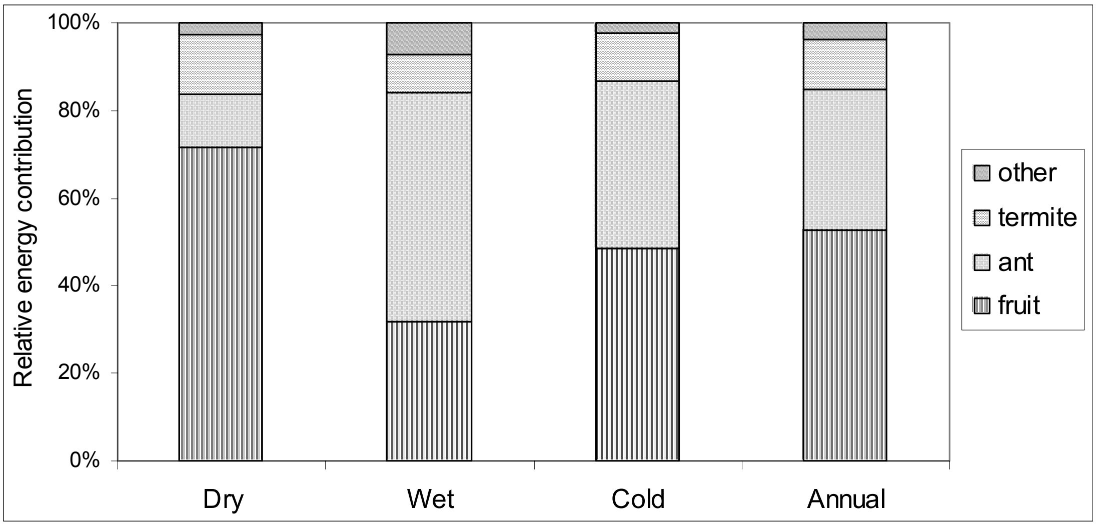


Fig. 7.3. Relative energy contribution (caloric values) of various food groups to sloth bear diet in different seasons and annually (*N* = 410).

Diet composition of sloth bears had considerable differences among months and seasons. The contribution of fruits, ants, termites and other food, in terms of relative ingested biomass, to the diet of sloth bears varied among months (Fig. 7.4). Fruits contributed to major part (70% to 80%) of the diet from April to July and in November and December. Ants formed a large portion of the diet from August to October (50% to 75%) and from January to March (35% to 70%). Termites contributed a small, but consistent portion (about 10% to 25%) to the diet from January to September and a minor portion during other months. Other food resources like honey and *Carabid* beetles contributed a small portion to the diet during the months of March, September and October (about 10% each). Fruits and ants complemented each other and together contributed from 70% to over 95% of the diet in all months (Fig. 7.4).

Among the fruits, *D. melanoxylon* was the highest contributor and it contributed from 45% to 80% of the diet from April to June (Fig. 7.5). *Z. mauritiana* comes next with a contribution of 40% and 65% during November and December. *C. fistula* fruits contributed 55% in July and about 10% to 20% in June and August. *L. camara* contributed 10% to 30% from October to January and about 15% in August. *A. marmelos* contributed from 10% to

20% in March, June and July. *M. longifolia* flowers contributed about 7% in April and other fruit species contributed less than 5% in any month.

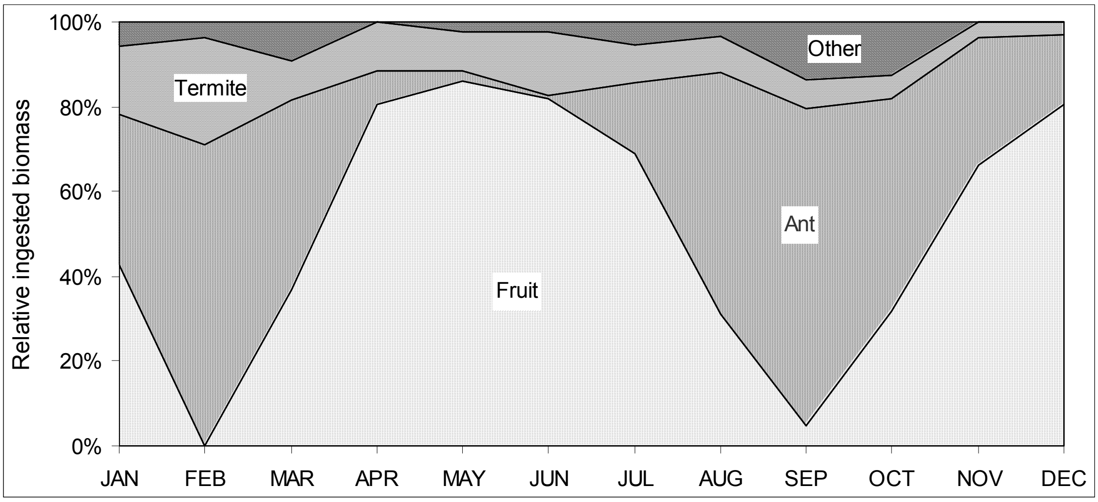


Fig. 7.4. Relative contribution (in terms of ingested biomass) of various food groups to sloth bear diet in different months.

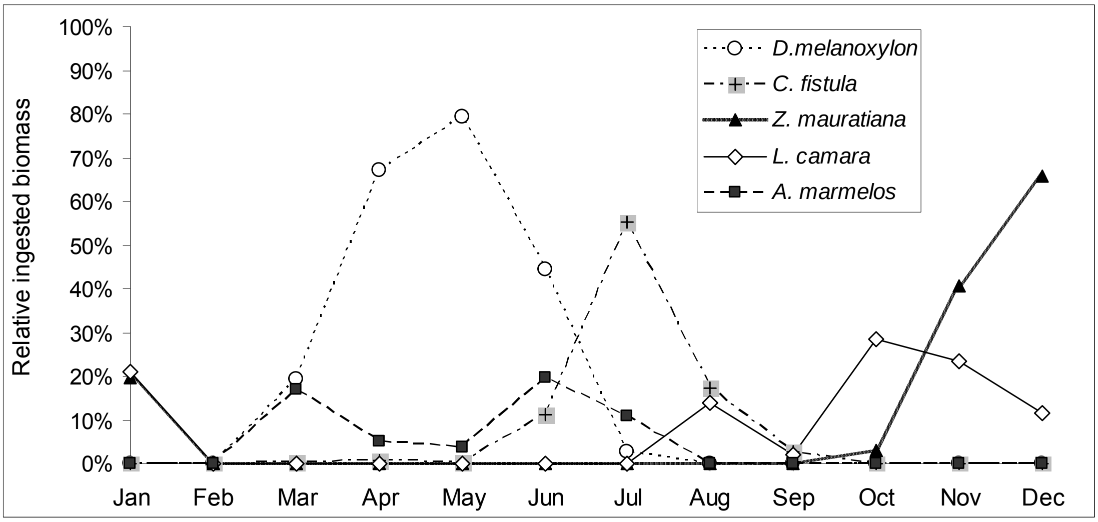


Fig. 7.5. Relative contribution (in terms of ingested biomass) of main fruit-yielding plant species to sloth bear diet in different months.

Of the insects, the ants *C. compressus* and *C. irritans* together made the greatest contribution to diet. From January to March and from July to November they made from 15% to 56% contribution to diet (Fig. 7.6). The pupal stage of *Camponotus spp.* ants were consumed at a considerable level from July to November, with its contribution ranging from 6% to 12% of the monthly diet. The consumption of *Camponotus* spp. pupa was positively correlated with consumption of *Camponotus* adults (Spearman's r_s =0.59, *P*=0.04). Another species of ant that contributed substantially, in terms of ingested biomass, is *D. labiatus*. This species of ant contributed from 5% to 20% of the diet during January, February and from August to November (Fig. 7.6). Consumption of *D. labiatus* was also correlated with consumption of *Camponotus spp.* (Spearman's r_s =0.82, *P*=0.001). However, consumption of termites was not significantly correlated with consumption of *Camponotus spp.,* or ants in general (Spearman's r_s = -0.13, *P*=0.70; for both).

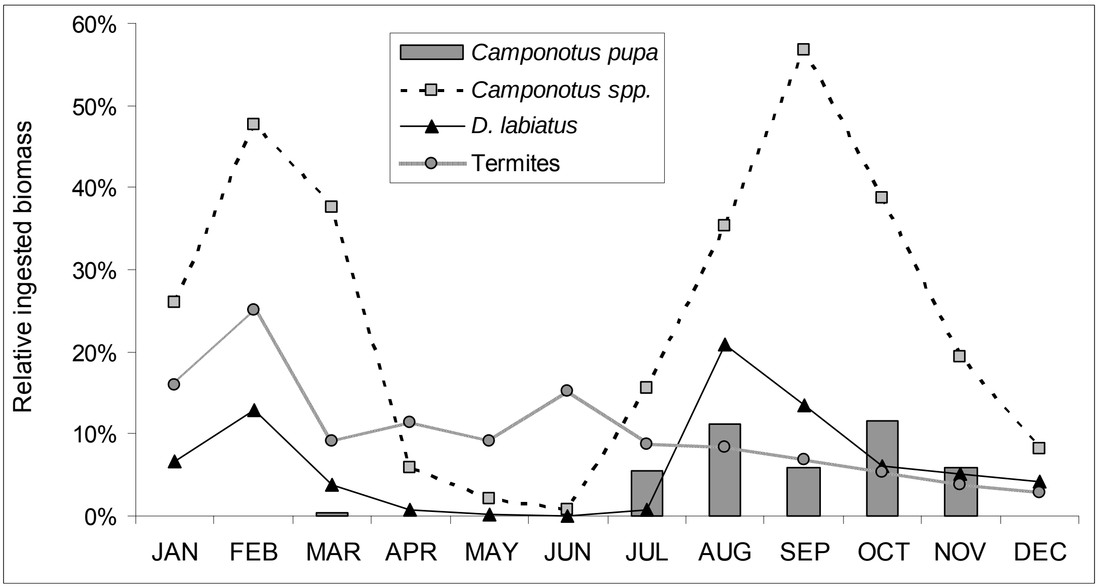


Fig. 7.6. Relative contribution (in terms of ingested biomass) of main insect taxa to sloth bear diet in different months.

Relationship of food consumption with phenology and productivity of food resources

Fruits

Relative consumption (ingested biomass; with respect to fruits consumed) of main fruit species was significantly and positively correlated to fruiting phenology (ripe fruits; proportion of sampled individuals fruiting) among months, except for *C. fistula* (Table 7.6). Relative consumption of *C. fistula* peaked after a lag of three months after the fruiting peak. Relative consumption of *A. marmelos* was low in April and May although the plants were fruiting. For the rest of the species there was a close relationship between relative consumption and fruiting phenology among months (Fig. 7.7). Relative consumption of main fruit species was also related to monthly relative biomass productivity (relative to biomass productivity of other species in a month; Table 7.6), except for *C. fistula*. The relative productivity of *C. fistula* (relative to other species) peaked twice, once in March and again in July, but the consumption was correlated only with the peak in July. Although *L. camara* was almost the only fruit produced (relative productivity reaching 100%) and was produced in abundance in August and September (20 kg/ha and 16 kg/ha respectively), the relative consumption was proportionately low. For the rest of the species, the relationship was similar to that of fruiting phenology (Fig. 7.7). A relationship between monthly relative consumption of all fruits together and relative productivity (out of annual) of all fruits could not be seen with the evidence I had (Spearman's r_s =0.4, P=0.1, N=12).

The relative consumption of various fruit species was not in concordance with relative productivity, for all months and year-round (Kendall's *tau-b*, null hypothesis of no relation could not be rejected at α=0.05). Some fruit species were consumed disproportionate to their productivity (Fig. 7.8). For example, in November, December and January, *Z. mauritiana* fruit was consumed at a higher proportion than its productivity and *Z. oenoplia* fruit was consumed disproportionately lower. Similarly, in April, May and June, *D. melanoxylon* fruit was consumed at a higher proportion than its productivity and *A. marmelos* fruit was consumed disproportionately lower than its productivity. In February, although fruits such as *L. camara* were produced, none was consumed. In contrast, *C. fistula* fruits were consumed in September even when they were not produced (but fallen fruits were available in the habitat).

Fruits of *D. melanoxylon* contributed about 22% of ingested biomass to the annual diet of sloth bears, although it accounted for only about 10% of annual relative productivity in the area (Table 7.7). Similarly, fruits of *Z. mauritiana* contributed about 11% to the diet despite it having formed only 2% of the food produced. In contrast, fleshy flowers of *M. longifolia* contributed less than 1% to the annual diet, while it constituted 44% of the food resource produced in a year. Overall, relationship between annual relative biomass contribution of various fruit species and their relative productivity was not significant (Kendall's *tau-b* = -0.21, *P*=0.23, *N*=8). *D. melanoxylon*, *Z. mauritiana* and *C. fistula*, were consumed in a higher proportion than their productivity and the rest in a lower proportion (Fig. 7.9).

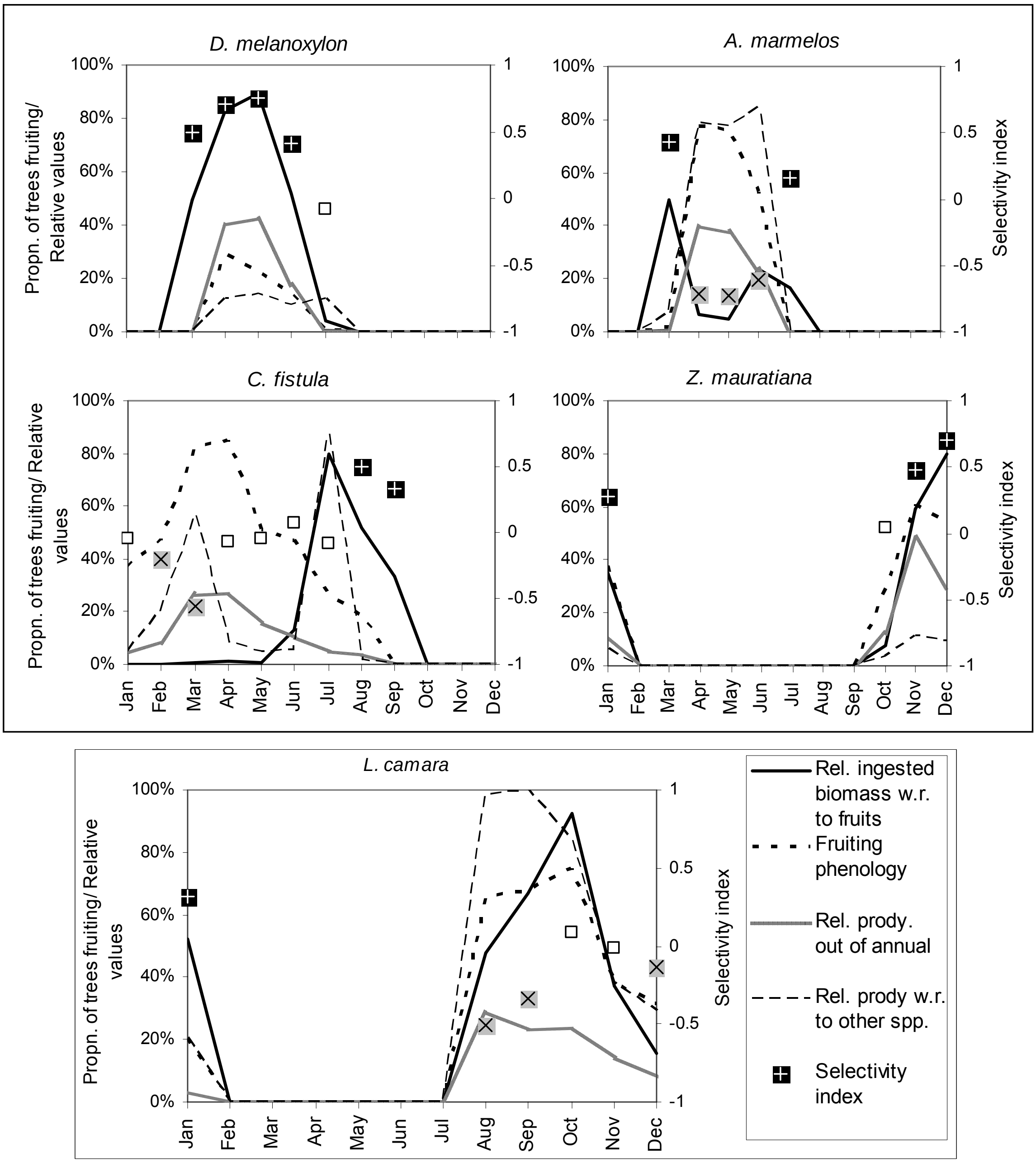


Fig. 7.7. Relationship between relative fruit consumption, fruiting phenology (ripe fruits) and relative fruit productivity of major food plants. Linear Selectivity Index value ranges from –1 to +1, indicating 'avoidance' (gray X) to 'selection' (black +). Values close to zero (within ±0.1) indicate random usage (blank square).

Table 7.6. Relationship between monthly relative consumption by sloth bears, fruiting phenology and monthly relative productivity of major fruit bearing species in Panna NP.

Species	Relative ingested biomass Vs. Proportion of population fruiting		Relative ingested biomass Vs. Relative productivity	
	Kendall's *tau-b*	*P*	Kendall's *tau-b*	*P*
D. melanoxylon	0.82	0.001	0.82	0.001
A. marmelos	0.58	0.01	0.68	0.005
C. fistula	0.17	0.23	0.29	0.11
Z. mauritiana	0.95	< 0.001	0.95	<0.001
L. camara	0.88	< 0.001	0.80	0.001

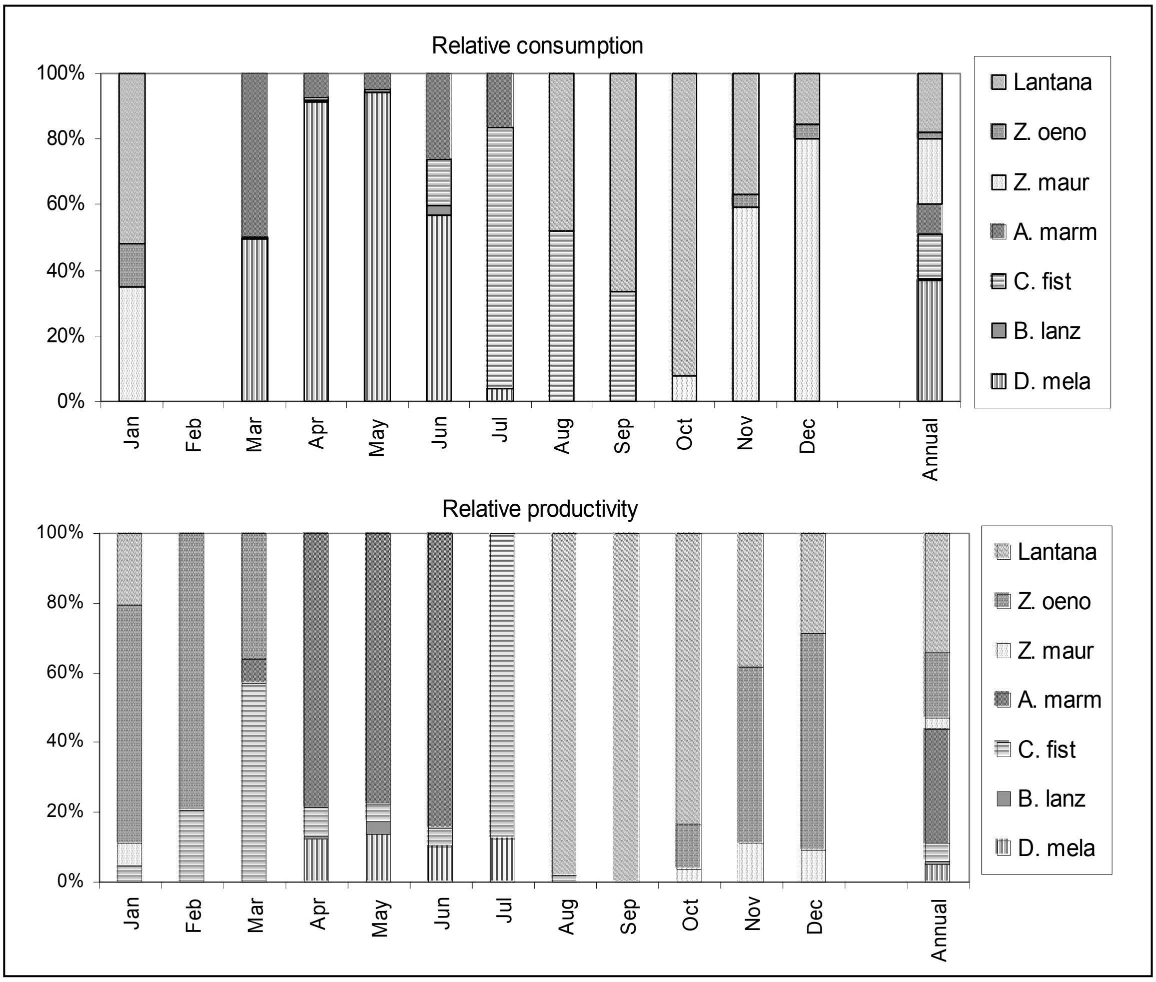


Fig. 7.8. Relative contribution of various fruit species and their relative productivity in Panna NP, in different months and annually.

Table 7.7. Relative ingested biomass contribution of common food items to annual sloth bear diet, and their relative productivity in the study area in Panna NP. Linear selection index values are calculated for within food groups (WG) and among all (AA) food items. The order of preferences of species was based on importance (within group) and productivity ranks. A '0' order of preference means no preference for an item among the group compared.

Species/taxa	Rel. biomass contribution % [a]	Relative productivity % [b]	Selection Index [c]		Importance rank [d]	Productivity rank [d]	Order of preference [e]
			WG	AA			
FRUIT							
D. melanoxylon	21.7 (38.6)	9.85 (9.93)	0.29	0.12	1	5	2
Z. mauritiana	11.4 (20.3)	1.72 (1.73)	0.19	0.1	2	7	1
C. fistula	7.4 (13.2)	1.09 (1.1)	0.12	0.06	4	8	3
L. camara	8.2 (14.6)	14.4 (14.6)	0	-0.06	3	3	4
A. marmelos	5.1 (9.1)	10.0 (10.1)	-0.01	-0.05	5	4	5
Z. oenoplia	0.63 (1.1)	15.7 (15.8)	-0.15	-0.15	8 (7) [f]	2	8
G. latifolia	0.76 (1.4)	*	--	--	6	*	--
M. longifolia	0.73 (1.3)	44.2 (44.6)	-0.43	-0.44	7 (6) [f]	1	7
B. lanzan	0.34 (0.6)	2.1 (2.15)	-0.02	-0.02	9 (8) [f]	6	6
INSECT							
C. compressus	12.9 (29.6)	0.4 (50.5)	-0.21	0.13	1	1	0
C. irritans	8.3 (19.0)	0.12 (14.9)	0.04	0.08	3	3	0
D. labiatus	5.3 (12.2)	*	--	--	4	*	--
L. processionalis	0.7 (1.6)	0.02 (2.3)	-0.01	0.01	8 (5) [g]	5	0
Pheidole spp.	1.6 (3.7)	0.03 (4.4)	-0.01	0.02	6 (4) [g]	4	0
Termites (mainly *Odontotermes spp.*)	10.0 (22.9)	0.22 (28.0)	-0.05	0.1	2	2	0
Honey & bees	3.3 (7.6)	*	--	--	5	*	--
Carabids	0.88 (2.0)	*	--	--	7	*	--
All fruits	56.2	99.2	--	-0.43	1	1	0
All ants	29.4	0.6	--	0.29	2	2	0
All termites	10.0	0.2	--	0.1	3	3	0

* – Productivity not measured

[a] – Relative biomass values are relative to all food items; values in parenthesis are relative to total for each food group (56.2 for all fruits and 43.6 for all insects)

[b] – Relative productivity values are relative to all food items; values in parenthesis are relative to total for each food group (99.2 for fruits and 0.8 for insects)

[c] – Index value ranges from –1 to +1, negative values indicate 'avoidance' and positive values 'selection'; values close to zero (within ±0.1) indicate random usage

[d] – Importance and productivity were ranked in descending order of relative contribution to diet (within food group) and relative productivity, respectively

[e] – Order of preference is the rank of differences between productivity and important ranks (tied values were ordered based on importance ranking); values in ascending order denote from most to least preferred

[f] – rank in parenthesis calculated after excluding *G. latifolia*

[g] – rank in parenthesis calculated after excluding *D. labiatus*, Honey bees and *Carabids*

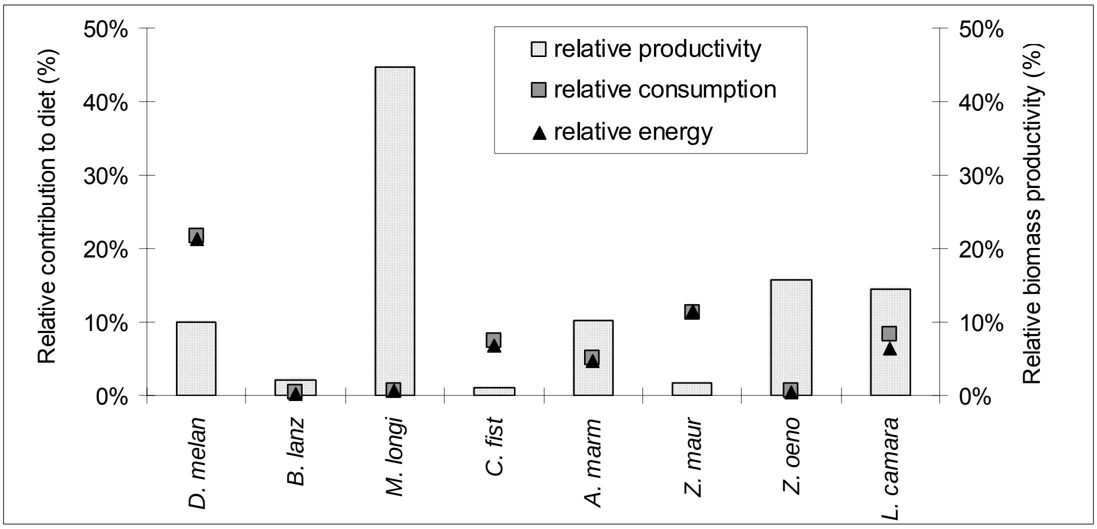


Fig. 7.9. The relationship between relative fruit biomass productivity, relative ingested biomass and relative energy contribution to annual sloth bear diet by various food plants.

Insects

Among the insects, *C. compressus* ant contributed about 13% of ingested biomass to annual sloth bear diet. *C. compressus* formed about 50% of the prey-insect biomass productivity, but only 0.4% of the total food (fruits and insects) biomass productivity (Table 7.7). Termites (mainly *Odontotermes spp.*) contributed about 10% ingested biomass to the annual diet and they formed about 28% of the prey-insect biomass productivity (0.22% of total food biomass). Another Formicine ant species, *C. irritans,* contributed about 8% biomass to the diet while it formed about 15% of the prey insect biomass productivity. Although the relative contribution of insects to annual diet is higher in proportion as compared to their relative biomass productivity (out of all food), among the insect species/taxa, the relative contribution to diet was very closely correlated with relative biomass productivity (out of prey-insects) (Kendall's *tau-b* =1, $P<0.001$, $N=5$). All the five main species/taxa of insects, for which productivity was measured, were consumed in the order of their relative productivity (Fig. 7.10).

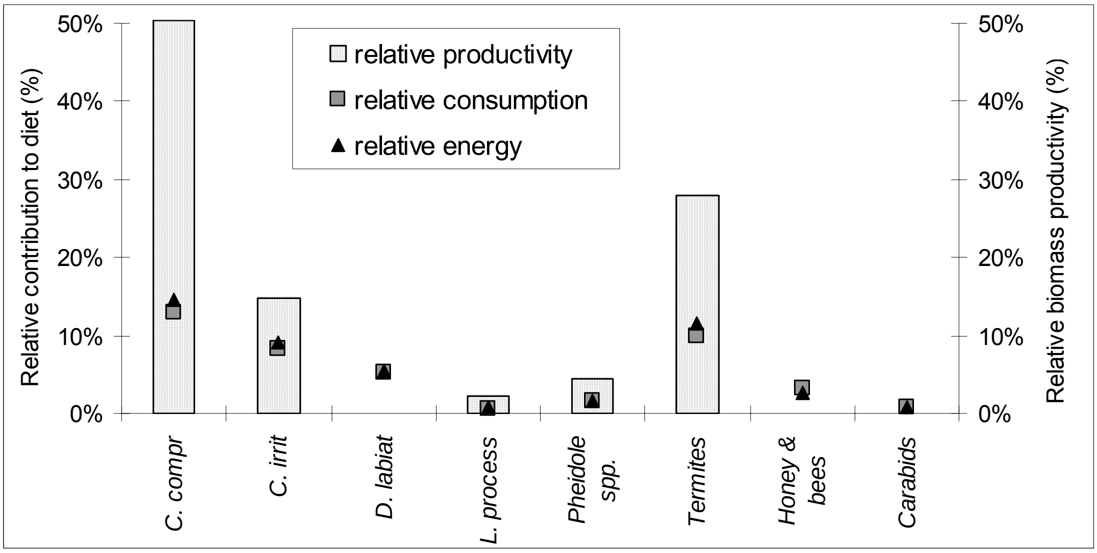


Fig. 7.10. The relationship between insect relative biomass productivity, relative ingested biomass and relative energy contribution to annual sloth bear diet by prey insect species. Biomass productivity was not measured for *D. labiatus*, Honey bees, and *Carabid* beetles.

Productivity could not be measured for an ant species *D. labiatus* and two other insect groups, honey bees and *Carabid* beetles. Further, monthly productivity of insects was not measured and so could not be compared with monthly relative consumption of insects. However, monthly relative consumption of all insects, or ants and termites together seemed to be inversely related to monthly relative productivity (out of annual) of fruits (Fig. 7.11), although a statistically significant relationship could not be observed with the small sample I had (for both, Spearman's r_S =-0.4, P=0.1, N=12). However, monthly relative consumption of termites alone did not seem to be related to monthly relative productivity of fruits (Fig. 7.11; Spearman's r_S = -0.28, P=0.2, N=12). The relative productivity of fruits peaked from April to June and again from August to December and dipped from January to March and in July.

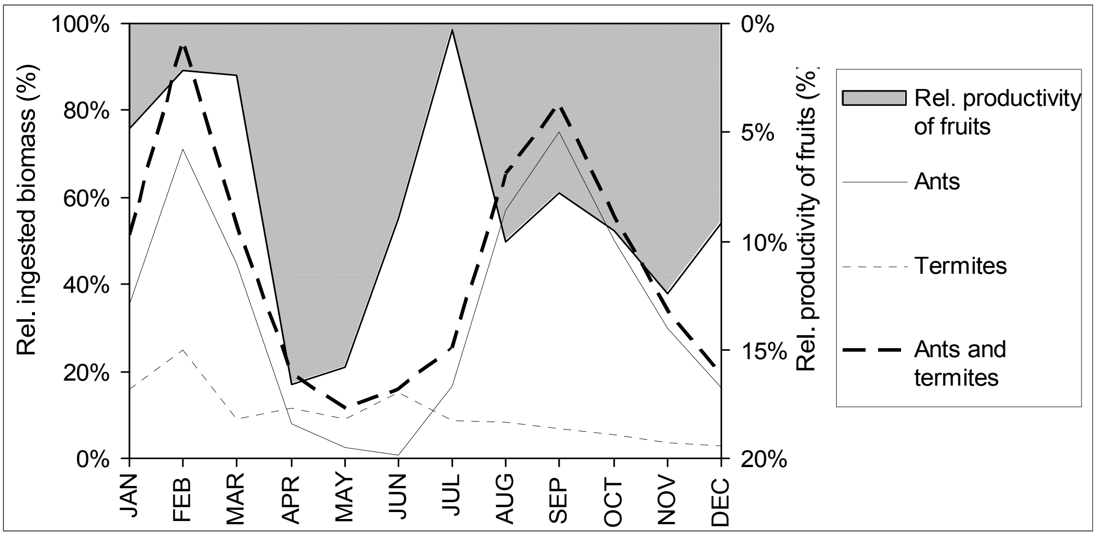


Fig. 7.11. Relationship between relative consumption of insects and relative productivity (out of annual) of fruits (2nd y-axis; values in reverse order) over the year.

Selection for food taxa and traits in plants and insects

Selection for Species/taxa

Within the fruit-group and among all food items, *D. melanoxylon*, *Z. mauritiana* and *C. fistula* were selected, as they were consumed in a higher proportion to their productivity, at the annual level. *A. marmelos, B. lanzan,* and *L. camara* were consumed in accordance with productivity (random usage). *Z. oenoplia* and *M. longifolia* were not selected (Table 7.7). However, the selection for a fruit species varied over months. For example, *A. marmelos* was selected in the months of March and July, but not selected from April to June. *C. fistula* was selected only in August and September, not selected in February and March, and was consumed in correspondence with productivity from April to July (Fig. 7.7).

Within the insect-group, *C. compressus* was consumed in lower proportion to its relative productivity (not selected), and other insects were consumed in correspondence with their productivity. However, when considered among all food items, *C. compressus* and termites were selected and other insects were subjected to random consumption. Among the three major food-groups, ants and termites were selected and fruits were consumed in lower proportion to their productivity (Table 7.7).

Preference for Species/taxa

Order of preference (within food groups) based on differences between productivity and importance ranks of each species/taxon placed *Z. mauritiana* as the most preferred species, for it has a higher importance as a diet component despite having a lower productivity, followed by *D. melanoxylon*, and *C. fistula*. *Z. oenoplia* was ranked as the least preferred fruit species, because of its much lower importance to diet and much higher productivity in the habitat (Table 7.7). Among the insects, all species/taxa had importance ranks the same as productivity ranks and consequently no species/taxa was shown to be preferred over the other. Among the three food groups, fruits, ants and termites, none was preferred over the other (Table 7.7).

Selection for plant and fruit traits

Among the fruit-bearing plant species that were consumed by sloth bears in Panna NP, characteristics such as plant form, dispersion pattern, phenology, and fruit traits varied (Table 7.8). The bears fed on fruits of sizes ranging from about 0.07 g to 120 g, of varying colours, from both trees and shrubs. The characteristics of some common plants or potential food plants in Panna that were not consumed by bears also varied among species (Table 7.9).

Plant abundance, dispersion, fruit bite-size, fruit presentation and ripe fruit taste are the characteristics that were notably different between food and non-food plant species (Table 7.10). Most food plant species were common and were patchily distributed. Bears selected large fruits or clustered fruits that offered large bite-sizes (Plate 13). They also selected for sweet taste in fruits. Other traits such as plant form, fruiting season, fruit type and colour were independent of being consumed by bears. I did not have data on fruit crop-size of non-food plants, but the crop-size distribution of food plants was different from a uniform distribution (chi-square =16.94, $P<0.001$), which suggested that the bears often selected for larger crop-sizes. Based on the traits that were selected, the probable factors that influenced sloth bears not to consume some common plant species or potential food species found in the study area were identified (Table 7.9). The relative biomass contribution of different species of fruits to the bear diet was significantly positively correlated to plant density, fruiting length and fruit bite-size (Table 7.11).

Table 7.8. Various plant and fruit characteristics of species whose fruits or flowers were eaten by sloth bears in Panna NP.

Species	Plant form	Parts eaten	Abundance & Dispersion	Fruiting period	Fruiting length	Fruit type	Fruit crop size (range)	Fruit size (mean)	No. of seeds (mean)	Pulp : fruit wt. ratio	Fruit presentation	Fruit bite-size [a]	Ripe Fruit colour	Fruit Taste
Diospyros melanoxylon	Medium tree	Ripe fruit	Abundant/ Moderately patchy	April – June	3-6 fortnight	Pulpy Berry	100 – 3,000	2.5 to 3.5 cm dia; 15 g	3	0.75	Drooping bunches at branch ends	Large	Orange /Yellow	Sweet
Zizyphus mauritiana	Shrub/ Small tree	Ripe fruit	Frequent/ Highly Patchy	Nov – Jan	4-6 fortnight	Pulpy Drupe	300 - 6,000	1.5- 2.5 cm dia; 2.4 g	1	0.83	On canopy surface; loose clusters	Large	Reddish orange	Sweet
Cassia fistula	Small tree	Ripe fruit	Frequent/ Non-patchy	Mar – Jun	8-10 fortnight	Indehiscent Pod	30-300	30-60 cm long; 2-3 cm dia; 85g	70	0.25	Hanging down in clusters	Large	Dark brown	Pulp sweet
Lantana camara	Shrub	Ripe fruit	Abundant/ Highly patchy	Aug – Dec	9-11 fortnight	Fleshy Drupe	2,000 – 10,000	0.5 cm dia; 0.07g	1	0.71	Clusters on the canopy surface	Large	Black	Sweet
Aegle marmelos	Medium tree	Ripe fruit	Frequent/ Patchy	Apr – Jun	6-7 fortnight	Hard-shell berry	50-200	10-15 cm dia; 120g	80	0.7	Hanging from branch ends	Large	Yellow	Sweet
Madhuca longifolia	Large tree	Flower petals	Frequent/ Non-patchy	Mar – Apr	2-3 fortnight	Fleshy petals	50,000-250,000	1.5-2cm long; 2.2g	--	0.99	Clustered at branch ends	Large	Cream/ Yellow	Sweet
Gardinia latifolia	Small tree	Ripe fruit	Frequent/ Patchy	Apr – Jun	4 fortnight	Leathery shell berry	30-300	5-8 cm long; 12g	600	0.52	At the ends of branches	Large	Grey	Sweet & sour
Z. oenoplia	Shrubby climber	Ripe fruit	Abundant/ Patchy	Oct – Jan	6-7 fortnight	Drupe (scanty pulp)	2,000-30,000	0.6 cm dia; 0.16g	1	0.5	uniformly spread on the surface	Small	Black	Sweet & sour

Species	Plant form	Parts eaten	Abundance & Dispersion	Fruiting period	Fruiting length	Fruit type	Fruit crop size (range)	Fruit size (mean)	No. of seeds (mean)	Pulp : fruit wt. ratio	Fruit presentation	Fruit bite-size [a]	Ripe Fruit colour	Fruit Taste
Buchanania lanzan	Medium tree	Ripe fruit	Frequent/ Non-patchy	Apr – May	2 fortnight	Pulpy Drupe	2,000-23,000	1-1.5cm long; 0.91 g	1	0.71	Clustered at ends of branches	Small	Black	Sweet
Flacourtia indica	Small tree	Ripe fruit	Frequent/ Patchy	Apr – May	2 fortnight	Berry	Unknown	1 cm dia	8	Unknown	not clustered	Small	Dark brown	Sweet

[a] – Bite size available to bears; clustered fruits on bushes allow large bite sizes, even though individual fruits are small

Table 7.9. Characteristics of some common plants or potential food plants that occur in Panna NP, but not eaten by sloth bears. Based on selected traits, the probable factors that influenced bears not to consume these fruits were identified.

Species	Plant form	Abundance & Dispersion	Fruiting period	Fruit type	Fruit size	No. of seeds	Fruit presentation	Fruit bite-size	Fruit colour	Taste	Probable factors for not being consumed
Phyllanthus emblica	Small tree	Frequent/ Non-patchy	Oct – Feb	Fleshy capsule	1.5-3 cm dia	1	Hanging down in clusters	Large	Pale yellow	Acidic	Acidic taste
Zizyphus xylopyra	Small tree	Abundant/ Non-patchy	Oct – Feb	Dry drupe	2.5 cm dia	1	On the surface; not clustered	Large	Green	Bitter/ acrid	No sugary pulp
Lannea coromandelica	Medium tree	Abundant/ Non-patchy	May-June	Thinly fleshy Drupe	1 cm dia	1	Clustered at the ends of leafless branches	Small	Red	Sour	Not sweet; thin pulp; fruits do not fall after ripening
Tectona grandis	Large tree	Abundant/ Non-patchy	Oct - Feb	Dry drupe	1.5 cm dia	1-4	Terminal racemes facing upwards	Small	Brown	Bitter/ acrid	No sweet pulp
Carissa opaca	Shrub	Occasional/ Patchy	Nov-Feb	Juicy berry	0.5 -1 cm long	2	On the surface; on the spines; not clustered	Small	Dark purple	Sweet	Plant not abundant; fruit presentation not favourable to forage

Species	Plant form	Abundance & Dispersion	Fruiting period	Fruit type	Fruit size	No. of seeds	Fruit presentation	Fruit bite-size	Fruit colour	Taste	Probable factors for not being consumed
Ficus spp. *(F.glomerata* etc.)	Medium to large tree	Occasional/ Non-patchy	Apr-June	Fleshy receptacle	1-3 cm dia	Numerous	Clustered on trunks and branches/ ends of branches	Large	Orange/ Red	Sweet	Plant not abundant; In some species fruits do not fall
Phoenix acaulis	Shrub	Occasional/ Patchy	Apr-June	Drupe	1-1.5 cm long	1	Clusters on spadix; hidden by leaves	Large	Black	Sweet	Plant not abundant; over grazed by cattle
Grewia hirsuta	Herb	Occasional/ Non-patchy	Nov-Feb	Fleshy drupe	1cm dia	4	On the branch surface; not clustered	Small	Brown/ whitish brown	Slightly sweet	Plant infrequent; over grazed; crop size small; presentation not favourable
Limonia acidissima	Small tree	Occasional/ Non-patchy	Nov-Jan	Fleshy berry	1 cm dia	1-4	Clusters on branches	Large	Black/ Purple	Bitter	Bitter taste
Manilkara hexandra	Medium tree	Frequent/ Patchy	Mar – May	Berry	1 cm long	1-2	On the canopy surface; not in clusters	Small	Reddish yellow	Sweet	Ripe fruits do not fall; Fruit presentation not favourable to forage
Syzigium cumini	Medium tree	Occasional/ Patchy	Aug-Sep	Pulpy drupe	<1 cm dia	1	Clusters under the leaves, end of branches	Small	Black/ Purple	Sweet	Plant not abundant
Bridelia retusa	Small tree	Occasional/ Non-patchy	Nov - Jan	Fleshy drupe	0.6 cm dia	1	Clusters in spikes	Small	Black	Sweet	Plant not abundant; ripe fruits do not fall
*Madhuca longifolia**	Large tree	Frequent/ Non-patchy	June-July	Fleshy berry	2 – 5 cm long	1-3	Clusters at ends of branches among leaves	Large	Red / orange	Sweet	Small crop size; fruits collected by people

* - *M. longifolia* flowers were eaten but not fruits.

Table 7.10. Selection of plant and fruit traits by sloth bears in Panna NP. Characteristics of 10 food plant, and 13 common plants or potential food plant species that occur in Panna but not eaten by bears, were compared. Chi-square tests were used where the expected frequencies were above permissible levels, or else Fisher's exact (FE) tests (for 2 x 2 tables) were used. For "2 x 3" tables, classes were combined (where it is biologically appropriate) to form 2 x 2 tables, if needed. For all tests, α was set at 0.1, to increase statistical power.

Variable	Plant group	Relative frequency (%)			Test & *P*
Plant form		Tree		Shrub	FE test, *P*>0.1
		Large	Small		
	Food	40.0	30.0	30.0	
	Non-food	46.1	30.8	23.1	
Plant abundance		Common		Occasional	χ^2 = 7.74, *P*=0.005; FE test, *P*<0.01
		Abundant	Frequent		
	Food	30.0	70.0	0.0	
	Non-food	23.1	23.1	53.8	
Dispersion		Patchy		Non-patchy	χ^2 = 3.49, *P*=0.06; FE test, *P*=0.07
		High	Moderate		
	Food	30.0	40.0	30.0	
	Non-food	0.0	30.8	69.2	
Fruiting period		Dry	Wet	Cold	χ^2 = 2.77, *P*>0.1
	Food	70.0	10.0	20.0	
	Non-food	38.5	7.7	53.8	
Fruiting length		Short (2-3 fortnight)	Medium (4-8 fortnight)	Long (8-12 fortnight)	χ^2 = 0.37, *P*>0.1
	Food	30.0	50.0	20.0	
	Non-food	23.1	46.1	30.8	
Fruit type		Drupe	Berry	Other	χ^2 = 0.44, *P*>0.1
	[a] Food	44.4	44.4	11.1	
	Non-food	53.8	30.8	15.4	
Pulp content (pulp proportion in fruit)		High (0.75-0.99)	Medium (0.5-0.75)	Low (<0.5)	χ^2 = 1.04, *P*>0.1
	[a] Food	33.3	44.4	22.2	
	Non-food	15.4	61.5	23.1	
Fruit size		Small (< 2 cm dia)	Large (> 2 cm dia)		FE test, *P*>0.1
	Food	40.0	60.0		
	Non-food	69.2	30.8		

Variable	Plant group	Relative frequency (%)			Test & P
Fruit bite-size		Small	Large		FE test, $P=0.1$
	Food	30.0	70.0		
	Non-food	61.5	38.5		
No. of seeds		1-2	3-10	>10	$\chi^2 = 2.35$, $P>0.1$
	[a] Food	44.4	22.2	33.3	
	Non-food	61.5	30.8	7.7	
Fruit crop size [b]		Small (100-500)	Medium (500-3000)	Large (> 3000)	--
	[a] Food	33.3	11.1	55.5	
	Non-food	--	--	--	
Fruit presentation		Clusters		Non-clusters	$\chi^2 = 3.49$, $P=0.06$; FE test, $P=0.08$
		Exposed	Hidden		
	Food	80.0	10.0	10.0	
	Non-food	30.8	23.1	46.1	
Ripe fruit colour		Red/Yellow	Black/Purple	Other	$\chi^2 = 0.22$, $P>0.1$
	Food	40.0	30.0	30.0	
	Non-food	38.5	38.5	23.1	
Ripe fruit taste		Sweet	Non-sweet		$\chi^2 = 4.91$, $P=0.03$; FE test, $P=0.04$
			Sour/acidic	Bitter/acrid	
	Food	100.0	0.0	0.0	
	Non-food	61.5	23.1	15.4	

[a] - only 9 food species were included

[b] - data was not available for non-food species

Table 7.11. Relationship between relative consumption (in terms of ingested biomass) and various characteristics of important food species/taxa. For all tests, α=0.1 was set to increase statistical power of detecting correlations.

	Characteristic (*N*)	Spearman's r_s	P
Fruit	Plant density (9)	0.57	0.06
	Fruiting length (10)	0.57	0.04
	Fruit crop size (9)	-0.45	>0.1
	Fruit weight (9)	0.35	>0.1
	Fruit bite-size (9)	0.53	0.07
	Pulp content (9)	0.25	>0.1
Insect	Colony density (7)	0.68	0.05
	Colony size (8)	0.76	0.01
	Colony biomass (8)	0.87	0.002
	Body weight (9)	0.54	0.07

Selection for insect traits

The population and ecological characteristics varied among prey-insect species (Table 7.12). The insect sizes ranged from 1 to 200 mg, colony sizes from a few hundred to over a hundred thousand, nest locations were in different microhabitats, etc. Characteristics of some potential prey insect species that were found in the study area but not preyed on by bears, also varied among species (Table 7.13).

Colony abundance, colony size and colony biomass size were significantly different between prey and non-prey insect species (Table 7.14). Most prey species were common and had large colonies or colony biomass sizes. Other characteristics such as insect size, nest location, foraging period and primary defence method were not found to be related to being consumed by bears. The characteristics that were selected were used to identify the probable factors that influenced some species of insects not being preyed on by bears in Panna (Table 7.13). The relative biomass contribution of different insect species/taxa to bear diet was significantly positively correlated with insect colony density, colony size, colony biomass and somewhat weakly correlated with insect body weight (Table 7.11).

Table 7.12. Population and ecological characteristics of insect species that were commonly preyed on by sloth bears in Panna NP.

Family/ Sub-Family	Species	Life stage eaten	Frequency of occurrence	Size (range)	Weight (mean)	Colony size (range)	Colony biomass[a]	Nest location	Foraging period	Defence method
Formicinae	*Camponotus compressus*	Adult, pupa, larva and eggs	Abundant	8-16 mm	24 mg	100-2,000	Large	Tree hole; under ground; under rocks	Day / Night*	Major-worker with strong mandibles; bite and spray formic acid
	C. irritans	as above	Abundant	6-10 mm	15 mg	100 – 2,000	Large	Under ground; under rocks; dead wood and tree hole	Largely night	Bite and spray formic acid
	Polyrhachis spp.	as above	Occasional	6-8 mm	8 mg	20 - 200	Small	Under ground; dead wood; on plants	Day & Night	Bite
Dorylinae	*Dorylus labiatus*	as above	Frequent	2-8 mm	4 mg	>10,000	Large	Deep under ground	Day & Night	Swarming; soldiers with strong mandibles; bite, sting
Aenictinae	*Aenictus spp.*	as above	Frequent	2-3 mm	2 mg	2,000 to >10,000	Large	Bivouacs; under rocks	Day & Night	Swarm; bite
Ponerinae	*Leptogenys processionalis*	as above	Frequent	7-9 mm	8 mg	500-1,500	Large	Under ground; leaf litter	Day/ Night*	Venomous sting
Myrmicinae	*Pheidole spp.*	Adult, larva	Abundant	2-4 mm	1 mg	200 – 4,000	Small	Under rock; under ground	Day & Night	Bite & sting; absconding reaction
Macrotermi-tinae	*Odontotermes spp.*	Adult, nymph	Frequent	2-4 mm	3 mg	50,000 to >100,000	Large	Under ground, mud mound	Day & Night	Soldiers present; bite
Nasutitermi-tinae	*Nasutitermes spp.*	as above	Frequent	2-3 mm	2 mg	> 1,000	Small	Under ground, under rocks, dead wood	Day & Night	Spray sticky secretion

Family/ Sub-Family	Species	Life stage eaten	Frequency of occurrence	Size (range)	Weight (mean)	Colony size (range)	Colony biomass[a]	Nest location	Foraging period	Defence method
Apidae	*Apis dorsata*	Adult, pupa, larva	Frequent	16-18 mm	200 mg	> 1,000	Large	On cliff faces; on large tree branches	Day	Venomous sting; swarming
	A. cerana	as above	Frequent	11-12 mm	> 50 mg	> 1,000	Large	Tree hollows; rock cavities	Day	Sting
Carabidae	*Carabid* beetles	Adult	Frequent	--	> 20 mg	--	--	Under rocks	Unknown	Unknown

* –Diel activity changed in relation to weather/season

[a] – product of insect size and colony size. Colony biomass > 10g are considered large

Table 7.13. Characteristics of some potential prey-insect species that were found in Panna NP, but were not preyed on by sloth bears. Based on traits selected by bears, the probable factors that influence bears not to prey on these insects were identified.

Sub-Family	Species	Frequency of occurrence	Size (range)	Weight (mean)	Colony size (range)	Colony biomass	Nest location	Foraging period	Defence method	Probable factors for not being preyed on
Formicinae	*Camponotus angusticollis*	Occasional	12-21 mm	30 mg	20 – 200	Small	Tree hole; under ground	Day & Night	Bite & spray Formic acid	Not abundant; small colony size
	C. parius	Occasional	5-10 mm	8 mg	50 – 200	Small	Ground	Day & Night	Bite	Not abundant; small colonies
Formicinae	*Polyrhachis spp.*	Occasional	6-8 mm	8 mg	20 200	Small	under rocks; rotting wood; on plants	Day & Night	Bite	Not abundant; small colonies

Sub-Family	Species	Frequency of occurrence	Size (range)	Weight (mean)	Colony size (range)	Colony biomass	Nest location	Foraging period	Defence method	Probable factors for not being preyed on
Formicinae	*Oecophylla smaragdina*	Frequent	7-11 mm	10 mg	>5,000	Large	Leaf nest on trees	Day	Bite & spray venom	Nests difficult to access; strong defence
	Prenolepis longicornis	Abundant	3-4 mm	2 mg	2,000 to >4,000	Small	Under rock; ground; leaf litter	Day & Night	Absconding reaction	Small colony biomass; absconding reaction
Ponerinae	*Leptogenys chinensis*	Occasional	8-10 mm	8 mg	> 50	Small	Ground	Day	Sting	Not abundant; small colonies
Dolichoderinae	*Tapinoma melanocephalum*	Frequent	1.5-2 mm	< 0.5mg	1,000 to > 5,000	Small	Ground; leaf litter	Day & Night	Repellent secretions	Small colony biomass
Myrmicinae	*Myrmicaria brunnea*	Frequent	6-8 mm	8 mg	> 500	Small	Ground; mound under vegetation	Day	Unknown	Nests difficult to access; small colony biomass
	Monomorium spp.	Frequent	2-3 mm	1 mg	>1,000	Small	Ground	Day & Night	Venomous secretions	Small colony biomass
	Tetramorium spp.	Occasional	2-3 mm	1 mg	> 1,000	Small	Ground; under rock	Day & Night	Unknown	Small colony biomass
	Crematogastor spp.	Abundant	2-4 mm	1 mg	100 to 1,000	Small	Ground; tree holes; rotting wood; cartons	Day & Night	Bite & Sting	Small colony biomass; difficult to access nests
Pseudomyrmecinae	*Tetraponera rufonigra*	Occasional	10-13 mm	10 mg	Unknown	Unknown	Tree hollows; dead wood of trees	Day	Venomous sting	Not abundant; strong defence; inaccessible nests

Table 7.14. Selection of insect traits by sloth bears in Panna NP. Characteristics of 12 prey insects and 12 potential prey insect species that were not eaten were compared. Chi-square tests were used where the expected frequencies were above permissible levels, or else Fisher's exact (FE) tests (for 2 x 2 tables) were used. For "2 x 3" tables, classes were combined (where it is biologically appropriate) to form 2 x 2 tables, if needed. For all tests, α was set at 0.1, to increase statistical power.

Variable	Insect group	Relative frequency (%)			Test & *P*
Colony abundance		Common		Occasional	χ^2 = 5.04, *P*=0.02; FE test, *P*=0.03
		Abundant	Frequent		
	Prey	25.0	66.7	8.3	
	Non-prey	16.7	33.3	50.0	
Colony size		Small (< 1,000)	Large (> 1,000)		FE test, *P*=0.03
	[a] Prey	9.1	90.9		
	[a] Non-prey	54.5	45.5		
Colony biomass		Small	Large		χ^2 = 9.21, *P*=0.002 FE test, *P*=0.004
	[a] Prey	27.3	72.7		
	[a] Non-prey	90.9	9.1		
Insect size		Small (< 8 mg)	Large (≥ 8 mg)		FE test, *P*>0.1
	Prey	41.7	58.3		
	Non-prey	41.7	58.3		
Nest location		Easy access [c]	Difficult access [d]		χ^2 = 1.51, *P*>0.1
	Prey	58.3	41.7		
	Non-prey	33.3	66.7		
Foraging period		Day	Night	Both	χ^2 = 1.63, *P*>0.1
	[a] Prey	18.2	9.1	72.7	
	Non-prey	33.3	0.0	66.7	
Primary defence method		Bite	Sting	Other	χ^2 = 0.56, *P*>0.1
	Prey	58.3	25.0	16.7	
	[b] Non-prey	50.0	20.0	30.0	

[a] – no data available for one species
[b] – no data available for 2 species
[c] – under rock/log; in leaf litter
[d] – under ground; inside mound; inside log

Food habits by various study methods

Information on diet composition was incongruous, when different methods of studying food habits were compared and when data from faecal analysis was presented in various forms. The relative contributions of various food-groups to sloth bear diet varied with the method, and thus resulted in varying importance being given to different food-groups when different methods were used to study food habits (Fig. 7.12).

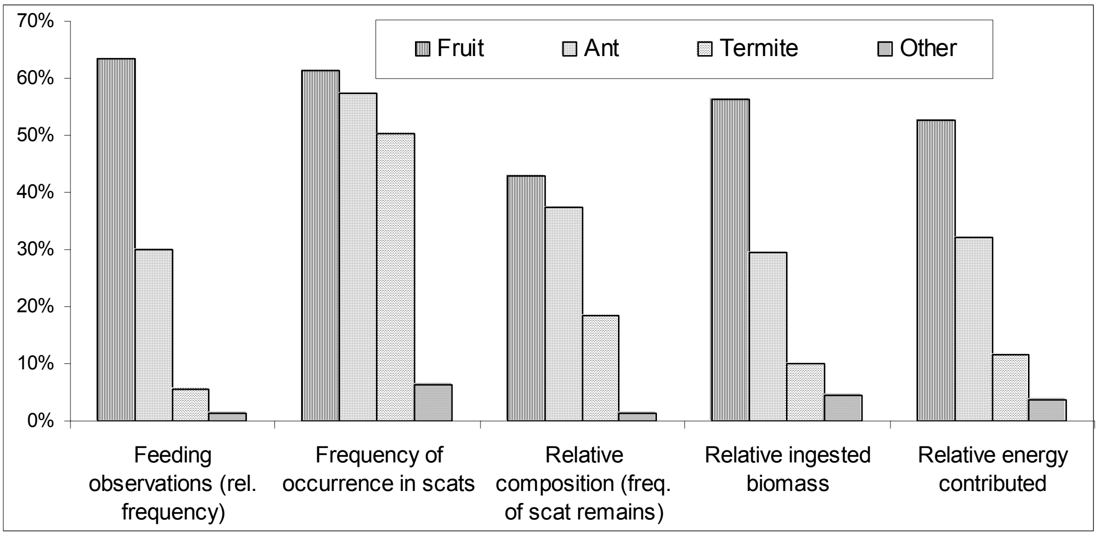


Fig. 7.12. Incongruity in annual diet composition of sloth bears in Panna NP represented by various methods that are commonly used in studies on food habits.

Diet composition reported in other studies

Relative contributions of fruits and insects to seasonal and annual diet varied among populations and habitat types (Table 7.15). All the ten studies that were compared were conducted in moist or dry deciduous habitats. In three studies (one conducted in fruiting season and two annually), fruits constituted a predominant part of the diet, and in two studies (one in non-fruiting season and another annually), insects constituted the major part. In five other studies, relative composition of fruits and insects were about equal. Food items other than fruits and insects constituted a minor part (<10%) of the diet in all studies.

Table 7.15. Sloth bear diet in various areas and habitats across its range, represented as relative composition (by frequency), relative volume or relative dry weights of scat remains, as measured in different studies.

Area & habitat type	Method & Period (*N*)	Fruit %	Insect %	Other %	Study
Kanha Moist deciduous	% composition; Annual (92)	61.0	39.0	0.0	Schaller (1967)
Bandipur Dry deciduous	% composition; Annual (95)	37.0	53.0	10.0	Johnsingh (1981)
Mudumalai Dry deciduous & thorn forest	% dry weight; Fruiting (350)	90.0	8.0	2.0	Baskaran (1990)
Mudumalai Dry deciduous & thorn forest	% dry weight Annual (567)	87.7	12.1	0.2	Baskaran *et al.* (1997)
Mudumalai Dry & Moist deciduous	% volume; Annual (474)	48.0	51.0	1.0	Desai *et al.* (1997)
Mundanthurai Dry deciduous	% dry weight; Non-fruiting (111)	25.0	75.0	1.0	Gokula *et al.* (1995)
Bilaspur Degraded moist deciduous	% dry weight; Annual (568)	85.0	10.0	5.0	Bargali *et al.* (2002)
Chitwan Moist deciduous & alluvial grassland	% composition; Annual (139)	42.0	52.0	7.0	Laurie & Seidensticker (1977)
Chitwan Moist deciduous & Alluvial grassland	% composition; Annual (627)	14.0	83.0	3.0	Joshi *et al.* (1997)
Panna Dry deciduous	% composition Annual (410)	42.8	57.2	0.01	This study
Panna Dry deciduous	% ingested biomass Annual (410)	56.2	43.6	0.2	This study

Plate 13. Plants that produced fleshy fruits and have large fruit-crop sizes such as *Diospyros melanoxylon* (left picture) and *Zizyphus mauritiana* (right) contributed a major part of the diet of bears in Panna NP. The bulk supply of food attracts opportunistic frugivores such as sloth bears and it could sustain them as frugivores in forest habitats.

Plate 12. During dry season, the fleshy petals of *Madhuca longifolia* (Mohwa) flowers drop off after blooming, and they are sought and eaten by sloth bears, as do a host of other animals and humans. The long pods of *Cassia fistula* (right picture) ripen in the dry season, but are frequently eaten by bears in the early wet season. In addition to providing sugary pulp, these fruits could also be a source of protein- and fat-rich *Microlepidoptera* (moth) larvae that is often found infesting these fruits.

Plate 11. Bears turn over rocks, deadwood and such microhabitats, rip open fallen logs, and earthen mounds to search for and feed on social insect colonies. The brood (larval, and pupal stages) of insects such as that of *Camponotus compressus* ants (left picture, foreground) are rich sources of fat and protein, found clumped together, and the bears could forage on them more efficiently than they could on adults. The brood and honey of rock bees (right picture) are excellent sources of food, but are often built on difficult to access sites such as on steep cliffs.

7.4. DISCUSSION

What did sloth bears forage on, how and why?

Sloth bears in Panna foraged on fruit-bearing plant species and insect taxa that were commonly found in the habitat. They mainly foraged on fruits that were produced in large numbers and on insect colonies rather than individual insects. In addition, bears sought broods of insects that were found concentrated inside nests. Most insects that they fed on are social insects, group-living or have a clumped occurrence. Foraging on these resources probably facilitated higher energy gains per unit time spent foraging. The only singly occurring resource that they fed on was the larva of dung beetle (*Scarabaeidae*). Sloth bears in southern Indian forests mostly fed on fruits of plants that occurred in high density, at least in some forest types within the study areas (Gokula *et al.* 1995, Baskaran *et al.* 1997, Desai *et al.* 1997). Joshi *et al.* (1997) observed during their study in Chitwan NP, Nepal, in the early 1990s that sloth bears fed only rarely on two species of fruits that were eaten commonly in early 1970s (Laurie and Seidensticker 1977), because those species were found to be uncommon during the later study. Sloth bears fed mostly on social insects, their brood and to a notable extent on beetles and their larva. Other omnivorous bear species also foraged mostly on common species of fruits and colonial insects (Landers *et al.* 1979, Hellgren and Vaughan 1988, Mattson *et al.* 1991, Schwartz and Franzmann 1991, Craighead *et al.* 1995, Noyce *et al.* 1997, Swenson *et al.* 1999a, Mattson 2001).

Commonly, ripe fruits fallen on the ground were eaten rather than those on trees, with the exception of fruits on shrubs. Several species of fruits fell after they ripened, and this may be a strategy of plants that produce large fruits to enhance their seed dispersal by large, ground-dwelling animals. Post-ripening abscission of fruits is considered a trait of plants dispersed by primarily carnivorous mammals (Herrera 1989), as opposed to bird-dispersed (Snow 1971). For sloth bears, foraging on the ground would have allowed higher feeding rates than foraging on trees. It also would have been energetically expensive for sloth bears to climb trees, unless the trees offered a large fruit biomass and allowed a high feeding rate. They also possibly avoided climbing trees to avoid the risk of being unable to run away from or pre-emptively charge at a large predator. However, honey from beehives was generally obtained by climbing trees. In Panna, sloth bears occasionally also climbed on *C. fistula* trees, the fruits of which did not fall soon after ripening. Sloth bears in Chitwan also foraged primarily on fruits on the ground or on bushes and climbed trees mostly to feed on honey (Laurie and Seidensticker 1977, Joshi *et al.* 1997). Laurie and Seidensticker (1977) noticed climbing signs on some fruiting trees in Chitwan NP, but they did not mention the tree species. Schaller (1970) reported that the Asiatic black bears (*U. thibetanus*) often climbed trees to feed on fruits and acorns of species such as *Celtis australis,* walnut and oak in Dachigam Wildlife Sanctuary in Kashmir. The bears in Dachigam could perhaps do so since a potential predator of bears, the tiger, does not occur there. Also, the fruit biomass available on trees was probably larger there. Sloth bear cubs do not climb trees as a defence strategy, unlike the American black bear cubs. This again might be related to the presence of large predators in sloth bear habitat (Laurie and Seidensticker 1977, Joshi *et al.* 1999).

Mostly ants that were available close to ground surface, such as *Camponotus* spp., were consumed. Only *D. labiatus*, an army ant species with a large colony biomass (Holldobler and Wilson 1990), was dug out from deep underground, for which the effort was considerable. In Panna, termites were generally found in underground colonies, with or without a mound over them. In either case, it would require a considerable effort to dig and access the nests. When ant nests were frequently available close to ground surface (during wet and cold seasons), termite consumption was relatively low. When ants were not available close to surface (during the dry season), termites were consumed at a higher frequency than ants, probably because the time needed for digging them out was not longer than the time needed for underground ants. Termite broods were available throughout the year, unlike ants, and this perhaps weighed in favour of termites. Termite colonies with mounds could also be more easily located during the dry season than underground ant colonies. Laurie and Seidensticker (1977) observed that the sloth bears in Chitwan foraged on ants and termites by digging shallow holes in the ground or digging into termite mounds. Joshi *et al.* (1997) also observed that the sloth bears in Chitwan foraged on ants mostly from the surface and termites from mounds or underground colonies. Thus, sloth bears generally seem to prefer to forage on insect nests closer to the ground surface.

Ant queens, in general, select ground under rocks to establish new colonies. The ants also frequently move, transporting brood, close to the ground surface beneath rocks during the seasonal brood peak (during wet season in Panna). Solar radiation heats up the nests and this helps in brood development and colony growth (Sanders 1972, Porter 1988, Roces and Nunez 1995). The thermo-regulatory properties of flat rocks make them suitable places for ants to colonise and the ants commonly selected these microhabitats for establishing nests (Wilson 1971, Brandt 1980). American black bears fed on ants that were mostly found inside or under the bark of partially decayed fallen logs (Noyce *et al.* 1997). Similarly, the North American brown/grizzly bears foraged more often on ants found in partially decomposed, moderate-sized logs rather than the ones found under rocks or in mounds (Mattson 2001). European brown bears foraged mostly on ants found in dead wood and mound nests (Swenson *et al.* 1999a). The ants preferred by these temperate species of bears largely nested in dead wood debris and this may be an important microhabitat for ants. However, availability of such dead wood is limited in Panna and this factor might be affecting the distribution and abundance of ants as was observed in North American habitats (Noyce *et al.* 1997, Mattson 2001). In contrast, plenty of rocks are found in Panna that replaced logs as nesting microhabitats for insects. The large ants that were preferred by the temperate species of bears, *Camponotus* spp., commonly nested on the ground in Panna and these ants formed a major portion of sloth bear diet too. Overall, it appears that bears everywhere preferred to feed on ants that were found close to the ground surface, and thus could be accessed easily. In general, sloth bears foraged on resources that appeared to have maximised rate of energy gain, given the constraints posed by risk of predation.

Are sloth bears optimal foragers?

The abundance of various fruit and insect resources that the sloth bears foraged on changed seasonally. Accordingly, the costs and benefits of foraging on those resources changed over time. The bears followed these changes and foraged optimally by changing their food choices seasonally. When fruits were abundantly available, sloth bears foraged in food-plant patches and fed mainly on fruits. During the wet and cold seasons, they foraged frequently on ants. They foraged consistently, but less frequently, on termites throughout the year. However, when ants were available in greater abundance they foraged less on termites. Their main foraging strategies appear to be to decrease 'search-time' by feeding on abundant and patchily distributed resources; to reduce 'handling time' by feeding on resources such as clustered or fallen fruits and on insects that were available close to surface and that had weak defence; if feeding on insects involved digging, then to minimise handling time per unit biomass by digging for colonies with large biomass. The bears also appear to increase the food 'intake rate' by foraging on resources that allowed a large bite-size or a high bite-rate. Although I did not accurately measure search and handling times, I have rough estimates of them. Search time for different resources was indicated by radio collared bear movement patterns to some extent. I also used the population and ecological traits of various food resources as indicators of relative search and handling times required.

In the case of less-frequent honey, the search-time may have been longer, but the handling-time was short and intake rate was high. The beehives may persist at the same sites, and the bears may remember hive locations and may even transfer the information across generations. This would reduce the search time and would make the resource cost-effective to forage on. The army ant, *D. labiatus* colonies involved long handling time, but since they had large colony biomass it would have been cost-effective. Diggings for *D. labiatus* ants were often done in the same locations periodically, indicating persistence of colonies at the same locations. Mound building ants and a few other forms with deep, secure nests are reported to remain at the same site for many years (Holldobler and Wilson 1990). The bears evidently remembered the locations of colonies and thereby reduced the search time.

Sloth bears also foraged on other less-frequent and seasonal resources such as termite reproductives and monitor lizard eggs. Although they may have involved high search time, these resources offered high nutritional benefits. For food resources that had similar nutritional value but different search and handling requirements, we would expect sloth bears to prefer those with lower search and handling times. A preference for fruit of *L. camara* over *Z. oenoplia,* feeding on which probably involved higher search and handling times (due to lower patchiness, poorer fruit presentation, and presence of thorns), may be related to such an optimal decision by bears. Conversely, for food resources that had different nutritional value but similar search and handling requirements, the bears would be expected to prefer those with higher nutritional value. This was shown in their preference for *C. compressus* ants, which had a higher nutritional value, over *L. camara* fruits, when both were in abundance during the wet season and may have had similar search and handling times. Similarly, among abundant resources having similar search times, foraging decisions may have been made based on nutritional value and handling time – clustered fruits and surface dwelling insects were selected by bears. If the handling times were equal, e.g., among fallen fruits, then the decision may have been based on nutritional value and search time – abundant species of fruits and common insects were chosen. Overall, sloth bears appear to be optimal foragers as they seem to follow the rules of foraging energetics (*sensu* Krebs and Davies 1993).

Sloth bears ceased feeding on food-patches (individual fruit plants and insect nests) long before the resources were completely exhausted. This may have helped the bears to maximise energy intake per unit handling time. The fallen fruit density under a tree or insect density within a colony would have diminished as the bears foraged (also more insects would have escaped from an excavated nest with time). Therefore, the bears could maximise intake per unit foraging time by moving to another patch rather than continuing in the diminished one ("marginal value theorem", Charnov 1976). However, this equation would be constrained if the time needed to search for the next patch were high (Stephens and Krebs 1986). Since the sloth bears fed on various food-groups during their seasonal abundance peaks, the time taken to search for subsequent patches could be assumed to be minimal. American black bears (Noyce *et al.* 1997), brown bears (Swenson *et al.* 1999a) and other myrmecophages (Redford 1985) also exhibited partial consumption of insect colonies. This kind of partial consumption perhaps also incidentally helped the insect colonies to persist at the same sites. Sloth bears often repeatedly dug out some *D. labiatus* ant and termite nest locations, at periodic intervals and this may be due to persistence of colonies of these taxa. This is also supported by the fact that the bear scats only rarely contained remains of queens of social insects. This indicates that the colonies were not entirely harvested by bears and the reproductive queens mostly escaped predation. This behaviour of not exhausting food patches also lends support to the hypothesis of optimal foraging by sloth bears.

Annual diet and the geographical variability in diet

Sloth bears in Panna fed mostly on fleshy fruits of commonly occurring plants and adult and brood of social insects such as ants, termites and honeybees. They also fed, in low relative proportions, on other food such as *Carabid* beetles and monitor lizard eggs that occurred in groups and on honey that was found in large volumes. They fed on 10 species of fruits, more than 10 species of ants, several species of termites, and two species of honeybees. Fruits contributed to over half of the annual diet and social insects, the rest. Some fruits, such as *D. melanoxylon* and *Z. mauritiana* contributed more than half of the diet for several months and some fruits contributed less than 10% of the diet and that too only for a month or two. *C. fistula* fruits were eaten for up to seven months and some such as *M. longifolia* flowers, for only a month. *Camponotus* spp. ants contributed a substantial portion to the diet for several months, whereas others such as *Polyrhachis* spp. only small amounts. Similarly, some insects, such as *Carabid* beetles, were eaten only for a few months, whereas others, such as termites, throughout the year (Fig. 7.1). This pattern of feeding was basically related to the availability of these food resources over time.

The relative contributions of fruits and insects to sloth bear diet varied among seasons and over the geographical range of the species (Table 7.15). In the moist deciduous forest and alluvial grassland habitat of Chitwan NP, insects formed a dominant portion of the annual sloth bear diet (83%) and fruits the rest (Joshi *et al.* 1997). However, the form that Joshi *et al.* (1997) used to represent diet (composition, in terms of frequency of faecal remains, rather than biomass of food consumed) would have overestimated the contribution of insects and underestimated that of fruits, to a considerable extent. In a dry deciduous forest in southern India (Baskaran *et al.* 1997), and a degraded forest in central India (Bargali *et al.* 2002), the proportion of fruit in scats (percent dry weight) was much higher (over 85%) than insects. In other studies, the proportions of fruits and insects in annual diet were more or less equal (Schaller 1967, Laurie and Seidensticker 1977, Johnsingh 1981, Desai *et al.* 1997). Overall, the variability in the diet of the sloth bear across its range may be related to the local availability of various insects and fruits. The relatively higher contribution of fruits to diet in the habitats south of Chitwan (in peninsular India) could be attributed to the higher abundance and diversity of fruiting plants and longer fruiting seasons. Sloth bears fed on several species of fruits in other areas in their range, as in Panna, and probably on several insect species too, although species-level data on prey insects is lacking in other studies. The contributions of food resources other than fruits and insects to sloth bear diet were low everywhere.

Other omnivorous bear species also fed heavily on several species of fruits and to a considerable extent on social insects (Schaller 1970, Peyton 1980, Rogers 1987, Hellgren and Vaughan 1988, Reid *et al.* 1991, Schwartz and Franzmann 1991, Craighead *et al.* 1995, Noyce *et al.* 1997, Mattson *et al.* 1991, Mattson 1998, 2001, Swenson *et al.* 1999a). Fruits are a major food source for all species of bears and probably for other omnivores too. Fleshy fruits, which are sugar-rich, provide immediate energy for these animals, and the excess sugar can be stored as fat tissue for future use (Rode and Robbins 2000, C. T. Robbins, *personal communications*). While most omnivorous bears meet their necessary protein and other nutrient requirements by feeding substantially on vertebrates, but feed only opportunistically on insects

(Mattson 1998, 2001, Swenson *et al.* 1999a), sloth bears obtain their protein requirements primarily from insects. This aspect of the food habit of the sloth bear makes it unique among bears.

Biases in foraging observations

The relative frequencies of observations of bears foraging on the main food-groups were comparable to diet composition (relative ingested biomass) from faecal analysis (Fig. 7.12). The seasonal relative frequencies of foraging observations were also comparable to seasonal changes in diet composition (Table 7.2). However, observations on consumption of termites were lower, probably because of difficulty in observing the bears feeding on small, non-mound-living termite colonies. The data from foraging observations were biased towards fruits, since it was easier to observe the bears feeding on fruits. Also, observations were more frequent in the dry and cold seasons when the bears fed more on fruits and for longer durations. Among the insects, the data was biased towards ants, particularly one species of ant, *D. labiatus*, because it took longer for bears to dig out the nests of these ants. This probably increased the likelihood of it being observed. Several of the diggings for *D. labiatus* were done on forest roads, roadsides and in open spaces, which were easier to observe at night. Foraging observations of Joshi *et al.* (1997) also had a bias towards fruits. Considering the biases discussed above, the similarity of data from foraging observations and faecal analysis in this study is perhaps just a coincidence. Were we to convert the data on relative frequencies of foraging observations to relative biomass consumed during the observed feeding events, the data will be heavily biased towards fruits. This is because the biomass consumed in a fruit-patch during a feeding event would be much higher than what would be consumed in an insect-patch.

Patterns in daily foraging

Frequency distributions of number of food-groups (fruits, ants, termites and other) and food-taxa (various fruit and insects species/taxon) contained in individual scats revealed the fashion in which sloth bears foraged within a day. The bears foraged frequently on two or more food-groups (56% of the scats had 2 or more food-groups; Table 7.3) or three or more food-taxa (58% of the scats contained three or more food-taxa; Table 7.4) in a day. Sometimes they foraged on all four food-groups or up to eight different food-taxa, in a day. During the dry season, when fruits were abundant, the bears foraged less frequently on multiple food-groups or food-taxa in a day, than in wet and cold seasons when food productivity was relatively low. This suggests that the bears were, in general, omnivorous within a day. However, they foraged frequently on a single, abundant resource during seasons of abundance.

When the bears foraged on just one food-group in a day, it was predominantly on a food that was available in large biomass (fruits). Fruit species such as *D. melanoxylon* were available in large biomass as compared to ants and termites. So, the bears did not have to search for other food when such species were available in abundance. When they foraged predominantly on fruit, they seldom fed on other food items. Also, when preferred fruit species such as *D. melanoxylon* and *Z. mauritiana* were fruiting, the bears probably fed primarily on them and when not, they fed on other things that were encountered. When they foraged on multiple food-groups in a day, it was on resources that were available in small biomass (e.g., termites). Also, when the bears fed on more than two food-taxa in a day, it was mostly combinations of ant and termite species/taxa. This is probably because when they foraged on insects that occurred in small biomass, they might have had to feed on several species that were encountered. Also, ants and termites appeared to have been considered similar by foraging bears, because they were often found together in mixed-diet scats. Overall, the sloth bears were omnivorous in a day, less so when fruits were abundant and more so when insects were the main food. This again suggests that they follow an optimal foraging strategy. Such a strategy, theoretically, is expected of all animals, and the more interesting part is to study how exactly it works. The information from this study, besides having indicated how it may be working in sloth bears, would be helpful to construct hypotheses for focused studies on this aspect of behavioural ecology.

The daily foraging patterns revealed by composition of individual scats are consistent with my observations on foraging bears. The Chitwan sloth bears that fed largely on insects (83% of the annual diet) had multiple food in about 71% of scats (Joshi *et al.* 1997). In contrast, I found multiple food-groups in only 56% of the scats. This indicates that the Chitwan bears that fed largely on insect food that occurred in small biomass per patch, had to feed more frequently on multiple resources than the Panna sloth bears that fed on more fruits than insects (56% and 40% respectively on an annual scale). This difference in daily foraging behaviour between the two populations perhaps reflected the difference in the relative abundance of food-groups between the two areas. Data on daily foraging patterns and the seasonal variations to it are hard to come by. Most data that exist on bears are on seasonal patterns of foraging (Landers *et al.* 1979, Hellgren *et al.* 1989, Mattson *et al.* 1991, Schwartz and Franzmann 1991, Craighead *et al.* 1995, Desai *et al.* 1997, Joshi *et al.* 1997). The patterns in daily foraging in sloth bears in Panna appear to be identical to patterns in seasonal foraging and these, in turn, appear to be identical to annual foraging patterns. A fractal pattern seems to exist at these different scales. Other large omnivores too might exhibit such a pattern. For instance, seasonal patterns of feeding were identical to annual feeding in grizzly bears (Mattson *et al.* 1991, Craighead *et al.* 1995).

Seasonal changes in diet and the factors that influence it

The relative contribution of various food-groups to sloth bear diet varied over time. They fed on fruits during the period when preferred species fruited, on ants mostly during the wet season months (August to October) and when fruits were not available (January to March) and on termites, in small amounts, throughout the year. Fruits and ants together contributed to over three-fourth of the diet throughout the year (Fig. 7.4). In Chitwan, insects formed most of the diet (95%) in the non-fruiting season and a large portion (58%) of the diet even in the fruiting season (Joshi *et al.* 1997). Fruits comprised a main portion (38%) in the fruiting season. Termites were the principal insect prey during all seasons, comprising about 60% in non-fruiting and 45% in fruiting seasons (Joshi *et al.* 1997). In peninsular India, insects formed most of the sloth bear diet during non-fruiting seasons and a relatively minor, but a substantial portion during fruiting seasons (Gokula *et al.* 1995, Baskaran *et al.* 1997, Desai *et al.* 1997). Among insects, ants formed a major portion in one area (Baskaran *et al.* 1997, Desai *et al.* 1997) and termite in another (Gokula *et al.* 1995). This difference could be due to habitat-related differences in the availability of these two insect groups.

The apparent variability in relative proportions of diet components could simply be due to the nature of compositional data obtained from faecal analysis studies, where an increase in one component (fruit) will show as a decrease in the other (insect). However, my observations of bears feeding and the seasonal changes in encounter rates of digging sign (Yoganand & Rice, unpublished MS) that the bears left when feeding on underground or mound-living insect colonies shows that the seasonal variability in consumption of insects is absolute, rather than being relative.

The temporal changes in consumption of various fruit species were related to changes in fruiting phenology and fruit-biomass productivity. Fruits were usually consumed only after they ripened and fell from trees. When several fruit species were available at the same time, e.g., during the dry season, the bears preferred some species to others. Consumption of *A. marmelos* dipped in April and May when *D. melanoxylon* became available. Fruits of *C. fistula* were consumed from July to September whereas the fruits ripened from March onwards. This lag in consumption (consumption was correlated to fruiting phenology with a lag of three months, Spearman's r_s =0.77, P=0.003) even after the fruits ripened, indicates that they were not preferred when other fruits were available and were consumed when availability of other fruits declined. The peak in relative productivity of *C. fistula* fruit during July shows that other fruits were not available in that period (Fig. 7.7). The ripe fruits of *C. fistula* remained on trees or on ground for long periods and this benefited bears. Also, grown-up larva of a *Microlepidoptera* moth that infested *C. fistula* fruits were available later in the season and this perhaps added nutritive value to the fruits when consumed later. A few fruits that I examined had an average of 20 – 30 larva or a larval biomass of 2 – 3 g per fruit.

D. melanoxylon and *Z. mauritiana* fruits were consumed in higher proportion than their relative productivity and *Z. oenoplia* fruit in a lower proportion than its productivity. *L. camara* fruit was available in large amounts in August and September but was not consumed proportionately during that period. This is apparently because the ant species such as *Camponotus spp.* and *D. labiatus* were available in abundance and were preferred to *L. camara* fruits. The consumption of *L. camara* was in proportion to its relative productivity in October and November. In January it was consumed in a higher proportion to its relative productivity, because *Z. oenoplia* that contributed most to the productivity in January was the least preferred among fruits. Similarly, some fruit species were preferred over the others and were also consumed in higher proportion to their relative productivity ('selected'). These differences were seen both within-months and annually (Fig. 7.8).

Insects contributed much to bear diet from August to October and from January to March. Insect colony abundance and population size of adult and brood increased substantially from August onwards and this was perhaps related to wet monsoon conditions (Levings 1983, Wolda 1988). During the wet season, the ant brood were also brought close to the surface and located beneath rocks and dead wood, where they could be heated by the sun, thus promoting brood development (Sanders 1972, Porter 1988, Roces and Nunez 1995). This possibly made the ants an abundant and easily available food resource. Phenological observations also indicated that ant colony abundance and brood presence started declining after the wet season, but remained at substantial levels until March, after which the surface activity or colony abundance of ants declined greatly. The insect populations either declined, their activity became restricted or the colonies moved deeper under ground during the dry season. Such population and behavioural responses to changes in temperature and moisture are known in soil-living termites (Ueckert *et al.* 1976) and ants (Sanders 1972, Torres 1984). The presence of brood in nests declined during the dry season and this corresponded with the complete absence of ant pupal remains in scats from April to June (Figs. 7.1 & 7.6). The consumption of *Camponotus* spp. adults was related to consumption of pupa, indicating that the bears fed more on ant colonies when brood were more. Other myrmecophagous bear species also fed preferentially on ant colonies when they were abundant and when brood were present (Noyce *et al.* 1997, Swenson *et al.* 1999a, Mattson 2001).

From April to June, a preferred fruit species, *D. melanoxylon,* became available and this may have resulted in a shift in food choice away from ants. During November and December, ant consumption declined, and that was apparently related more to the availability of another preferred fruit species, *Z. mauritiana,* and not due to a decline in availability of ants. *Z. mauritiana* is an optimal food choice of bears because of its various traits (see later section on food selection) and it would be more beneficial to feed on it than feed on ants during its fruiting period. The myrmecophagous American black bears and grizzly/brown bears also shifted their food choice, away from ants and towards fruits when fruits became available (Mattson *et al.* 1991, Noyce *et al.* 1997, Swenson *et al.* 1999a). The observed peak in ant consumption from January to March is probably due to the unavailability of preferred fruit species. *Z. oenoplia* and *L. camara* were the fruits available during that period and they were low in energy content compared to insects. In particular, *Z. oenoplia*, the species that contributed most to productivity during that period, allowed only lower intake rates because of its poor fruit presentation and presence of thorns. Consequently, the relative consumption of ants showed an increase, which did not necessarily mean an increase in absolute consumption of ants. This peak in ant consumption was consistent among the main prey ant taxa, *Camponotus* spp. and *D. labiatus.* The apparent inverse relationship between consumption of ants and productivity of preferred fruits corresponded with this overall pattern (Fig. 7.11). Thus, the seasonal changes in ant consumption are confounded by changes in both preferred and unpreferred fruit availability and consumption.

The consumption of termites, however, was roughly constant throughout the year and was not strongly related to either fruit productivity or ant consumption. The increased consumption of ants from August to October and that of *Z. mauritiana* fruits in November and December possibly made the relative consumption of termites appear less during these months. Termites contributed majority of the insect food in May and June, when ant consumption was low. Termites seem to have been more readily available to bears than ants during these months. This may be because the termite population cycle did not as closely follow the rainfall cycle as ants, or the cost of foraging on termites became less as compared to ants (see section on foraging). Termites manipulate the environmental conditions of their nest microhabitat by building mounds (Josens 1983). Hence their colony locations or colony size may not change as much with climatic conditions as ants. Although termite foraging activity has been known to be related to factors such as soil moisture and temperature (Ueckert *et al.* 1976), this may not affect the frequency of bears predating on their nests. However, the question of why sloth bears foraged on termites even when fruits were abundant, probably incurring relatively higher costs than foraging on preferred fruits like *D. melanoxylon,* is interesting. A discussion of this is presented in a later section.

Is consumption related to productivity?

A lack of significant correlation between relative contribution of fruit species to annual sloth bear diet and their annual relative productivity indicates selection among them. Fruits such as *D. melanoxylon* and *Z. mauritiana* were selected and some others were not. The traits that influenced such selection are discussed later (see section on food selection: p228). Among insects, the relative contribution to annual diet corresponded with relative productivity, which indicates that the bears, in general, fed on insects in proportion to their abundance. Although there was selection for prey insect species from the ones available in the habitat, based on colony size and other traits that would be discussed later (see section on food selection: p231), there seems to be no preference for any prey insect taxa over the others (Table 7.7).

Sloth bears everywhere fed on various species of fruits during their seasonal abundance, as do other bear species that feed on fruits. However, selection relative to abundance has not been dealt with in most studies. Further, comparable data on sloth bear fruit and insect preference and productivity does not exist for any sloth bear population. In American black bears and brown/grizzly bears, certain species of fruits were selected from what was available (Mattson *et al.* 1991, Schwartz and Franzmann 1991, Craighead *et al.* 1995). Some have found a positive relationship between relative consumption by bears and relative availability of fruit species (Schwartz and Franzmann 1991, Baskaran *et al.* 1997, Desai *et al.* 1997). Among insects, relative consumption of various species was related to relative abundance of species in some cases (Swenson *et al.* 1999a), and in others, a selection for species based on their traits such as insect size and strength of defence was exhibited (Noyce *et al.* 1997, Swenson *et al.* 1999a). Those bears also showed a preference for certain species over others from among the prey insects (Noyce *et al.* 1997).

Sloth bears in Panna fed more on insects when they were seasonally abundant, when brood abundance increased and fed less on insects when preferred fruits became available, but fed consistently on low amounts of insects even when preferred fruits were available. Overall, several factors such as insect availability, reproductive cycle, relative availability of other food, and nutritional requirements seem to have influenced insect feeding in Panna. Joshi *et al.* (1997) related the seasonal shifts in home ranges of sloth bears in Chitwan to seasonal changes in accessibility of termites in different habitat types, rather than changes in productivity. Seasonality in myrmecophagy and other insect-feeding by American black bears and brown bears has been known to be related to factors such as seasonal abundance of insects (Mattson 2002, White *et al.* 1998), abundance of brood (Noyce *et al.* 1997), or low relative abundance of other food (Schwartz and Franzmann 1991, Noyce *et al.* 1997, Swenson *et al.* 1999a).

There is a possibility that insect biomass was under-estimated in this study and this could affect the conclusion that sloth bears selected for insects (relative to their availability and that of fruits). The measured social insect productivity was much lower as compared to fruits in the study area (2.1 kg/ha and 271.2 kg/ha, respectively). However, productivity could not be measured for all prey insect taxa, because of difficulty in sampling some, such as the entirely sub-terranean *D. labiatus,* and because of the frequent absence in sample plots for some, such as honeybees. Biomass of subterranean ants and termites, which were potentially available for sloth bears, may have been high in the study area, but could not be measured. *Dorylus* spp. ant colonies were reported to be numerous in parts of Africa. Their colonies may contain millions of workers and their queens can lay up to 2 million eggs in a month (Holldobler and Wilson 1990). These ants may be an abundant and renewable resource for sloth bears in Panna. The insect productivity that I measured was the biomass that was available at microhabitats usually foraged by sloth bears and not the total biomass present in the habitat. The total biomass may be much higher. Also, I measured insect productivity at one point in time (during wet season, when productivity was probably the maximum). The insect colony density and colony size would change or get replenished over time and thus was not as straightforward to measure as fruit biomass. However, even if the total productivity of insects were ten times the productivity that I measured, it would still be much lower than fruits. If it were fifty times the productivity, it would still indicate a selection for insect food.

Monthly productivity of insects was not measured systematically, but information on insect seasonal activity and phenology was collected. The relative productivity of prey insects in some months, particularly during the wet season, could have been high. Only one fruit species, *L. camara*, fruited in wet season and it was not a preferred fruit. Thus, the high seasonal relative productivity of insects could have resulted in high relative consumption of insects. Data on monthly productivity of insects might have revealed the pattern of preference between fruits and insects better.

Although productivity may determine how much of it is theoretically available for sloth bears, the actual availability may vary among taxa. Differential accessibility, differential abscission of fruits, consumption by other frugivores or insectivores, and differential degradation or decay rates of fruits would determine what proportion of the food resource produced would be available for bears. Competition for fruits from frugivorous birds might affect fruit availability for bears. Frugivorous birds are known to remove a large percentage of fruits produced (Davidar and Morton 1986, Izhaki 2002). Small-sized fruits as that of *L. camara* were heavily eaten by birds in Panna (*personal observations*). However, most fruits eaten by bears were of large size and the extent of frugivory on them by birds and mammals such as langurs, rodents or civets is unknown, although I observed this. Birds and arboreal mammals consumed the fruits of a majority of plants that produced fleshy fruits and pre-dispersal fruit predation by primates and squirrels was high in a wet forest in southern India (Ganesh and Davidar 1999). This kind of competition could have a significant effect on fruit availability for bears. In contrast, competition for social insects is low in Panna. Only one species of specialised myrmecophage that could break into insect nests, i.e., the pangolin *Manis crassicaudata*, occurred there and that was very low in abundance. The myrmecophagous niche, thus, was relatively vacant in Panna, as it is in most parts of the sloth bear range (Laurie and Seidensticker 1977).

Plant and fruit traits that were selected and the probable influences

Analysis of fruit traits indicated that the sloth bears selected for traits such as plant abundance, dispersion, fruit presentation, bite-size and taste in the fruit species they consumed. The frequency with which bears encounter the abundant fruit species would be high. The bears can be expected to know the locations of fruit plant patches. Within a patch, the rate at which bears encounter individual fruiting plants of a species would also be high. These factors would result in a reduction in the time and energy spent in searching for abundant or patchy fruit plant species. Clustered or large fruits that offered large bite sizes and plants that had large fruit-crop sizes would have led to higher feeding rates and lower handling time. All these traits indicated that the sloth bears in Panna chose optimal food species, similar to the pattern found in the seasonal foraging choices made by them (see section on foraging). Frugivores, in general, are attracted to plants with large fruit-crop sizes (Snow 1971, Howe and Estabrook 1977, Howe and De Steven 1979, Izhaki 2002). Production of large quantities of fruit is considered a trait of plants to attract opportunistic frugivores from other sources of food, as may happen with sloth bears, by providing them an opportunity to feed on a large supply of food, at little cost in search and handling times (Howe and Estabrook 1977). In addition, plant abundance and fruit energy were positively related to intensity of frugivory by birds (Izhaki 2002). Abundant species are also expected to produce large fruit crops because of intraspecific competition for dispersers (Howe and Estabrook 1977). In forest habitats, this kind of evolutionary feedback would benefit sloth bears greatly and could sustain them as frugivores to a large extent.

Sloth bears selected sweet tasting ripe fruits, indicating choice for sugar-rich fruits and avoidance for starch-rich unripe fruits or sour fruits with high acid content. Simple sugars contained in ripe fruits could be easily assimilated by bears, whereas starch, like cellulose, may be digested poorly by the simple digestive system of bears (Pritchard and Robbins 1990). Among the food species of fruits, the relative contribution to diet increased with plant density, fruiting length and fruit bite-size. These relationships again suggest that the bears selected fruit species to reduce search time and increase intake rates. Sloth bears in other areas also fed more on fruit species that were available for longer periods (Laurie and Seidensticker 1977, Desai *et al.* 1997). The longer the plant had ripe fruits, the higher and more frequent would be the chance for the bears to feed on it. Long fruiting period was suggested as a strategy of plants to enhance seed dispersal by specialised frugivores (Howe and Estabrook 1977). However, it also appears to benefit omnivores such as sloth bears. Fruit size and relative pulp richness are considered as traits of carnivorous-mammal dispersed fruits (Herrera 1989) and these seem to be traits of fruits consumed by sloth bears too. In general, fruit traits are associated with consumer taxa and are supposed to have been evolved under consumer pressure (Gautier-Hion *et al.* 1985). Sloth bears dispersed seeds of fruits they consumed (unpublished data). By selection of traits in the fruits they dispersed, the bears, to some extent, may have influenced the evolution of persistence of traits that favoured them. Overall, as the energy values of (food-plant) fruits were more or less similar, the selection of fruit species appear to have been influenced by other factors of optimal food choice, namely, search and handling times.

Fruit species that were selected and others that were not

The fruits that were selected, *D. melanoxylon*, *Z. mauritiana* and *C. fistula* have all or most of the traits that the bears selected for as optimal food traits. Of the fruits that were consumed commensurate with their productivity, *A. marmelos* had a small fruit-crop size and required a longer handling time because of its hard shell, resulting in a slower intake rate. The fruit is also acidic to some extent, probably limiting its consumption. *B. lanzan*, although a fruit with potential to be selected, had a short fruiting period and the fruits were also collected extensively by people for its market value. This limited its availability to bears. The shrubby weed *L. camara* was highly patchy and was restricted to the peripheries of the study area. Thus, it may not have been accessible to all the bears in the study area. Also, *L. camara* has lower energy values as compared to other alternative food resources (*Z. mauritiana* fruits and *Camponotus spp.* ants) that were available during the period it fruited.

Other fruit species that were 'avoided' (consumed in lower proportion to their productivity) did not have most of the traits that the bears selected. Fruits of the shrubby climber *Z. oenoplia* offered small bite-size due to its poor fruit presentation, presence of thorns, and low fruit-fall rates after ripening. It also allowed only a low intake rate of ingestible pulp due to its low pulp to fruit ratio, and probably had a low energy value as compared to the alternative food (fruits of *Z. mauritiana*) that was available when it fruited. *Z. oenoplia* was of a lower preference as compared to even *L. camara*, in the months from November to January (Fig. 7.8). Fleshy flowers of *M. longifolia* had most of the traits to be an optimal food, however, its flowering period was short (less than a month). This limited the amount the bears could feed on them, although its flower-crop sizes were very large (>50,000/tree). Also, the flowering trees were less abundant as compared to *D. melanoxylon*, which fruited during the same period. Water content of *M. longifolia* flowers is high (about 80%) and this would have made the absolute energy obtained per unit time of feeding much less compared to *D. melanoxylon* fruits. Thus, the total biomass consumed would have been higher for *D. melanoxylon* than *M. longifolia*, making the former a preferred fruit. In addition, the presence of large number of people collecting *M. longifolia* flowers even at night would have disturbed bears from feeding on several of the trees in the study area. Competition from other flower consumers too might have been high. The main factors that influenced the bears not to feed on some potential fruit species in the study area appear to be either their infrequent occurrence or their non-sweet fruits.

Insect traits that were selected and the probable influencing factors

Colony abundance, colony size and colony biomass-size were the traits selected by sloth bears in the prey species of insects. Feeding on insect species whose colonies occurred frequently would have led to a reduction in search time. Large number of insects or a large biomass in a colony (product of number and weight of insects) would have resulted in a higher intake rate and a lower handling time per unit biomass. Excluding the reproductives and brood, the insect taxa had similar energy values among themselves, but overall a higher value than fruits (Table 7.5). Therefore, it would have been beneficial for bears to exercise optimal insect choice (based on search and handling times), while preferring to feed on the high-energy insect stages. The insect traits selected by sloth bears indicate that this was as expected. Comparable data on insect traits is not available from other studies on sloth bears. Sloth bear scats frequently contained the widely distributed *Camponotus* spp. ants and *Odontotermes* spp. termites, in some forest areas in southern India (*personal observations*). It is likely that the sloth bear populations everywhere select for these optimal traits. The relative contribution of prey insect taxa to sloth bear diet increased with colony density, colony size, colony biomass and insect size (Table 7.11). These relationships also indicate a choice for lower search and handling times in prey-insect selection. Colony density and insect sizes were also found to be related to consumption in American black bears and brown bears (Noyce *et al.* 1997, Swenson *et al.* 1999a, Mattson 2001). Swenson *et al.* (1999a) observed that although the colony sizes of *Formica* ants were high, it was not related to consumption, and the *Camponotus* ants that were larger in body size were preferred.

Insect taxa that were consumed and others that were not

Camponotus spp. ants and *Odontotermes* spp. termites were consumed in higher proportion to their productivity. These species had most of the traits that were selected by sloth bears. Termites were small but their colony biomass-sizes were large. *L. processionalis* and *Pheidole* spp. ants, the other taxa for which productivity was measured, were consumed in proportion to their availability. Although *L. processionalis* colonies were frequent, and the insect size and colony biomass sizes were large, the swarming defence and venomous sting of these army ants may have limited their consumption by sloth bears. *Pheidole* spp. insect size and colony biomass sizes were small, but they were consumed in proportion to availability probably because of their colony abundance. However, some other similar sized *Myrmicine* ant species were not eaten, probably because of their small colony biomass sizes and speedy evacuation of nests when attacked by predators. Thus, the prey defence methods too influenced prey choice by bears. Noyce *et al.* (1997) and Swenson *et al.* (1999a) also observed that the bears in their study areas consumed the ant species with weak defence and passive reaction to disturbance, more often than others. Among the species for which productivity data was collected, there was no evident preference exhibited by bears. This suggests that except for the difference in search and handling times that influenced relative consumption of different species, most prey-insects were probably recognised to be similar by bears. The main factor that influenced bears not to feed on some common insect species that occurred in the study area seems to be (small) colony biomass size. However, in the case of the leaf-nest building Asian weaver ant, *Oecophylla smaragdina*, which had a large colony biomass, the factor could be its strong defence or its largely inaccessible nests that were located on thin branches of trees.

Choice between fruits and insects

Sloth bears fed preferentially on fruits when they were available and on insects either when they were abundant or when fruits were not available.

This pattern corresponded with the inverse relation consumption of insects had with production of fruits, except in the wet season months of August and September (Fig. 7.11). However, the bears also fed on considerable amount of insects throughout the year, irrespective of availability of fruits. Among all food-groups, ants and termites were consumed in higher proportion to their annual relative productivity (‘selected’) and fruits were not selected. The apparent non-selection of fruits is possibly because fruits were only seasonally available, despite having been produced in much higher biomass as compared to ants and termites. In non-fruiting periods the bears have had to feed largely on insects. Further, insect productivity might have been higher than fruits during some months. Also, a considerable amount of insects were eaten even during fruiting seasons. These factors might have influenced a high annual relative consumption value given to insects. Therefore, the selection calculation based on annual values does not seem to reveal the real pattern. Seasonal values could instead be used for identifying selection. Further, due to the relative nature of the measure that I used, fruits were given a high relative productivity value and insects a very low relative productivity value, despite the insects not having had a low absolute productivity. Similarly, relative consumption values too can be misleading when they are used to compare between food groups. Thus, the relative measures resulted in an overall selection for insects and non-selection for fruits. An absolute measure of consumption and productivity would reveal the true relationship. However, an absolute measure of consumption is difficult to obtain for sloth bears.

The measure of preference that I used is also handicapped by the relative measures of consumption and productivity. However, preference was definitely shown towards insects in February, when fruits such as *Z. oenoplia* were produced, but the diet was composed almost entirely of insects. *Z. oenoplia* is least preferred among fruits and was perhaps not preferred compared to insects too. Similarly, in September, when *L. camara* fruits were available in large amounts, insects were preferentially consumed, although the absolute insect abundance was also probably high during that month. The apparent preference for insects during certain months may be due to their abundance in those months, and the consequent optimal foraging choice by bears, and not necessarily a real preference for insects over fruits in those months. American black bears and brown/grizzly bears fed on insects generally when fruits or other high quality foods were not available (Noyce *et al.* 1997, Swenson *et al.* 1999a, Mattson 2001). However, some bear populations also fed on insects somewhat consistently to obtain protein and other nutrients (Rode and Robbins 2000).

Sloth bears may have consumed plentiful fruits, but how much of it had been digested and efficiently converted to tissue is a further question. I observed that the fruits were often not digested fully and a lot of pulp was voided in faeces. This means that although the bears were feeding abundantly on fruits, they may not have got all the energy from it. The importance of various food-groups to sloth bear ultimately depends on how much of energy derived from each gets translated to new body tissues. Metabolizable energy from berries was calculated to be about 60% in American black and grizzly bears (Pritchard and Robbins 1990). This measure probably is higher for insects, in which case the relative importance of insects to sloth bears would increase.

Why consistently feed on insects? Mixed-diet strategy or patchiness of fruit plants?

Feeding on a mixed diet has been considered a strategy of fruit-eating animals to reduce the increased maintenance energy requirement, and the consequent need for increased dietary intake that happens when on fruit-only diet (Rode and Robbins 2000). I examined if the mixed diet of sloth bears observed in this study conformed to this strategy. During the fruit productivity peaks, e.g., in April, May and November (Fig. 7.11), although the bears could have obtained all their energy from fruits, they still fed on a considerable amount of insects (Fig. 7.4). This supplementary feeding on insects and a consistent relative consumption of a minimum of about 15 to 20% insects each month by sloth bears suggests that they may be adopting a mixed diet strategy, as has been proposed for North American bears (Rode and Robbins 2000). Alternatively, it may be to obtain the minimum requirements of protein that is necessary for growth (Robbins 1993, Welch *et al.* 1997, Witmer 1998), or to get essential amino acids. For, adult bears, however, the protein requirement for growth may not be high (Robbins 1993). North American bears that have fruit as a dominant seasonal food have been reported to include about 13% protein in their diet and thus seem to have followed a mixed diet strategy (Rode and Robbins 2000). Most frugivorous birds, except a few highly specialised ones, consume insects along with fruits, at least during some part of their life (Izhaki and Safriel 1989). Some frugivorous primates too supplement their fruit diet with insects (Williamson *et al.* 1990).

An alternative explanation for the behaviour of consistent feeding on insects even during fruit abundance could be that for a part of the bear population in the study area, fruits may not have been available in greater abundance than insects within their home ranges, because of spatially patchy distribution of fruit plants. Hence, the bears that had their home ranges in areas with low fruit abundance (such as in degraded habitats, see Chapter 6: Space Use and Habitat Selection), or where fruiting had seasonally failed might have foraged considerably on insects in fruiting seasons. Studying food habits of individual bears and relating it to fruit and insect productivity within their home ranges could detect such differences in individual resource use. However, with the method of studying food habits by faecal analysis, which I followed, only the food habits of the population could be evaluated. Further, even for individual bears, availability of fruit would vary on a daily basis within the fruiting season and spatially within their home ranges. This also might have led to consumption of insects, albeit less frequent, by bears during fruiting seasons. However, daily foraging patterns of bears shown by the heterogeneity of food items in individual scats, and the observations on some foraging bears indicated that the bears fed on insects even when fruits were available to them in their daily ranges. This points to a purposeful, rather than random, feeding on insects.

Are sloth bears obligate myrmecophages or mere omnivores?

Sloth bears in Panna exhibited optimal foraging behaviour, i.e., they tended to maximise the rate of energy intake by foraging on resources that resulted in a reduction in search and handling times and enhanced the nutritional benefits. The traits selected by them in the fruit and insect species they fed indicated that they exercised optimal food choice. The bears also foraged on some infrequent resources when they were available in large biomass per food-patch. The primary strategy seems to be that they attempted to spend minimal energy in foraging for low-energy food such as fruits and insects. Foraging theory dictates that the decisions about prey choice and when to eat a prey should be based on the costs of obtaining a food resource compared to the nutritional benefits that the food provides (Krebs and Davies 1993). Sloth bears appear to follow these principles. Although, omnivory can be, in general, considered optimal feeding (Schoener 1971), the diet composition would be determined by relative availability of different kinds of food. There are also other constraining factors such as competition and predation risk that would restrict the diet of an omnivore (reviewed in Sih 1992, Krebs and Davies 1993). Studies on feeding behaviour of omnivores, along with estimation of productivity of various diet components are rare. In my search of the literature, I have not come across any work that investigated whether any other omnivorous bear species exhibited optimal foraging or food choice.

Sloth bears feed primarily on two types of food, fruits and social insects – both are relatively abundant and easily accessible. It would be cost-effective for the large bodied sloth bears to feed on such abundant resources and this would also make them an energy conserving omnivore. Foraging on fruits is probably done more for the quick energy from sugar and the efficient conversion of it to fat (McDonald *et al.* 1981, Rode and Robbins 2000, C. T. Robbins, *personal communications*). As compared to insects, fruits would also require low foraging costs. Foraging on social insects is probably done for nutritional benefits (to get essential protein and other nutrients). There would be energy benefits too, in the seasons when insects are abundant, and in the habitats where insect availability is high. Further, in habitats where fruit availability is low, or the seasonal and annual variability in fruit availability is high, insects could be a dependable resource. Many of the distinctive physical characteristics of sloth bears (i.e., long and naked muzzle, long front claws, short hind legs, absence of upper middle incisors) are related to adaptations for feeding on social insects (Laurie and Seidensticker 1977). This suggests that the social insects have been a critical resource for sloth bears.

The abundance of fruit and insect resources that sloth bears fed on varied seasonally and the relative composition of diet varied accordingly. On the whole, fruits contributed more to bear diet than insects and this corresponded with their higher relative productivity in forest habitats. Fruits are probably the most abundant food resource in forests, after foliage. A large proportion of trees in tropical forests produce fleshy fruits (Howe and Smallwood 1982), and these fruits could sustain many frugivores. Insects were consumed by sloth bears more during the periods when they were abundant or when fruits were not available. The only paradoxical pattern that was observed is the consumption of considerable amount of insects during the periods when fruits were probably abundant enough to constitute the entire diet. This consistent feeding on insects could be because of a mixed diet strategy, which might offset the disadvantages of a fruit-only diet (Rode and Robbins 2000). The required protein could potentially be obtained by sloth bears from resources other than social insects. However, they probably feed on these social insects because of their widespread distribution, abundance and population stability (Wilson 1971). These factors ensure a reliable resource for bears. In addition, the myrmecophagous niche is without much competition in its range. Sloth bears seldom feed on carrion (a high-energy resource and a possible source of protein), probably because of the risk of predation by sympatric predators, tiger and leopard, which generally guard their kills (Laurie and Seidensticker 1977). There could also be competition for carcasses from efficient scavengers such as the striped hyaena and wild pig. Carcasses also decay rapidly in tropical conditions.

Frequencies of occurrence of food-groups in scats indicated that ants and termites were found in similar frequency to fruits (Fig. 7.12). Although the insects were eaten in lower quantities than fruits, they were foraged on frequently by bears. This points to the omnivorous foraging disposition of sloth bears rather than the biomass contribution of these insects to their diet.

Alternatively, it is an indication of qualitative as opposed to quantitative importance of these insects to sloth bear diet.

In summary, data on foraging behaviour and food habits of sloth bears in Panna suggest that they are omnivores with adaptations for myrmecophagy, rather than obligate myrmecophages. However, they obtained necessary nutrients from social insects alone and hence can be classified as “facultative myrmecophages”. Other omnivorous bear species obtain protein from several resources such as ants, termites, wasps, moths, small and large mammals and carrion (Landers *et al.* 1979, Hellgren and Vaughan 1988, Mattson *et al.* 1991, Schwartz and Franzmann 1991, Craighead *et al.* 1995, Noyce *et al.* 1997, White *et al.* 1998, Swenson *et al.* 1999a, Mattson 2001, 2002). Sloth bear is the only bear species that is almost entirely dependent on social insects for its protein requirements and in this respect, is unique among bears.

Relative contributions of fruits and insects to seasonal and annual diet varied among populations and habitat types (Table 7.15). Of the ten studies compared, all except two, (one from an alluvial grassland habitat (Joshi *et al.* 1997) and another from a study during non-fruiting season (Gokula *et al.* 1995)), the relative contribution of fruits was higher or about the same as insects. The sloth bears fed mostly on fruits in fruiting seasons and on insects in non-fruiting seasons. They included some insects in diet even during the fruiting season (Baskaran 1990). Where fruits were low in abundance, they fed more on insects (Joshi *et al.* 1997). These results indicate that most sloth bear populations exhibited feeding behaviour similar to Panna sloth bears (although food habits of bears in somewhat ‘extreme’ habitats – wet evergreen forest and scrubland have not yet been studied). This concurrence supports the proposition that they are, in general, omnivores, but with a facultative dependence on social insects. Thus, the proximate factor that determines their feeding behaviour appears to be the relative availability of different kinds of food, over time and space, and the additional need for essential nutrients.

The evolutionary question of what made the sloth bear adapt to the myrmecophagous niche leads me to speculate. The monsoon driven, seasonal tropical habitats (with marked seasonality in fruit and insect abundance) of the Indian subcontinent may have played a role in their seasonal dependence on social insects. The morphological characteristics for myrmecophagy in the sloth bear probably evolved under the influence of the following factors: the need to obtain an alternative food (that is abundant and with few competitors) in the seasons when fruits were not available; to obtain protein and other nutrients from social insects; to survive in habitats with abundant insects or with few fruiting plants; to deal with seasonal and annual failure in fruiting; and to harvest insect colonies having large biomass. The same selective pressures, in addition to the sympatric large carnivores (Laurie and Seidensticker 1977), could have even led to the evolution of this species within the limits of the seasonal tropics.

7.5. SUMMARY

- Keeping with its *Ursid* lineage, the sloth bear is expected to be an omnivore. However, its characteristic physical and physiological features indicate an adaptation to myrmecophagous (feeding on ants and termites) niche. In this study, I attempted to answer if the sloth bear is an obligate myrmecophage or just an omnivore with a diet including insects.
- I studied the food habits and foraging behaviour of sloth bears in Panna National Park, by observing radio-collared and other bears and by estimating diet composition from faecal remains. I further examined if seasonal changes in diet followed seasonal changes in food productivity.
- Sloth bear scats were collected fortnightly from about 100 km of jungle trails that were uniformly spaced over the study area. I estimated diet composition at monthly, seasonal and annual levels. I converted relative frequency of scat remains into relative ingested biomass contributed by each food item to diet, and as a further extension, the total energy (in calories) contributed by each food item was estimated.
- I assessed if the bears selected for certain taxa, and specific traits in the fruits and insects they foraged. In addition, I assessed if they showed a preference for some food, and if the preference was related to foraging costs or nutritional quality. Selection for a food taxa was assessed based on its relative contribution to diet and relative productivity in the habitat. Preference for a taxa was relative to other food. Selection for traits was assessed based on a comparison of traits of taxa that were consumed by bears and that were not.
- In addition, I developed a method of faecal analysis for studying food habits of sloth bears that could be a potential standard method.
- Sloth bears were observed foraging primarily during crepuscular periods and at night. The relative frequencies of foraging on three main food-groups (fruits, ants and termites) changed with seasons. During the dry season, most foraging was on fruits, and in the wet and cold seasons, it was about equally divided between fruits and ants.
- About 44% of all scats contained one food-group and another 37% were made up of two food-groups. About 25% of scats were composed wholly of one food-taxon, mostly of one of four species of fruits. Sloth bears foraged frequently on two or more food groups or three or more food taxa

in a day. This suggests that bears were omnivorous within a day, less so when fruits were abundant and more so when insects were the main food.

- The bears foraged frequently on a single, abundant resource during seasons of abundance, and otherwise foraged on multiple resources. When the bears foraged on one food-group in a day, it was predominantly on a food that was available in large biomass (fruit), and if on multiple food-groups in a day, it was on resources that were available in small biomass (e.g., termites).
- Fruits contributed 56%, ants 29%, termites 10% and other food 4% to the annual diet (in terms of ingested biomass) of sloth bears in Panna. Fruits contributed 75% of the diet during dry, 37% in wet, and 52% in cold season. Ants and termites together contributed 54% and 46% of the diet, during the wet and cold seasons, respectively. The relative contribution to annual diet in terms of energy was similar to ingested biomass.
- Among the fruits, *D. melanoxylon* was the highest contributor, followed by *Z. mauritiana*. Of the insects, *Camponotus* spp. ants made the greatest contribution to diet, followed by *D. labiatus* ant. Termites contributed a smaller, but consistent portion (about 10% to 25%) to the diet during most months. Fruits and ants complemented each other and together contributed from 70% to over 95% of the diet in all months.
- Monthly relative consumption of main fruit species was positively correlated with its fruiting phenology and relative biomass productivity. A fruit species was consumed more than others when a greater percent of its population was fruiting, and its relative productivity was more than others.
- The relative consumption of various fruit species was not in concordance with their relative productivity, for all months and annually. Some fruit species were consumed disproportionately more or less than their productivity in any month.
- Fruits of *D. melanoxylon* contributed 22% of ingested biomass to the annual diet, although it accounted for only 10% of relative fruit productivity in the area. Similarly, fruits of *Z. mauritiana* contributed about 11% to the diet despite it having formed only 2% of the fruit produced.
- Overall, a relationship between relative biomass contribution of various fruit species to annual diet and their relative productivity was not observed. This indicated selection by bears among the fruits. *D. melanoxylon*, *Z.*

mauritiana and *C. fistula* fruits were selected, as they were consumed in a higher proportion to their productivity. *A. marmelos, B. lanzan,* and *L. camara* were consumed in accordance with their productivity (random usage), and *Z. oenoplia* and *M. longifolia* were not selected.

- *Z. mauritiana* was the most preferred species, for it has a higher importance as a diet component despite having a lower productivity, followed by *D. melanoxylon*, and *C. fistula*.
- Among the insects, *C. compressus* ant contributed 13% of ingested biomass to annual diet, and it formed about 50% of the prey-insect biomass productivity, but only 0.4% of the total food (fruits and insects) productivity. Termites (mainly *Odontotermes spp.*) contributed about 10% ingested biomass to annual diet and they formed about 28% of the prey-insect productivity (0.22% of total food).
- All the five main insect species/taxa for which productivity was measured were consumed in the order of their relative productivity. This indicated that the bears fed on insects in proportion to their abundance. Although there was selection for prey insects from the ones available in the habitat, there seems to be no preference for any prey insect over the others.
- Plant abundance, dispersion, fruiting length, fruit bite-size, fruit presentation, and ripe fruit taste are the plant traits that were selected by bears. Most food-plant species were common, patchily distributed, had longer fruiting seasons, large fruits or clustered fruits that offered large bite-sizes, and had sweet-tasting fruits. All these selected traits suggested that the sloth bears in Panna made optimal food choice.
- As the energy values of (food-plant) fruits were similar, the selection of species appears to have been influenced by the other factors of optimal food choice, namely, search and handling times.
- Colony abundance, colony size, and colony biomass size were the traits selected by bears in insect prey. Most prey species were common, had large colonies, and large colony biomass. The selection of these traits by bears again indicated their choices for lower search and handling times and higher intake rates.
- The abundance of fruit and insect resources that the sloth bears fed on varied seasonally. Accordingly, the costs and benefits of foraging on

those resources changed over time. The bears followed these changes and foraged optimally by changing their food choices seasonally.

- On the whole, the sloth bears in Panna exhibited optimal foraging behaviour, i.e., they foraged on resources that appeared to have maximised the rate of energy intake. Their main foraging strategies appear to be to decrease 'search-time' by feeding on abundant and patchily distributed resources; to reduce 'handling time' by feeding on resources such as clustered or fallen fruits and on insects that were available close to surface and that had weak defence; if feeding on insects involved digging, then to minimise handling time per unit biomass by digging for colonies with large biomass.
- The bears fed preferentially on fruits when they were available and on insects either when they were abundant or when fruits were not available. However, they consistently fed on a considerable amount of insects even when fruits were abundant. This consistent feeding on insects suggests that they may be adopting a mixed diet strategy (Rode and Robbins 2000). Or, this may be to obtain the minimum requirements of protein that is necessary for growth, or to get essential amino acids.
- Foraging behaviour and food habits of sloth bears in Panna suggest that they are omnivores with adaptations for myrmecophagy, rather than obligate myrmecophages. However, they obtained necessary nutrients from social insects alone and hence can be classified as "facultative myrmecophages". Sloth bear is the only bear species that is almost entirely dependent on social insects for its protein requirements and in this respect, is unique among bears.
- Relative contributions of fruits and insects to seasonal and annual diet of sloth bears varied among populations and habitat types. Out of 10 studies on sloth bear food habits, conducted primarily in moist or dry deciduous forests, except for two (one in non-fruiting season, and another in grassland dominated habitat), the relative contribution of fruits was higher than or about the same as insects.

CHAPTER 8. SLOTH BEAR CONFLICT WITH HUMANS

8.1. INTRODUCTION

An important factor affecting the behaviour of wild animals living in human-use landscapes is the extent of human activity in their habitats. Animals react to humans in several different ways and the responses vary under varying conditions (Whittaker and Knight 1998). The responses may depend on the animal's instincts, cognitive and learning abilities, its experiences in past interactions with humans, and the level of cultural transmission of learned behaviour in the species. In general, the response is avoidance, and this may be due to the aversive stimulus (humans) itself or, frequently, to the aversive consequences associated with humans. The human – animal interactions mostly manifest as conflict rather than being compatible. Conflict resolution influences the survival of a species in a fundamental way and therefore has crucial conservation implications. Wildlife management itself, frequently, is about managing these conflicts at various levels. The study of an animal's behavioural ecology cannot be complete without dealing with the question of how that animal interacts with humans, why it reacts the way it does, and what factors lead to such interactions. With this premise, I studied the conflict between sloth bears and humans in Panna NP and assessed the patterns and underlying factors.

There are different kinds of conflicts between humans and bears and these occur at different scales. The impact of such conflict can be either on bears, caused by humans directly or indirectly, or can be a direct impact on humans caused by bears. Indirect impacts on bears caused by humans are chiefly through destruction or modification of habitat. Fragmentation of forests, degradation of habitat through over-use by humans, fire-damage and destruction of essential micro-habitats such as den sites, constitute conscious destruction. In contrast, modifying or manipulating the habitat as a wildlife management measure, with an objective of resource extraction or improving conditions for some other species, either without regard to the habitat needs of the bear or giving it a lower priority, constitute unintended destruction of habitat.

Direct impact on bears caused by humans include, mortality and injury through hunting, poaching for trade, persecution killing, road accidents, to name a few. (Herrero 1970, Mills and Servheen 1994, Mattson *et al.* 1996, McLellan *et al.* 1999, Mattson and Merrill 2002). Humans may also harvest food resources of bears and thus cause a reduction in the food available to bears. Additionally, human activity in bear habitat causes modifications in the various aspects of bear behaviour; for example, a shift in activity (McLellan and Shackleton 1988, Gibeau *et al.* 2002), displacement from important habitats (McLellan and Shackleton 1988, Mace and Waller 1996, Olson *et al.* 1997, White *et al.* 1999, Gibeau *et al.* 2002) and reduced feeding (White *et al.* 1999). Bear impact on humans include physical attack on humans during “encounters” or by “pursuit” (Herrero 1970, 1985, Laurie and Seidensticker 1977, Baptiste *et al.* 1979, Garshelis *et al.* 1999, Swenson *et al.* 1999b), attacks on livestock (Peyton 1980, Johnson and Griffel 1982), crop depredation (Laurie and Seidensticker 1977, Peyton 1980, Rajpurohit and Krausman 2000), other property damage, and the nuisance created by some bears such as the ones attracted to human-generated food (Pelton *et al.* 1976, Baptiste *et al.* 1979, Gniadek and Kendall 1998).

Indirect impacts on sloth bears caused by humans (such as fragmentation of habitat, modification of habitat due to management actions) needs to be studied at a scale beyond the scope of this study. Direct impacts of human activity on sloth bear behaviour, namely, on activity patterns, habitat use and food habits (competition for food) has been discussed in earlier chapters (Chapters 5, 6, and 7). It was not possible to get reliable data on human-caused mortality or injury to sloth bears in the study area and so this could not be dealt with here. Livestock killing (I could not find any report implicating the sloth bear of livestock killing, anywhere in its range), crop damage, and nuisance bear problems did not exist in the study area. “Pursuit attack” on humans was not reported in the study area and is rare elsewhere (one instance was reported by Dunbar-Brander 1923 and another area, where such attacks were probably occurring was reported by Murthy and Sankar

1995). Therefore, the main aspect that is addressed in this chapter is the "encounter attack" by sloth bears on humans.

Sloth bear attacks on humans are reported frequently and attacks occur throughout the sloth bear range, where humans live close to bear habitats (Laurie and Seidensticker 1977, Iswariah 1984, Krishnaraju *et al.* 1987, Gopal 1991, Garshelis *et al.* 1999, Rajpurohit and Krausman 2000, Yoganand *et al*. in press). The encounters and resultant attacks have been happening in the wild habitats in India for at least two millennia. References to the sloth bear behaviour, the danger of suddenly encountering a bear and the fear that humans had for bears, are many in the ancient Tamil literature of southern India, dating from 2nd century B.C. to 5th century A.D. (Samy 1970). The human fear of bears that probably has developed due to historical interactions and instances of fierce attacks by bears has translated into several beliefs, exaggerated stories and myths about bears. Such references have been traditionally propagated and still abound in Indian literature and popular beliefs.

In the modern times, sloth bear attacks on people during the 19th and early 20th centuries have been reported by sportsmen and naturalists (Dunbar-Brander 1923, Champion 1934, Phythian-Adams 1950, Gee 1964, Prater 1965). On the other hand, humans have persecuted, caused mortality and injury to bears all along. Sport hunting of sloth bears and persecution killings because of fear of the bears have happened frequently in several parts of India (Dunbar-Brander 1923, Phythain-Adams 1950, Rangarajan 1996, 2001). The long history of conflicts and subsequent adverse impacts on each other have probably caused behavioural modifications in both bears and humans. From this perspective, it is even more interesting to study the behavioural ecology of the conflict.

Although there have been reports of sloth bear attacks all along, the reasons for such attacks were not critically examined and further, unverified assumptions and false beliefs have mostly been propagated on this subject. The commonest reason that has been given to explain the attacks is that the sloth bear is dangerous and unpredictable (Bargali *et al.* 1999, Rajpurohit and Krausman 2000). Chauhan *et al.* (1999) even commented that the sloth bear is a fearless animal not afraid of any species including humans. The “unpredictability” hypothesis has been traditionally used and without much change either. However, one of the original proponents, Dunbar-Brander (1923), has then qualified it by observing that the bears are unpredictable when encountered suddenly and then they mostly attack. Untested beliefs such as poor sight and hearing in sloth bears were also proposed and the bears were said to become aware of humans only when approached very closely (Chauhan *et al.* 1999, Rajpurohit and Krausman 2000). However, these authors did not consider other factors such as poor visibility in the habitat that might be favouring sudden encounters. Broad assertions or unsubstantiated explanations for attacks, such as human entry into sloth bear habitat and sloth bear entry into crop fields, human harvest of sloth bear forage, camping in sloth bear habitat (Rajpurohit and Krausman 2000), reduction in food availability and presence of new-born cubs (Chauhan *et al.* 1999) were also made. These claims have been speculative and have not identified the causal factors clearly.

In contrast, studies on other bear species had focussed questions and critical analysis on the reasons for conflicts and consequently helped improve management of the problem. Three types of human activity in wildlife habitats, wildlife viewing, camping and hiking have been identified as main activities during bear attacks in North America and surprise encounters caused many grizzly bear attacks on hikers (Herrero 1970, 1985). McLellan and Shackleton (1989) reported that bears may react more strongly to people on foot when they were in the open than when in cover. The reactions were also more extreme in low human-use areas as compared to high-use areas (Jope 1985, McLellan and Shackleton 1989). Presence of cubs and surprise encounters comprised most attacks in Glacier National Park (Gniadek and Kendall 1998). Habituated or food-conditioned bears were those most often involved in attacks on people in North America (Herrero and Fleck 1990, Mace and Waller 1996). Mattson (1990) further summarised that the individual and population response of bears to human activity, in North

America, is a function of several factors, including the nature and extent of historical interactions with humans, accessibility of food belonging to people, demographics and size of the bear population, and the distribution of native habitats and foods. Attacks resulting in human injury are very rare among Eurasian brown bears in Europe (Swenson *et al.* 1999b). Wounded bears were involved in a majority of brown bear attacks in Scandinavia and this is considered the only truly dangerous situation. However, presence of cubs, proximity to carcass, or proximity to winter den contributed to an increased level of aggressiveness in bears. Also, the activities of humans prior to attacks would have influenced the chance of encountering bears or the chance of getting injured (Swenson *et al.* 1999b).

Under most circumstances, bears flee upon detecting humans (Herrero 1970, 1985, McLellan and Shackleton 1989, Swenson *et al.* 1999b, *personal observations*). When people presume that the bears attack as a habit, they tend to forget that there are energetic and survival costs associated with attacking humans. The instinctual responses or decisions to attack would mostly be based on the risks and benefits. Therefore only certain set of conditions or stimuli should lead to attacks and it should be possible to predict the conditions, with properly designed studies and analyses. Various hypotheses that were proposed in the past, such as bears being unpredictable, assumed a random probability of encountering them in the forests. Whereas, the probability of encounters would vary over space and time and can be predicted from the behavioural ecology of the bears and the patterns of human use of forests. It may be difficult to predict when the bears attack and how they decide whether to attack or not (which may warrant some dangerous experiments). There may be several factors influencing the bear to act aggressively, which may be too complex to build into a prediction model. A far more practical option is for the humans to avoid certain situations that lead to high probabilities of encountering a bear. As the probability of attacks is likely to be strongly correlated to probability of encounters, an assessment of encounter probability is appropriate for the practical purpose of resolving conflicts. The management implications of detecting the causal factors of attacks and identifying measures to avoid attacks are multiple, including reducing human and bear mortality or injury and gathering local support for conservation.

In this context, I studied the human – sloth bear conflicts in Panna NP, from 1996 to 2000. I describe here the patterns in attack incidents, relevant aspects of sloth bear activity, habitat use and patterns of human use of the forests. I further test certain working hypotheses on the likely ecological and behavioural conditions leading to attacks, which I developed based on preliminary observations on the behaviour of sloth bears in Panna NP and the literature from similar studies elsewhere.

My working hypotheses are:

1. The attacks do not randomly occur within the forest. Certain habitat types, either with poor visibility or which the bears and humans use at the same time would have more attacks.
2. The attacks would be more frequent during certain times of the day, either when bears and humans use the same habitat concurrently or when the activities of bears and humans overlap.
3. The attacks would be more frequent in certain months or seasons of the year, when the human-use of bear habitat is greater or the period of overlap of human and bear activities is longer.
4. Daytime attacks would be more common in habitats where bears frequently rested during daytime.

8.2. METHODS

Bear-human encounter records

I surveyed 35 villages located in and around my study area in Panna National Park to study frequencies of sloth bear – human encounters, encounter locations and other associated parameters. In addition, I examined the records of Panna National Park and other Forest Department offices in Panna District to search for recorded encounters. These records specified the names and places of the people who were injured or killed during encounters with bears and other associated information. I visited the villages and interviewed over 200 people who had close encounters with sloth bears and who use the forest areas intensively for various purposes such as grazing livestock. I gathered information on the date and time of encounters, the kind of habitat, the activity of humans and bears at the time of encounters, number of bears and people involved, (reported) sex and size of the bears, the kind of injuries suffered and the circumstances that led to the encounters. I also gathered information on the local people's perception on this issue.

Encounter location and time characteristics

Most recent encounter locations were visited and location coordinates, habitat and terrain type, vegetation cover, visibility, presence of bear dens, proximity to trails or roads were recorded. For some locations with known landmarks, such information was obtained from topographic and vegetation maps. Date and time of encounters were gathered from interviewing the people involved. For the encounters involving injury, Park records were used to crosscheck the information gathered from interviews. The encounter time characteristics were put into seasonal and diurnal time classes that were used in this study (described in Chapter 4: General Methods).

Encounter type

From the information given by people on the circumstances leading to each encounter and on the activity of bear and people at the time of encounter, I classified the encounters into surprise/abrupt or deliberate encounters.

Surprise/abrupt encounter: An encounter is classified as a surprise/abrupt encounter, when humans and bears involved in the encounter were not aware of each other prior to the encounter and they chanced upon each other suddenly. If a bear attacked in a surprise encounter or a deliberate encounter initiated by human, it was classified as a 'defensive attack'. The attack is categorized as 'offensive' if the bear initiated a deliberate encounter. Sometimes, human fleeing from an encounter invited pursuit by bears. This too was classified as a 'defensive' attack.

Conscious/deliberate encounter: When either the human or the bear were aware of the other prior to the encounter, it is classified as conscious/deliberate encounter. It may happen when a human approached a bear so as to provoke it, harm it or to poach it or its cubs; or when a bear approached a human or a human habitation in search of food or in pursuit of a human. Other potential circumstances that may lead to a deliberate encounter such as, sport-hunting, wildlife feeding, close-range viewing or photographing, camping or hiking in bear habitats, habituation to humans, attraction to garbage food, etc. that are common in North American conditions (Herrero 1970, 1985, Baptiste *et al.* 1979, Jope 1985, Gniadek and Kendall 1998) seldom occurs in the range of the sloth bear.

Activity pattern and habitat use of bears

I gathered data on sloth bear activity (>10,000 activity logs), home ranges and habitat use by radio tracking (9 bears; >4,000 radio relocations in all) and other observations (see methods in Chapters 5: Activity Patterns, and Chapter 6: Space Use and Habitat Selection). Activity logs and habitat use data from the radio-collared bears were pooled to describe the overall diurnal, monthly and seasonal activity and habitat use of bears. Bears in the study area generally rested during mid-day, more or less in all seasons. Their resting locations were recorded by homing in or by triangulation, and the resting sites were grouped into different habitat cover classes: escarpment, knoll/hillock, dense *Lantana* shrub thicket, and other dense cover habitat. Each bear with a functioning radio collar was recorded at its resting site for at least 10 days each month, but usually for over 20 days each month, throughout the study period.

Habitat classes (escarpment, knoll, dense *Lantana*, other dense, and open habitat) of radio relocations were identified based on field observations and using topographic and habitat maps. These classes are somewhat different from the habitat types used in Chapter 6: Space Use and Habitat Selection, which are largely based on vegetation type (structure and density). The habitat classes used in this Chapter (8) included terrain features along with vegetation type, because these were more appropriate to assess the factors influencing conflict between bears and humans. However, both classifications are closely related: 'escarpment' and 'knoll' classes of this Chapter (8) are a major part of 'dense forest' type of the earlier Chapter (6); 'dense *Lantana'* class includes 'dense shrub' and dense patches of *Lantana* within 'open shrub' types; 'other dense' class is a subset of 'dense shrub' type; and 'open habitat' class includes parts of 'open forest', and 'open shrub', and whole of 'open savannah', and 'degraded scrubland' types. A total of 1,540 relocations pooled from all bears were classified this way and used in this Chapter to describe the relative use of different habitats by bears during different times of day and seasons.

Human activity and use of forests

Activity patterns of humans inside the forest and the locations that they used in various times of day and seasons were obtained from observations made during the course of radio tracking and other fieldwork, and by interviewing local people. The knowledge of local people, who assisted me in field work for several years, on the traditional activity and forest spatial usage patterns of humans were also collated. In addition, two Trailmaster® infra-red electronic trail counter units, mounted with camera, were used to monitor roads and trails at night for animal, human and vehicle usage. The units were moved among trails every 2 – 7 days to get coverage of large number of roads/trails spread over the study area. Based on these data, the intensity of human activity in the forests, during each hour of the day in a season was ranked.

The geographical locations of villages, bear-human encounter sites and usage by people were obtained with a GPS unit and from topographic maps. The various human activities and the resulting disturbance to the habitat were assessed at uniformly spaced (2-km interval) locations across the study area (see Chapter 4: General Methods; and Chapter 6: Space Use and Habitat Selection). These data were used to identify the diurnal and seasonal habitat-use patterns of humans in the study area. Each type of human use in each habitat was given a score based on intensity of usage, for each season. The total score for each habitat was used to calculate the relative use of different habitats in each season. Based on the overall intensity of forest usage, human use in each month was given a rank.

Habitat map of the study area

Satellite imageries of the study area were used to map the various habitat types and to delineate human degraded areas (see Chapter 4: General Methods). Habitat attribute data for the various locations and other delimited space (such as grazing range) were obtained from this habitat map.

Sloth bear interactions with conspecifics, predators and humans

Observations on sloth bear interactions with conspecifics, predators and humans were made during radio tracking and other fieldwork. I observed the bears and their interactions primarily from vantage points such as ledges and treetops, from jeeps, or sometimes by following them on foot and by riding elephants. Several encounters between sloth bears and tigers were also observed while observing radio-collared tigers in the study area. Sloth bear and predator mortalities during the study from in and around the study area were examined and the possibilities of any bear-predator interaction prior to mortality were determined from field evidence. Other established records of such mortality were collated from official records.

Observations of encounters between sloth bears and humans, and responses of bears to indications of human activity (noise, artefacts, etc.) were made while observing bears. The several direct interactions that our research team had with bears during the study complemented the observational data. Some of the encounters that we had were surprise encounters, but some were deliberately caused so as to observe the responses of bears. I also observed the responses of bears to human artefacts, scent, noise and other indications related to humans. These were either inadvertently left by us or by deliberately leaving them in the travel paths of bears. Responses of humans to indications of presence of bears in the locality or the prior knowledge of bear presence (provided by us) along their travel route were also recorded. The responses of bears to each other and to predators were used to interpret their responses to humans.

Statistical issues

Frequency data were analysed with contingency tables (Siegel and Castellan 1988, Sokal and Rohlf 1995). When expected frequencies did not meet the chi-square test of independence requirements, classes were combined (where biologically relevant) to form tables of smaller dimension. Since relationships between monthly frequencies of attacks and monthly averages of various explanatory attributes were assessed, and since some relationships may not have been linear, rank correlations were used to test the strength of relationships. An *a priori* type I error rate of 5% ($\alpha=0.05$) was set for all statistical significance tests, unless indicated otherwise.

8.3. RESULTS

Frequency of attacks

Out of the 35 villages surveyed, 30 villages had reports, totalling 80 incidents of bear attacks. Of these, 58 happened between 1981 and 2000, and the rest between 1950 and 1980 (Fig. 8.1). Although there may have been some error in the years reported by respondents and many incidents may have gone unrecorded or forgotten, the data still indicated that there was a minimum of three to four attack incidents each year. Humans injured in attacks had mostly severe (51%) or moderate (46%) level of injuries and only one attack was fatal.

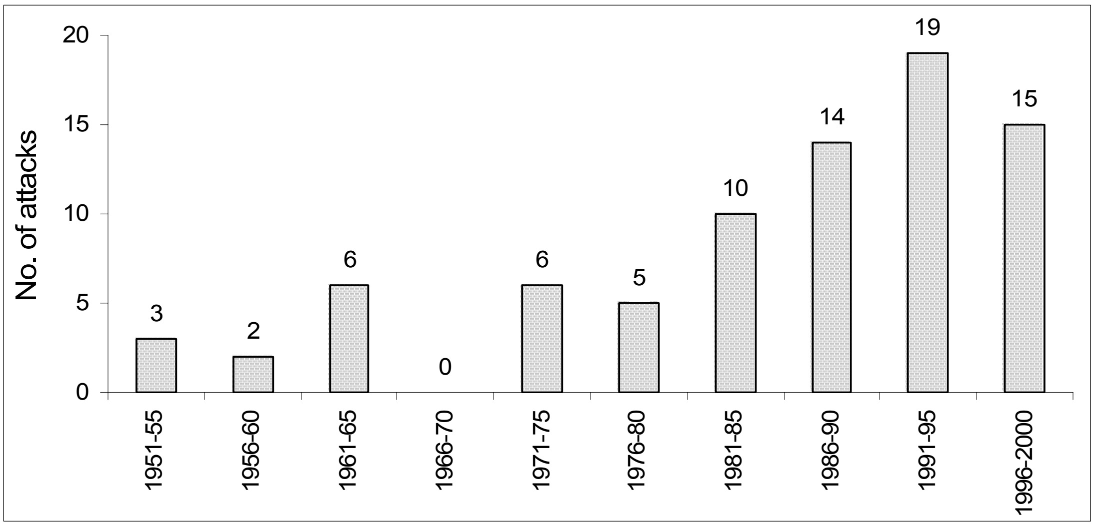


Fig. 8.1. Number of reported sloth bear attacks on humans during the past 50 years in the study area in Panna NP, as gathered by interviews. Fewer attacks in the period 1950 to 1980 does not indicate that the attack frequency has increased after that, rather it indicates that more information on recent incidents is presently available, as many people who lived in the forests in the past have since moved out or many attack incidents have been forgotten.

Bear and human responses

In most encounters bears fled but some times they charged at humans and then either attacked or retreated without making physical contact. The humans also usually fled upon perceiving a bear. If the bear fled in an encounter, then the humans also moved away or if the bear rushed towards or attacked, then they either panicked and passively gave in, or occasionally, held their ground and chased it away or attacked it in return. In summary, the bear response to an encounter with humans was to flee, bluff charge and retreat, or to attack. Human response to an encounter with a bear was to flee, confront or yield.

Type of encounter

All attacks happened when humans encountered bears abruptly in the forests or, in two cases, in the vicinity of villages. Most attack victims reported that they realised the bear's presence only at a close range (when the distance between them often was less than 50 m). Most other humans who were interviewed reported that they too often encountered bears in the forests suddenly. The bears also may have sensed the humans mostly immediately prior to the encounter. There were no incidents of human-habituated bears, bears attracted to human-origin food or to crop fields in the area, nor were there any incidents of bears pursuing and attacking humans. All attacks, therefore, were defensive in nature and none were deliberate. In some cases the bears repeatedly attacked and retreated or pursued the humans for short distances when they fled. However, this too may have rather been a defensive reaction.

Season, time of day and habitat of frequent attacks

Most attacks occurred during cold (41%) or wet (39%) seasons (Fig. 8.2). More than 70% of the attacks happened in the crepuscular period (evenings and mornings), and about half were in the evenings alone. About 25% of the attacks occurred in the day time and only 2 attacks were at night. Forty three percent of the attacks occurred in the escarpment habitat, 30% in *Lantana* shrub patches and another 15% in other habitats having dense vegetation cover (Figs. 8.2, 8.3).

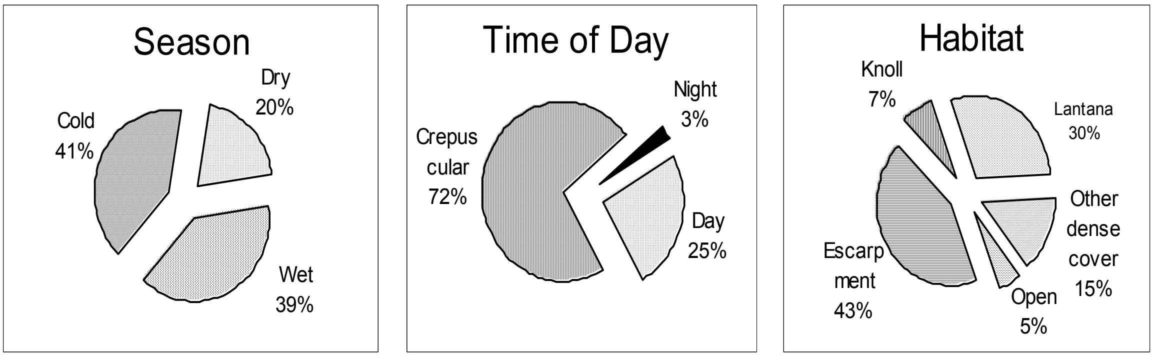


Fig. 8.2. Relative frequencies of sloth bear attacks on humans in Panna NP in different seasons, times of day and habitat types.

About 75% of the dry season and 50% of the cold season attacks happened in the escarpment and knoll habitats, whereas about half of the wet season attacks were in *Lantana* patches (Fig. 8.4). The other half of the cold season attacks were in habitats with dense cover, either having *Lantana* or other vegetation. About 60% of the day time attacks were in escarpment or knoll habitats and another 35% in habitats with dense cover. Two-thirds of the attacks in *Lantana* patches were in the wet season and the rest in cold season. Overall, the majority of the attacks took place in escarpment or other dense vegetation cover habitats, in the crepuscular period of wet and cold seasons. There were more frequent attacks in the wet and cold season months of October, September, December, January and August, decreasing in that order, than other months, although some attacks happened in all the months (Fig. 8.5).

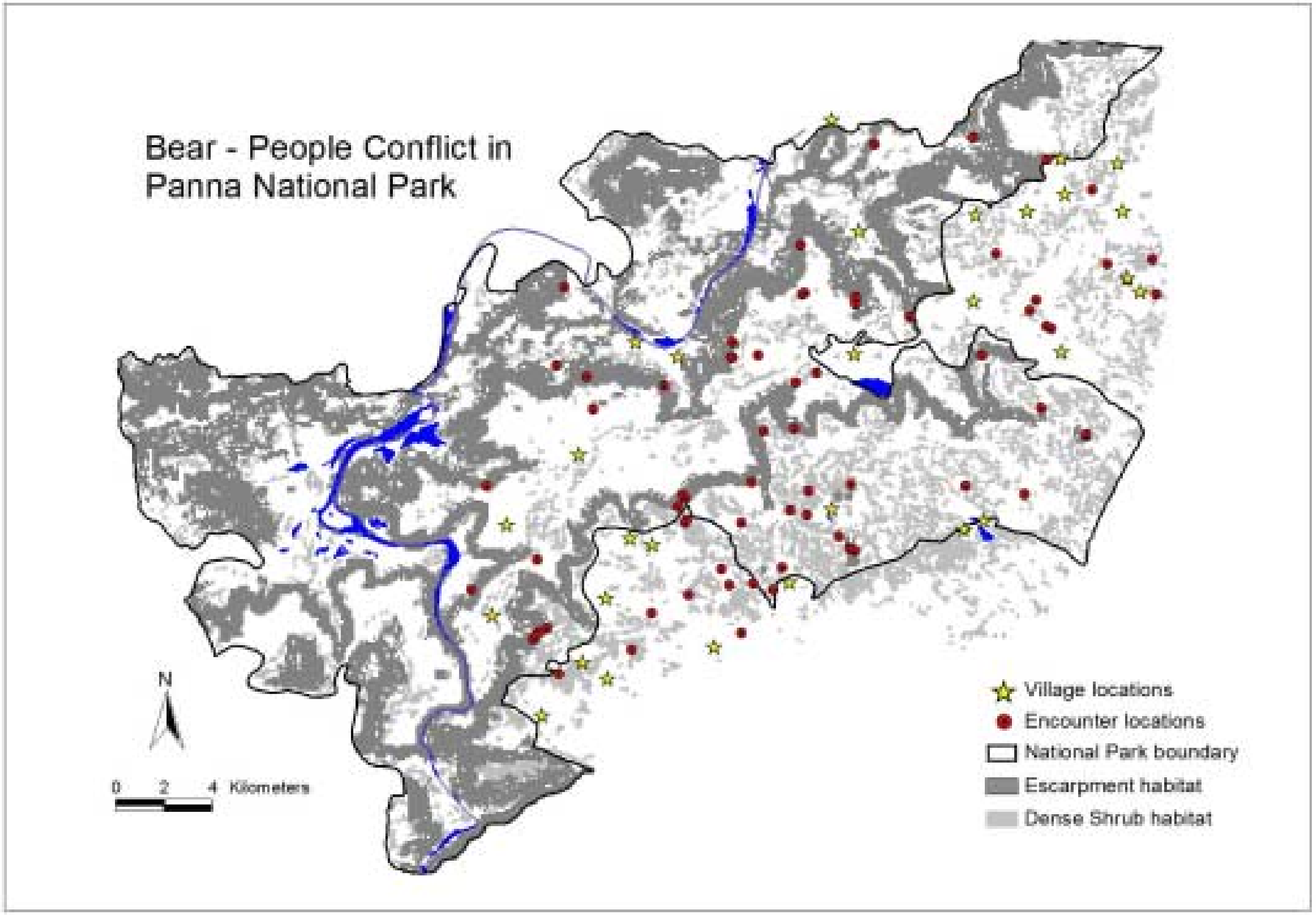


Fig. 8.3. Locations of encounters between humans and sloth bears that resulted in injuries to humans, in Panna National Park and adjoining areas. Most encounters were in escarpment (sloppy terrain with dense forest cover) and dense shrub cover (dominated by *Lantana camara*) habitats.

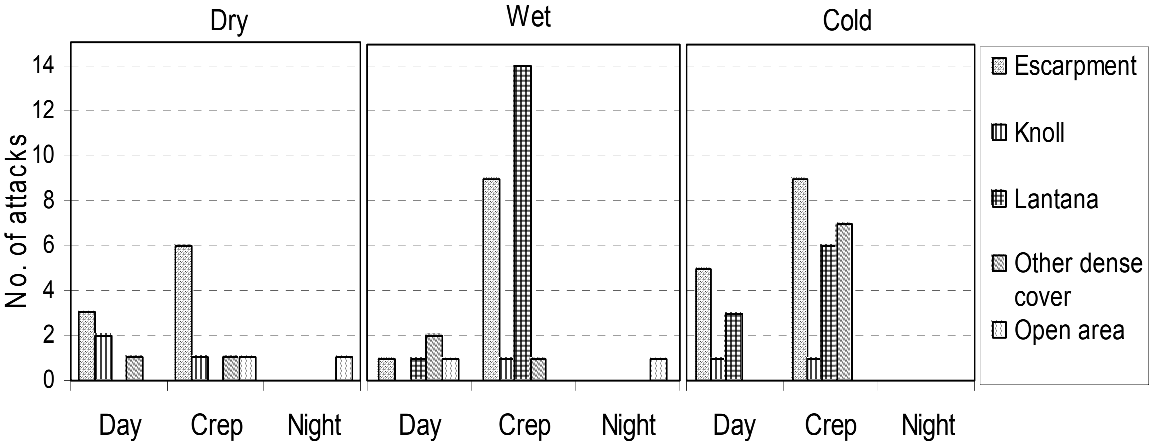


Fig. 8.4. Number of reported sloth bear attacks on humans in Panna NP in different habitats, times of day and seasons.

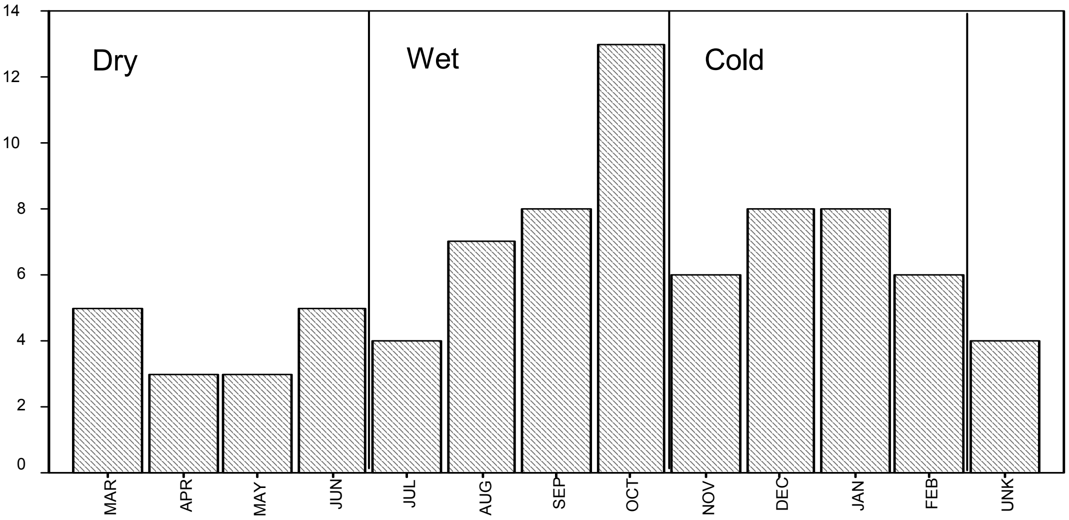


Fig. 8.5. Number of reported sloth bear attacks on humans in Panna NP during different months and seasons. (UNK denotes that the month was not known).

Human and bear activity prior to attack

About 40% of the humans that were attacked were tending cattle in the forests, 30% were collecting minor forest products (MFP, such as edible fruits, honey, fodder, firewood, etc.) and 24% were travelling along footpaths in the forests that connected villages. Attacks on humans tending cattle were disproportionately more in the wet season and less in the dry season, whereas attacks on humans collecting MFP were disproportionately more in the dry season and less in the wet season (Table 8.1). Relative frequency of attacks on humans travelling was in proportion among the seasons. While the attacks on humans engaged in various activities were related to seasons, they did not show any relation to time of day (chi-square tests, α=0.05; Table 8.1). More than 40% of the attacks on humans tending cattle occurred in *Lantana* habitat, whereas a majority of attacks on humans engaged in other activities occurred in the escarpment habitat (Table 8.2). The human attacked was alone during most (86%) of the attacks and in only 9% of the time humans were in pairs and in fewer times they were in groups. Solitary bears were involved in half of the attacks, sows with dependent young were involved in about 30% of the attacks and pairs (of unknown sex and age) in 13% of the attacks (Table 8.3). While attacks involving sow and cubs were disproportionately more in the wet season, attacks involving other cohorts had no apparent relation to season. Also, attacks by different bear cohorts showed no relation to time of day or habitat type or bear activity state (resting or foraging). Bear cohorts involved in attacks or bear activity prior to attacks showed no relation to human activity prior to attacks (Chi-square tests, not significant at α=0.05).

Table 8.1. Number of reported sloth bear attacks on humans engaged in various activities in different seasons and times of day, in Panna NP.

Human activity	Season			Time of day			Total
	Dry	Wet	Cold	Day	Crepus cular	Night	
Cattle tending	2	16	12	7	23	0	30
MFP collection	8	4	12	7	17	0	24
Travelling	3	9	7	5	14	0	19
Other	3	2	1	1	3	2	6
Total	16	31	32	20	57	2	79

Table 8.2. Number of reported sloth bear attacks on humans engaged in various activities in different habitats, in Panna NP.

Human activity	Habitat					Total
	Escarpment	Knoll	*Lantana*	Other dense cover	Open	
Cattle tending	8	4	14	3	1	30
MFP collection	13	1	4	5	1	24
Travelling	10	1	4	4	0	19
Other	2	0	2	0	2	6
Total	33	6	24	12	4	79

Table 8.3. Number of reported sloth bear attacks on humans by different sloth bear sex-age cohorts in different seasons and times of day, in Panna NP.

Bear cohort	Season			Time of day			Total
	Dry	Wet	Cold	Day	Crepuscular	Night	
Solitary	7	13	20	11	27	2	40
Pair	5	2	3	3	7	0	10
Sow and cubs	4	14	6	6	18	0	24
Unknown	0	2	3	0	5	0	5
Total	16	31	32	20	57	2	79

About half the bears were foraging and a little over 40% of the bears were resting prior to encounters that led to attacks. Attacks involving bears resting or foraging was related to season and time of day (chi-square tests, significant at α=0.05). Of the foraging bears, disproportionately more were involved in attacks during the crepuscular period and in the wet season, whereas, of the resting bears disproportionately more were involved in attacks during the day and in the cold season (Table 8.4). Attacks involving resting bears were disproportionately more in escarpment habitat, whereas, in the attacks involving foraging bears, no such relationship with habitat type could be discerned (Table 8.5).

Table 8.4. Number of reported attacks on humans by sloth bears resting or foraging, in different seasons and times of day, in Panna NP.

Bear activity	Season			Time of day			Total
	Dry	Wet	Cold	Day	Crepus cular	Night	
Foraging	6	20	12	2	34	2	38
Resting	8	8	17	16	17	0	33
Unknown	2	3	3	2	6	0	8
Total	16	31	32	20	57	2	79

Table 8.5. Number of reported attacks on humans by sloth bears foraging or resting, in different habitats, in Panna NP.

Bear activity	Habitat					Total
	Escarp-ment	Knoll	*Lantana*	Other dense cover	Open	
Foraging	15	2	14	4	3	38
Resting	17	4	8	3	1	33
Unknown	1	0	2	5	0	8
Total	33	6	24	12	4	79

Effect of village proximity to escarpment

Frequency of attacks in different habitats had a distinctive relationship with the proximity of villages that the humans were from to the escarpment habitat (chi-square =27.01, *df*=3, *P*<0.001). About 60% of the attacks on humans from villages near escarpment (within 2 km) happened in escarpment habitat, whereas about 60% of the attacks on humans from villages far from escarpment happened in *Lantana* habitat and fewer attacks happened in the escarpment habitat (Table 8.6).

Table 8.6. Number of reported sloth bear attacks on humans from villages near or far from escarpments, in different habitats and seasons, in Panna NP.

Village proximity to escarpment	Season	Habitat					Total
		Escarp-ment	Knoll	*Lantana*	Other dense cover	Open	
Near	Cold	11	0	0	6	0	17
	Dry	8	2	0	1	1	12
	Wet	8	0	4	2	1	15
	Total	27	2	4	9	2	44
Far	Cold	3	2	9	1	0	15
	Dry	1	1	0	1	1	4
	Wet	2	1	11	1	1	16
	Total	6	4	20	3	2	35

Human use of forests

There were 15 villages located inside, and about 50 villages located within 5 km of Panna NP. Humans from these villages and even from villages farther away used the forests for various purposes. The main uses included, livestock grazing, collecting MFP, and travelling along footpaths connecting villages. Livestock grazing comprised the bulk of human activity in forests, followed by MFP collection, travelling and others. Some villages had grazing rights over certain areas of the Park and they regularly let the livestock graze in those areas. Some MFP collection had been allowed in the Park in the past and it continued to go on in the forests outside the Park. Inside the Park, collecting MFP was illegal, but the restrictions were not strictly enforced, as the village economy depended considerably on MFP (Plate 14a). Human use of forests for travelling was frequent and it happened throughout the year. However, humans preferred to use shorter routes along footpaths cutting through forests, in the dry and later part of cold seasons when the vegetation was less dense, but preferred broader jungle roads, even if longer, in the wet and early part of cold seasons when the vegetation cover was dense. Although the frequency of usage of footpaths decreased in the seasons of dense vegetation, many humans nevertheless continued to use them.

Livestock grazing in the forests was acute in the wet and early part of the cold season, due to the influx of cattle from villages even far outside the Park.

As the outside cattle left the Park in the later part of cold season, the grazing intensity decreased substantially, but still remained at a considerable level through the dry season. MFP collection was intense in the dry season as several products of importance to local economy, (e.g., *Buchanania lanzan*, *Diospyros melanoxylon* and *Madhuca longifolia* fruits, *M. longifolia* flowers, and *D. melanoxylon* leaves) became available. In the wet season, MFP collection dropped to a low level, with humans collecting mainly grass and browse for fodder. In the cold season, human activity related to MFP collection again increased to a considerable level, as the fruit of *Phyllanthus emblica*, fodder and firewood were collected frequently.

The various major occupations in different seasons took humans to different habitats and this determined their relative use of habitats across seasons. In the dry and cold seasons, open forest and escarpment habitats together comprised over half of the human use areas and further the relative use of habitats was similar in these seasons, except that the dense *Lantana* habitat was used much less frequently in the dry season (Fig. 8.6). In the wet season, dense *Lantana* habitat was used more often and the escarpment was used less. Overall, the intensity of human use of forest was highest in the wet and cold season months of August to December and remained at a moderate level during the rest of the year (Fig. 8.7).

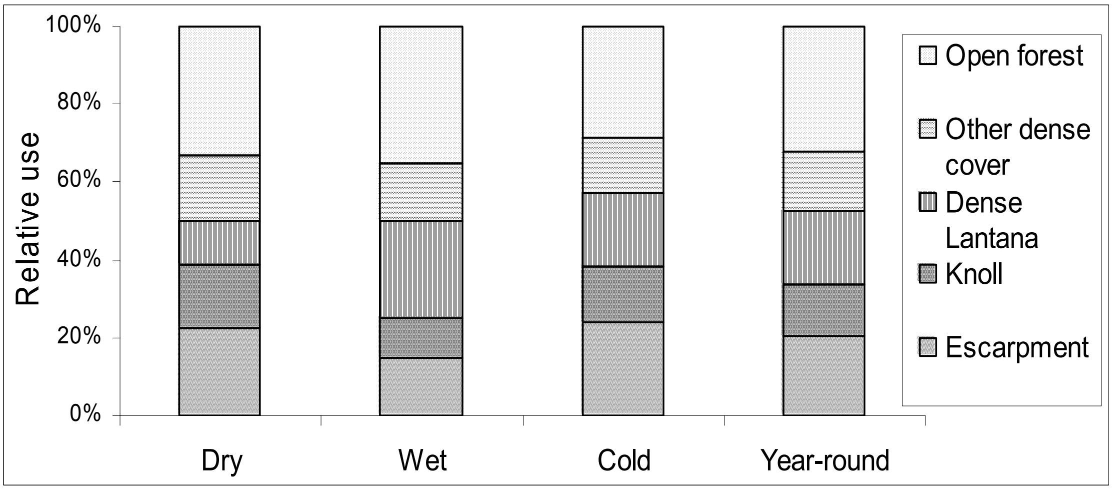


Fig. 8.6. Relative use of different habitats by humans for various purposes in different seasons and annually, in Panna NP.

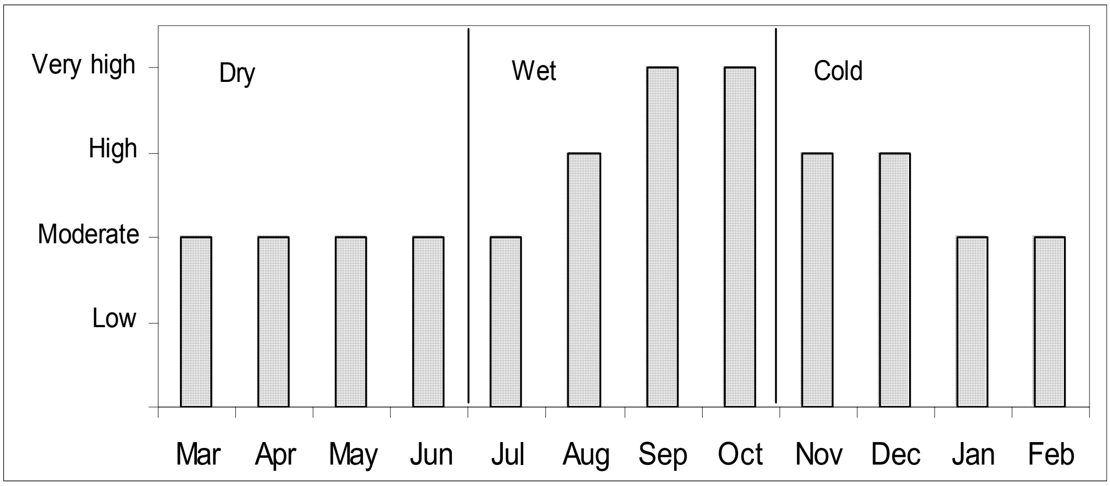


Fig. 8.7. Intensity of human use of forest during different months and seasons, in Panna NP.

Diel activity of humans

Human activity usually started at about 4:00 and went on until about 21:00, with activity peaking in the morning (about 8:00) and in the evening (about 17:00) with a moderate level throughout the mid-day (Fig. 8.8). Activity in the cold season, when the days were shorter, generally started an hour later and ended about an hour earlier as compared to the wet and dry seasons. There was a drop in activity in the extremely hot mid-days in the dry season. Activity related to MFP collection began as early as 3:00 in the dry season, whereas livestock grazing started about two hours later and went on until about 20:00, with a mid-day rest. Humans travelled through forests until even later in the dry season. On the other hand, buffalo grazing started as early as 3:00 in the wet season and the evening grazing extended until 21:00 and sometimes beyond. MFP collection was mostly done in daylight and travelling did not extend late beyond the evening in wet and cold seasons. Overlap in the time of different activities and engagement of more humans in the different activities in mornings and evenings resulted in the activity peaks.

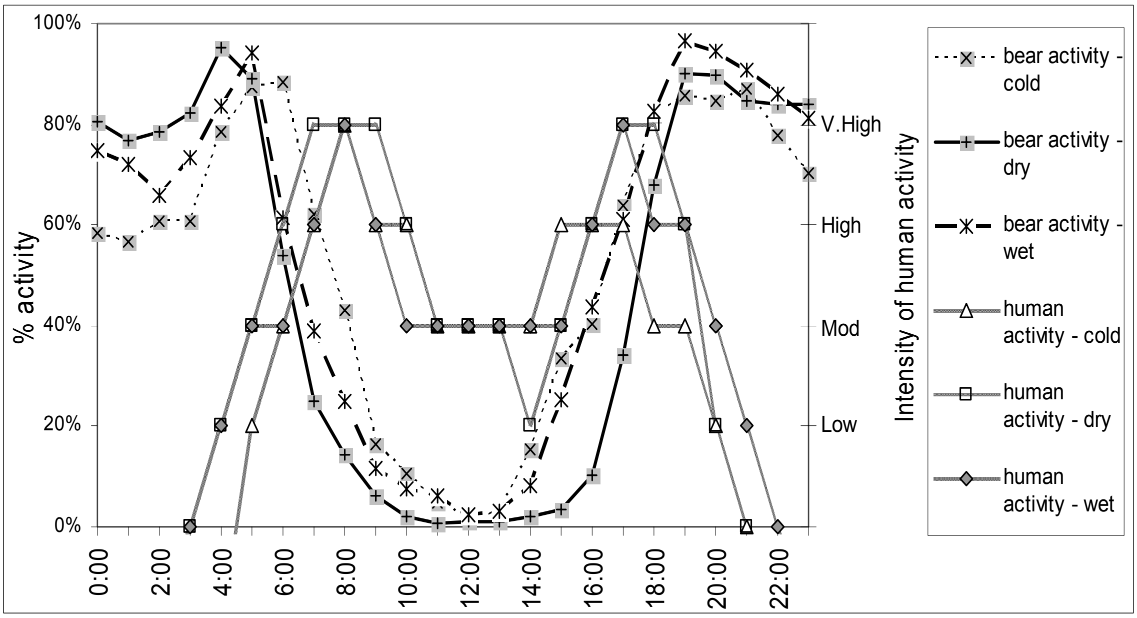


Fig. 8.8. Sloth bear and human diel activity patterns in the forests of Panna NP, in different seasons. The period of overlap of human and bear activities was longer in the evenings than in the mornings in all seasons.

Sloth bear diel activity

Detailed descriptions of diel activity of bears are presented in Chapter 5: Activity Patterns. A summary of it is presented here. Bears were usually active during the crepuscular period and at night, and rested during mid-day. After the mid-day rest, they became active in the late afternoons or evenings, continued their activity through the night and ended by morning (Fig. 8.8). This routine in diel activity was similar in all seasons, although, with some variation. Bears showed >80% activity throughout the night in the dry season, but reduced their activity in the post-midnight, pre-morning hours, in the wet and cold seasons. Considerable daytime activity by bears, particularly in the afternoons, was observed in the wet and cold seasons, whereas the bears rested almost throughout the mid-day in the dry season.

Bears started their activity later and ended it earlier in the dry season than the other two climatic seasons (Chapter 5: Activity Patterns, Figs. 5.11a, b). The earliest activity start and latest activity end was in the cold season. The differences among climatic seasons in both timings were statistically significant (Chapter 5: Activity Patterns, Table 5.2). Wet season activity start time with reference to sunset was much earlier than the other two seasons, whereas the difference between cold and dry seasons was small and not statistically significant. The difference in activity end times between cold and dry seasons too became much smaller after adjusting for sunrise time.

Sloth bear habitat use

Sloth bear habitat use varied with time of day, season and their activity state (see Chapter 6: Space Use and Habitat Selection, for detailed descriptions). During the daytime, bears used escarpment about 75% of the time and dense *Lantana* habitat about 20% of the time, on an annual scale (Fig. 8.9). However, in the daytime of dry season, relative use of escarpment was over 90%, while in the wet season it was only about 50%. Relative use of dense *Lantana* habitat in the daytime was low in the dry season and increased in the wet season. In the crepuscular period, relative use of other dense and open habitats increased, with a corresponding decrease in the relative use of escarpment. At night, when the bears were highly active, they moved away from escarpment and used open habitats such as open forest and open shrub frequently for foraging (also see Chapter 6: Space Use and Habitat Selection).

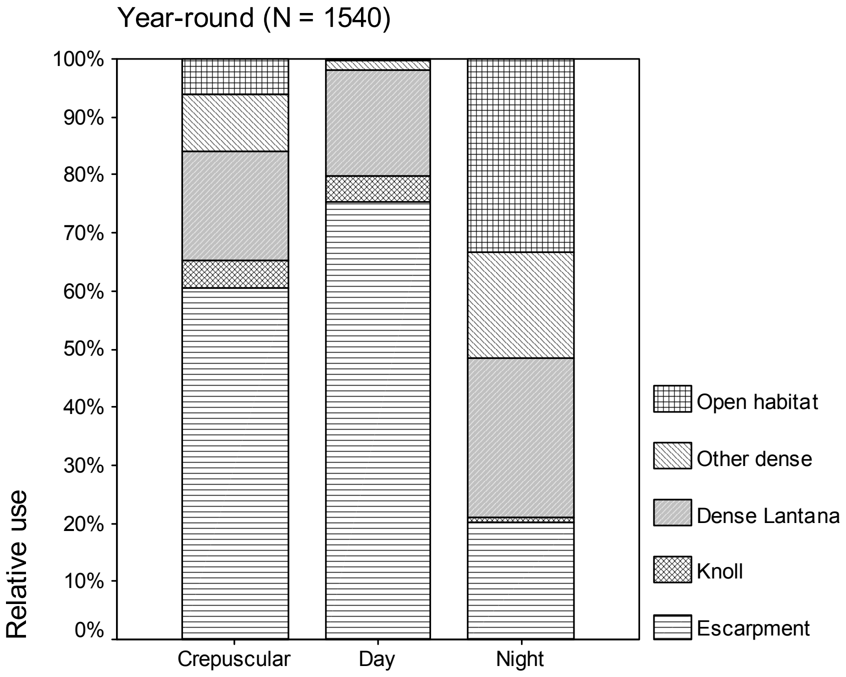


Fig. 8.9. Relative use of different habitats by sloth bears (based on 1,540 relocations pooled among bears) during different times of day.

When the bears were active, their use of escarpment was substantial in the dry and cold seasons, while in the wet season, bears used dense *Lantana* habitat more than any other habitat (Fig. 8.10). Open habitats were used about 20% to 30% of the time when they were active (generally night hours) in all seasons. However, open habitats were seldom used for day-resting. Escarpment with dense vegetation cover, boulders and natural cavities that acted as dens and the dense *Lantana* shrub habitat constituted most of the day-resting habitat of bears in all seasons (Chapter 5: Activity Patterns, Fig. 5.12). In the dry season, escarpment was used over 80% of the time and even in the wet season, it was used about 60% of the time for day-resting. Dense *Lantana* habitat was used as day-resting habitat in over 30% of the time in the wet season and about 15% of the time even in the dry season. Relative usage of dense *Lantana* habitat for day-resting increased from August onwards and reached a peak usage of about 50% in October and then declined to a level below 20% after January (Fig. 8.11). Relative use of escarpment as day-resting habitat correspondingly declined as the wet season progressed and increased as the dry season approached.

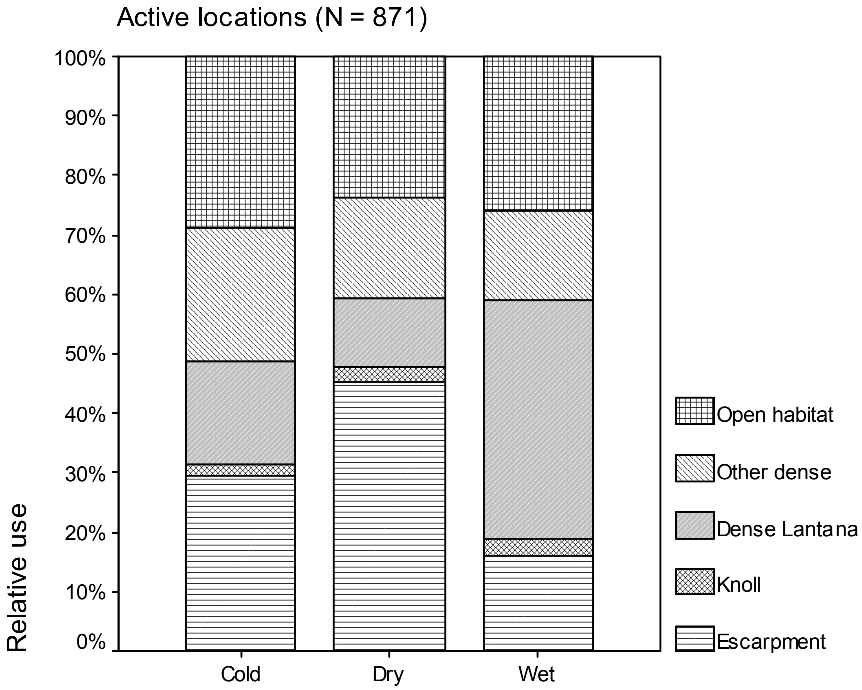


Fig. 8.10. Relative use of different habitats by sloth bears when they were active (based on 871 relocations obtained when bears were active, pooled among bears), in different seasons.

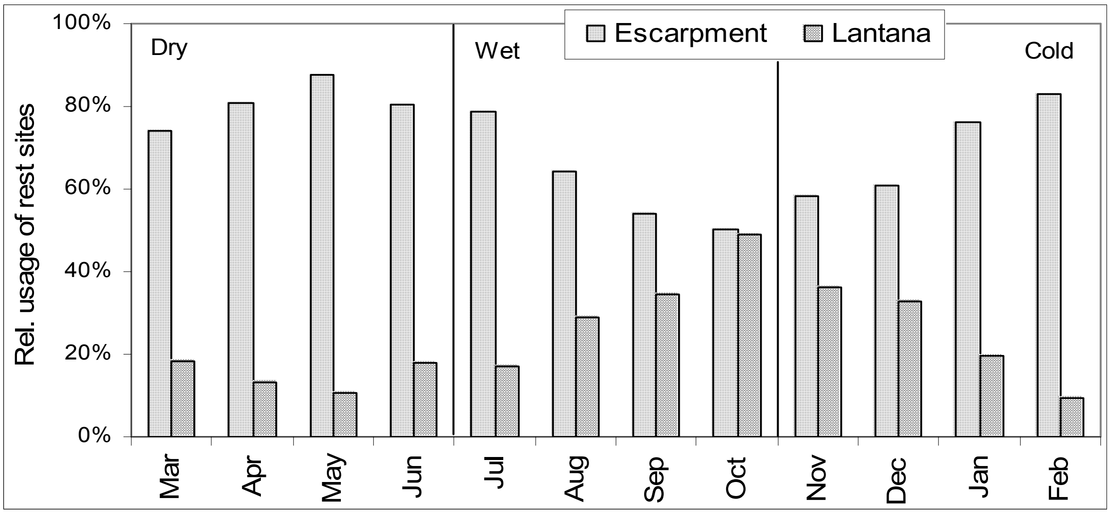


Fig. 8.11. Relative usage of escarpment and dense *Lantana* habitats as day-resting sites by radio-collared sloth bears in Panna NP, in different months and seasons.

Overlap in human and sloth bear activity periods and habitat use

Human and bear activity were both high in the mornings (between 5:00 and 8:00) and in the afternoons and evenings (between 15:00 and 20:00). The overlap period was longer in the evenings than in the mornings in all seasons (Fig. 8.8). In the evenings, human and bear activity peaked at about the same time, whereas in the mornings, human activity peaked much after the bear activity started declining. There was a longer period of activity overlap in the wet and cold seasons as compared to the dry season. There also was a considerable activity overlap in the day in wet and cold seasons, due to some day-activity of bears in those seasons. Intensity of human use of forest was also higher in the wet and cold seasons (Fig. 8.7).

Bears mostly used escarpments or other habitats of dense vegetation cover (including *Lantana*) in the crepuscular and day times, when their activity overlapped with humans (Fig. 8.9). Even the bears that were resting during these times used escarpments or dense *Lantana* habitats mostly (Fig. 8.11; Chapter 5: Activity Patterns, Fig. 5.12). This pattern of usage was largely similar for all seasons, but with some variation. Humans used escarpments and dense cover habitats about 60% to 70% of the time, in all seasons (Fig. 8.6). During these times the habitat use of bears and humans overlapped, irrespective of whether the bears were resting or active. About 30% to 40% of the time humans used open habitats and there was little overlap in habitat use in those times. While bears used escarpments over 80% of the time and *Lantana* habitat over 60% of the time in the day and crepuscular periods of dry and wet seasons respectively, humans used escarpments only about 20% of the time and *Lantana* habitat about 25% of the time during the same diurnal periods and seasons. Therefore, as with the partial overlap in activity, only some of the human use of forest habitats overlapped with that of bears. The overlap in activity and habitat use was nevertheless substantial.

Relation between frequency of attacks and attributes of bear behaviour and human use of forests

Monthly frequency of attacks was significantly positively correlated with intensity of human use of forest, daytime activity of bears, activity start time before sunset, length of combined day and crepuscular activity periods (sum of the differences between bear activity start time and the end of evening period, and between activity end time and the beginning of morning period) of bears, and relative usage of *Lantana* habitat for day-resting by bears (Table 8.7). Although activity end time was positively correlated, the relationship did not hold when adjusted for sunrise time. Activity start time and relative usage of escarpment habitat for day-resting were inversely correlated with monthly frequency of attacks. In summary, more the use of forest by humans, more the daytime activity of bears, earlier the bears started activity before sunset, longer the day and crepuscular activity period of bears, and more the usage of *Lantana* habitat (or conversely, less the usage of escarpment) for day-resting by bears, the higher were the frequency of attacks.

Table 8.7. Relationship between monthly frequency of sloth bear attacks on humans in Panna NP and the various explanatory variables (monthly means) of bear behaviour and human use of forest (*N*=12, for all).

Explanatory variable	Correlation coefficient (Spearman's r_s)	*P*
Human use of forest	0.74	0.006
Bear – % daytime activity	0.63	0.03
Bear – activity start time	-0.68	0.01
Bear – activity start time before sunset	0.63	0.03
Bear – activity end time	0.70	0.01
Bear – activity end time after sunrise	0.36	0.25
Bear – day & crepuscular activity length	0.57	0.05
Bear – % day-resting in escarpment	-0.78	0.003
Bear – % day-resting in *Lantana*	0.77	0.004

However, some of the explanatory variables that were correlated with frequency of attacks were also strongly correlated (statistically and biologically) with each other (e.g., % daytime activity and length of day and crepuscular activity period). Therefore, those correlations do not necessarily mean a real relationship with frequency of attacks. The relationship of each variable with frequency of attacks was hence assessed after controlling for the effect of other variables with which each was strongly correlated, by partial correlation analysis (Table 8.8). Although, human use of forest was statistically correlated with other explanatory variables, no biological relationship is expected, and therefore it was not included in this analysis. This analysis showed that two variables, relative usage of *Lantana* habitat for day-resting (and the converse of it, relative usage of escarpment habitat), and intensity of human use of forest had the strongest correlation with frequency of attacks. Further, the explanatory importance of the variable, relative usage of *Lantana* habitat for day-resting intrinsically implies (in an ecological sense) that bear activity start time is also a chief variable related to frequency of attacks.

Table 8.8. Relationship between monthly frequency of sloth bear attacks on humans in Panna NP and the explanatory variables of bear behaviour, after controlling for the effect of other variables with which each was strongly correlated, by partial correlation analysis (Pearson's *r;* for all, *df*=9).

Relationship with variables	Controlled for variables				
	% *Lantana* resting	% Escarpment resting	% Daytime activity	Day & crepuscular activity length	Activity start time before sunset
% *Lantana* resting	--	0.44 (*P*=0.18)	--	--	0.77* (*P*=0.005)
% Escarpment resting	0.12 (*P*=0.72)	--	--	--	-0.70* (*P*=0.02)
% Day activity	--	--	--	0.39 (*P*=0.24)	0.20 (*P*=0.53)
Day & Crepuscular activity length	--	--	-0.08 (*P*=0.83)	--	-0.12 (*P*=0.74)
Act start time before sunset	-0.21 (*P*=0.54)	-0.09 (*P*=0.79)	0.13 (*P*=0.71)	0.36 (*P*=0.28)	--

* – significant at α=0.05

High overlap in activity and convergence in the peaks of activity of bears and humans occurred in the evening times and that was when about 50% of the attacks happened. Another 20% of the attacks happened in the mornings, when there was substantial overlap in activity. Also, overlap in activity was high in wet and cold seasons and most attacks by foraging-bears occurred in these seasons. However, a third of the crepuscular attacks and about 80% of the day attacks were by bears that were resting. Most of the attacks by resting-bears happened in the escarpment and *Lantana* habitats, where the bears day-rested usually. Human use of these two habitats was substantial and the pattern of relative use of escarpment and *Lantana* habitats by humans in different seasons matched a similar pattern in bear use of these habitats for day-resting. Further, during the period of activity overlap too, the use of habitats overlapped substantially and most attacks by foraging-bears took place in these habitats.

Plate 14a. Humans use forest habitats for various purposes, including collecting forest-products such as Mohwa flowers, which gives them nutritional and economic benefits, but also puts them in conflict with bears. In the habitats simultaneously used by both bears and humans, encounters between them occur frequently, which sometimes results in injuries or even mortality to one or both.

Plate 14b. Aggression in the sloth bear has evolved probably as a defensive strategy against predators like the tiger and leopard that co-occur in its habitat. In surprise encounters, they react to humans as they would to a predator and often launch a defensive attack.

8.4. DISCUSSION

Humans and sloth bears in Panna NP avoided direct encounters, given an option, and only a small proportion of encounters between them resulted in attacks. Bears attacked primarily when the encounter was sudden and the attacks were probably a defensive response. No attack in Panna NP appeared to have been deliberate. Most attacks happened in cold and wet seasons, in crepuscular periods and in escarpments or other habitats with dense vegetation cover. The frequency of attacks on humans engaged in various activities was related to the intensity of usage of different habitats in different seasons. Foraging bears were involved in attacks more often during crepuscular time in wet season and resting bears during daytime in cold season.

Sloth bears in Panna NP followed a daily routine of activity, with some seasonal variability, as did human activity. Bears were active in the night and crepuscular periods and usually rested during mid-day in escarpment or dense *Lantana* habitats. They were active for a longer period in the evenings than mornings and began their activity earlier in the evening in the wet season. Humans started their activity early in the morning and ended it late in the evening. They had peaks in activity in the morning and evening and were moderately active in the forests throughout the mid-day. Sometimes, their activity extended into the night considerably, in wet and cold seasons. Human use of forest was also higher in wet and cold seasons.

Similar to season, time of day also affected key bear and human behavioural attributes. Human and bear activity overlapped in the crepuscular periods, often greatly in the evenings and the period of overlap was longer in the wet and cold seasons. Bears mostly used escarpment or other dense cover habitats during the periods of overlap in activity. They more frequently used escarpment in the dry and cold seasons and *Lantana* or other dense cover in the wet and cold seasons. Humans also used escarpment and other dense cover habitats frequently and during these times, their habitat use overlapped substantially with that of bears. Most attacks happened during the period of high overlap in habitat use or activity and in the habitats where the simultaneous use was greater. On the whole, interacting behavioural factors placed the humans and bears in circumstances leading to encounters. The habitat setting often made the encounters sudden and the behavioural response of bears during such encounters resulted in attacks. In summary, the behavioural and ecological factors influenced both the probability of encounters and also the possibility of an encounter resulting in an attack.

Why are there more attacks in certain seasons, times of day and habitats?

During wet and cold seasons, more humans used the forests and particularly the same habitats that the bears used. New flush of grass and browse in the forests during wet season attracted livestock and the humans who tended them. Due to the higher abundance and better nutritive quality of forage, there were also more people harvesting it during these seasons. Due to the denser vegetation cover in habitats such as *Lantana* shrub patches in these seasons, bears tended to use these habitats more frequently for day-resting (see Chapter 5: Activity Patterns). Some of the bears also shifted their seasonal ranges to dense shrub (*Lantana*) and open shrub habitats in the wet season (Chapter 6: Space Use and Habitat Selection). Also, with smaller range of daytime temperatures in wet season, bears began their diel activity earlier, thereby increasing the length of day and crepuscular activity period. Since, humans also had activity peaks in the crepuscular period, the extent of activity overlap between the humans and bears was longer in the wet and cold seasons. These factors likely increased the probability of encounters and consequently the frequency of attacks in these seasons.

The diel activity of sloth bears follows a routine: they rest during the mid-day, more or less in all seasons, and forage in the crepuscular and night times. During the crepuscular period, human activity, especially the peaks in it coincided with bear activity. Also, during this period, bears were active mostly in the vicinity of day-resting habitats (escarpments or other dense cover). The cattle grazing ranges often extended up to escarpments in the wet and cold seasons, particularly in the evenings, because of the abundant browse available there. Due to the topographic position of escarpment habitat in Panna NP, people from many villages were constrained to use escarpments to travel back to their villages. Consequently, humans often used escarpments in the evenings. Areas surrounding many villages are degraded and invaded by dense *Lantana* shrub patches (Fig. 8.3). Cattle that return after ranging farther and those that graze close to villages use *Lantana* patches in the evenings. Therefore, humans who tended cattle and those travelling back to villages use this habitat in the evenings. The use of escarpment and *Lantana* habitats in the crepuscular period overlaps dynamically with the use by bears. This overlap probably resulted in a higher frequency of encounters and consequently, more frequent attacks on humans during the crepuscular period. During the day time, the bears usually rested either in dens in escarpment habitat or in dense *Lantana* cover, sheltered from heat and other disturbances. However, in the cold season some bears frequently rested outside dens, among vegetation cover in escarpment habitats. Humans engaged in MFP collection or cattle tending used these habitats during the day time. This overlap in space use and the increased possibility of encountering bears in escarpments in the cold season may have resulted in attacks during the day time.

Most sloth bear attacks happened in escarpment or other dense cover habitats and few in open cover habitats. Sloth bears mostly used escarpments or such dense cover habitats for day-resting and for foraging in the crepuscular period. These habitats offered suitable shelters for day-resting and abundant food in some seasons. Fruits were abundant near escarpment habitat in the dry season. In the wet season, social insects and fruits of *Lantana* were abundant in dense *Lantana* habitat. Due to the abundance of both food and cover, bear usage of these habitats was high. Humans too used escarpments frequently to collect MFP and in travelling through. In the wet season, new flush of grass became available in open patches within *Lantana* habitats and in the fire-burnt areas surrounding villages and these attracted cattle. Also, *Lantana* habitat occurred mostly near villages and on the peripheries of the forests. Therefore, it acted as an intervening habitat for humans returning after tending cattle, collecting MFP, or just travelling. Consequently this habitat was used much in crepuscular periods and in wet and cold seasons. The simultaneous use of these habitats by bears and humans increased the probability of encounters and consequently the frequency of attacks.

The associations that sloth bear attacks had with season, time of day or habitat type were also reported from other areas. Rajpurohit and Krausman (2000) reported that in Madhya Pradesh State in central India, the attacks that occurred in forest habitats were more frequent between April and October and the attacks in village gardens and crop fields were more common in October. Chauhan *et al.* (1999) reported that in North Bilaspur Forest Division (NBFD), an intense conflict area in eastern central India, attacks were more frequent from August to October, January and May. However, both these studies have not related the seasonal variations in attacks to probable ecological or behavioural factors underlying them. In NBFD, most attacks were reported to have happened during morning activity of humans in bear habitat, when the bears were also known to be active (Bargali *et al.* 1999). Further, a majority of attacks (about 65%) in NBFD were reported to have occurred in vegetable gardens, crop fields or in the vicinity of villages, while most attacks (over 90%) in areas other than NBFD were in forest habitats (Chauhan *et al.* 1999, Rajpurohit and Krausman 2000). However, plain descriptions of such seasonal or spatial variations, without an evaluation of factors causing them or at least a measurement of the correlated ecological factors, are not very informative for understanding the situation or for managing the conflict.

Does some activity make humans more prone to attacks than others?

Although people engaging in different activities were attacked in different frequencies in different seasons, this does not indicate a direct relationship the kind of activity had with the likelihood of being attacked. Rather, the different activities took the humans to different habitats in different seasons and being in those habitats in those times determined the probability of being attacked. Many people who used the forests were alone, although there may have been others in the vicinity. Humans tending cattle or collecting MFP spread out in the grazing areas or resource patches, perhaps as a means of segregating resources or due to competition. Humans often travelled in pairs or in groups but they were also alone many times. Although there were fewer instances when humans were in pairs or groups in forests than being alone, there may have been fewer attacks on them because they made enough noise that the bears could hear them and move away. Or, they may have been more able to protect themselves when a bear attacked them. Humans from villages near escarpments used that habitat frequently for various purposes and hence the frequency of attacks on them was higher in that habitat. Whereas, humans from far off villages used escarpments less often and used the *Lantana* habitat that was found in the peripheral areas more often. The attacks were, therefore, more frequent in the habitats used most. This pattern reinforces the idea that the intensity of usage of particular habitats by humans was the factor that chiefly influenced the probability of encounters and consequently the frequency of attacks.

Do some bears attack more often than others?

The results suggest that the bear that gets into a sudden encounter with humans, in a dense habitat, is the likely one to attack and that the attack probability had no discernible relation to the sex or age of the bear or composition of a pair or group. Since the solitary bears were not sexed, this cohort had the highest likelihood of meeting a human, given randomness, and there were more attacks by this cohort, as expected. Next to solitary bears, the mother and cub association was the most likely cohort to be encountered and the attack frequencies matched this pattern. Since the sloth bears are mostly solitary and the intraspecific associations other than mother and dependent young were mostly among siblings or adults during the breeding season (Laurie and Seidensticker 1977, Joshi *et al.* 1999, *personal observations*), fewer attacks were to be expected by such pairs and the results were in agreement with this. Attacks by the mother and cub cohort were disproportionately more frequent in the wet season and this was probably because they needed to range over a wider area to meet their combined energy demand and this season offered cover and resources to do that. Due to the denser vegetation of the wet season, more humans probably also intruded into the extended individual distances that the mothers with cubs may have maintained (Herrero 1970, 1985) and consequently, were attacked.

The overlap in human and bear use of habitats was longer during the day than the crepuscular period and during this overlap period, more bears were resting than were active. However, there were more attacks by foraging than resting bears. This is probably because the chance of encountering a foraging bear would be much higher than that of a resting bear, even if both were present in a habitat. Bears often rested in secure cover such as dens or dense thickets, which the humans do not enter often. However, despite the lower probability of resting bears being encountered, there were still frequent attacks by them. This could have happened because human disturbance caused bears to come out of the den, or as is common, bears may have been resting outside the dens, in some seasons and times of day. There was also a possibility that while it was reported that the bears were resting prior to attacks, some bears actually may have started their foraging in the evenings and perhaps had a pause in their activity when humans noticed them. There is little information available from other areas on whether foraging or resting sloth bears attacked more often. Grizzly and European brown bears feeding on or near a carcass have been considered potentially dangerous situations to encounter (Herrero 1985, Swenson *et al.* 1999b). Mother bears were involved in most grizzly bear attacks that happened during sudden encounters (Herrero 1985). In general, a positive relation seems to exist between the aggressiveness of mother bears and the presence of cubs (Herrero 1985, Swenson *et al.* 1999b). However, even other bears can be equally aggressive, because being aggressive is important throughout the lives of bears, be it for securing territory, mates, protection of young, protecting themselves from other bears, predators or humans (Herrero 1985).

Why do the bears attack?

When the encounter is sudden, (i.e., the distance between the bear and the human before the bear senses the human, and consequently, the time to react is short), the bear tends to attack. Also, it is very likely that the visibility level in a habitat determines whether a human or a bear sense each other's presence in advance or meet suddenly. Although a bear may hear the sounds made by humans from far off, if the sounds are not clearly associated with humans, the bear may wait to be guided by sight or scent. By which time, the distance and time to respond might become too short. A common factor that underlies the habitats where most attacks occurred is the dense or sheltered cover and the consequent poor visibility. The visibility factor explains why the encounters in these habitats often turn out to be sudden.

Surprise at close range is an important factor in many grizzly bear attacks in North America, particularly the ones on hikers (Herrero 1970, 1985, Gniadek and Kendall 1998). Garshelis *et al.* (1999) observed that the sloth bear attacks in Nepal happened mostly when people suddenly encountered bears inside forests and there were no attacks outside forests, nor were there any instances of sloth bears entering crop fields in recent times. Gopal (1991) observed that in Kanha NP in central India, the sloth bear attacks occurred when humans suddenly encountered bears or when encounters were near fruit trees. Attacks due to sudden encounters may be more widespread and may even be the cause for most attacks by sloth bears in India. The main deviants from this may be the attacks by bears that are habituated to humans, attracted to human-generated food or crop fields, bears that have been wounded or the ones that react to an aggressive approach by humans.

The sloth bear is aggressive in nature and this trait probably has a survival value and has evolved under certain evolutionary ecological pressures. Therefore, in certain conditions, it is probably an innate reaction that a bear attacks to defend itself from a possible threat. If the conditions permit the bear to sense a human well in advance, then the bear may avoid rather than confront a human. However, the reaction could also be influenced by an individual bear’s past experiences in such circumstances (Herrero 1985). The variability in the reactions shown towards humans, even during close encounters can perhaps be explained by this learning factor. Individual bears may also have a personal space (or “individual distance”, defined as the “minimum spacing between themselves and conspecifics or humans”) around them, which if trespassed, may make the bear attack almost as a reflex

(Herrero 1970, 1985). This distance might vary with an individual bear's social status, its physiological condition and it may change with circumstances. Grizzly bear sows with cubs are known to enforce large individual distance, up to several hundred metres, especially with respect to certain males or humans (Herrero 1970). The variability in the minimum distance before a bear attacked could be explained by this factor.

Why are the sloth bears aggressive?

While sudden encounters in poor visibility habitats may be a proximate factor determining the probability of attacks, the ultimate factor might be the defensive response of sloth bear to humans that manifests as an aggressive disposition. Sloth bears probably evolved within the Indian subcontinent sympatrically with larger predators such as the tiger. The evolutionary pressures of predators may have influenced the development of aggression in sloth bears (Plate 14b). Laurie and Seidensticker (1977) suggested that the aggressive behaviour of sloth bears may be a consequence of not being able to rely on trees for escape, in a habitat that holds tree-climbing predators like the leopard, and also makes it advantageous to live in fairly open habitats. Incidents of sloth bear mortality caused by predators have been reported from several places in its range (reviewed in Joshi *et al.* 1999). In Panna, sloth bears had several agonistic interactions with tigers and were also occasionally killed by tigers (unpublished data). Sloth bear cubs seldom climb trees to avoid predators. Therefore, offence may be the mother bears' best defence strategy and this strategy has been considered to have important survival value for the grizzly bear cubs (Herrero 1970). However, there are also costs associated with attacking humans. Therefore, the bears may be making decisions based on the risks and benefits of attacking (or may have developed it over evolutionary time) and might not be acting arbitrarily, contrary to popular belief.

Aggression may have also developed due to competition among conspecifics over resources. The aggressiveness of the sloth bear is perhaps adaptive in their interactions with conspecifics, predators like tiger, leopard and other sympatric mammals like elephants and rhinos, and the bear may show the same kind of reaction to humans (Laurie and Seidensticker 1977, Herrero 1985, Garshelis *et al.* 1999). Humans might have been occupying the Indian subcontinent for at least 4000 years and probably have had regular agonistic interactions with the sloth bears. As a consequence, sloth bears may have evolved aggressive reactions towards humans. In the last 200 years or so, human persecution of bears has been more severe (Dunbar-Brander 1926, Rangarajan 1996, 2001) and these interactions might have reinforced the negative perceptions of humans. Sloth bears have been observed to have low tolerance towards people and conflicts with humans are common in most of its range (Garshelis *et al.* 1999, Yoganand *et al.* in press).

My observations on interactions that sloth bears had with conspecifics, tigers and humans in Panna indicate that there are several responses that are common in these interactions, particularly in the way sloth bears reacted to both tigers and humans. Sloth bears actively avoided tigers and humans when they became aware of their presence in advance. When they heard suspicious sounds made by humans, tigers, or even alarms raised by other animals such as sambar (*Cervus unicolor*) or common langur (*Trachypithecus entellus*) to the presence of predators or humans, the bears became vigilant. They paused their activity and waited for further sounds or scents, looked in the direction of the sound, or exhibited such vigilant behaviour. When the bears sensed the presence of adversaries, they stopped their activity, moved in a different direction or even took shelter under secure cover. Sometimes, they did not emerge out of dens until long after their usual times of start of activity. Occasionally they also fled on sensing a threat, or at other times, they rushed towards the tiger or the human. Similar reactions were also observed in Chitwan NP, Nepal. At close quarters, sloth bears reacted to humans and tigers similarly, often by roaring and running away, or roaring and attacking before retreating (Laurie and Seidensticker 1977). These observations indicate that the bears perhaps perceived humans as predators or equivalent to predators. However, a peculiar behaviour that I observed that may confound other observed patterns to a considerable extent is that the bears while foraging, were often quite preoccupied and did not pay attention to things other than searching for food, unless there was sound or scent coming by its way. Several times, when I was still and silent the bears approached me (mostly when in a jeep or treetop, but sometimes even when on foot) without noticing me, coming as close as a distance of 10 m, usually after which I made noise and scared it away.

How to avoid encounters with sloth bears?

Although it is difficult to predict if a bear will attack or not when encountered, it is possible to predict where the probability of encountering bears would be higher. The best way to avoid encounters is to avoid such places, during the times when the bears are likely to be there. The likelihood of being attacked by a bear is determined primarily by being in the wrong place (habitat) at the wrong time (season and time of day) than anything else. Sudden encounters can be avoided best by avoiding habitats with poor visibility, those with dense vegetation cover or rocky slopes having natural cavities that may act as dens, at all times. If indispensable, then using these habitats as a group or by making enough noise to announce human presence might help avoid running into resting or “preoccupied” foraging bears. Avoiding being on footpaths in the crepuscular periods, particularly in the wet and cold seasons may help in reducing encounter frequencies, as would avoiding night usage of any forest habitat. Even just being alert for sounds in the forests, as foraging bears make a lot of noise, and circumventing dense vegetation patches that might harbour resting bears, can go a long way towards avoiding encounters with bears. Making noises while being in grizzly bear country and hiking as groups have been suggested as good measures to alert bears of human presence (Herrero 1985). Even in places like Panna, many humans, as a traditional habit, sing loudly or make noises while walking through dense habitats. This way, a good proportion of people using the forests may actually be avoiding encounters with bears. The measures that I have discussed here apply only to areas where the attacks are by bears that are defensive. Where the attacks are by food-attracted, crop raiding, human habituated or other ‘offensive’ bears, then the avoidance measures may have to be quite different.

If not successful in avoiding an encounter and if a bear attacks, there are certain things that the humans could do to minimise injury. When the bear rushes to attack, running may not be a good option unless the distance to the bear is great. Climbing trees to escape would not be an option either, in contrast to grizzly bears, as sloth bears are good climbers. Distracting the bears by dropping objects might help to some extent. Herrero (1970, 1985) observed that the extent of injury caused by attacking grizzlies was related to the behaviour of the person during the attack. He found that playing dead or showing minor resistance stopped or lessened grizzly attack and this may be effective in cases related to "individual distance" violation. Since distance violation in sudden encounters is a probable cause for many attacks by sloth bears, this way of responding to attacking bears might be an option. While being attacked, one can reduce injury by assuming a position so as to minimise exposure of vital body parts. Standing one's ground and fighting back may be an option too. However, the effectiveness of these different options remains to be tested with sloth bears.

How intense is human – sloth bear conflict across India?

Although attack incidents are widespread, their frequency varies over the range of the sloth bear in India. Considering the number of people using the forests in India and the widespread occurrence of sloth bears, the probability of humans encountering sloth bears in the forests can be expected to be high. However, attack frequency is only moderate in most places across India (unpublished data). For example, in Panna NP, the attack frequencies were not high, despite the high human use of forest. Most humans using the forests may not be encountering sloth bears because the overlap in activity and space use is probably limited, except under certain conditions, as in Panna. Also, most encounters probably do not end in attacks and the chance of a person being injured or killed in an encounter should be further small. There are only a few areas that are known to have high frequencies of attacks and these are primarily concentrated in eastern central India (Bargali *et al.* 1999, Rajpurohit and Krausman 2000). However, there are also a few areas elsewhere that experience high-conflict (e.g., a degraded forest area in southern India; Iswariah 1984). Interestingly, most of the known high-conflict areas are located where the forests have been severely degraded and fragmented (in terms of forest cover). Also, in these areas, attacks often occur in human habitats such as crop fields. These high-conflict areas may exhibit patterns of attack quite different from Panna and might need special studies to assess the causal factors. On the whole, the intensity of conflict in an area may depend on bear density, number of humans using bear habitat, the quality of bear habitat and more importantly, the extent of conditions promoting the interactions between them.

Management implications

Sloth bears are not inherently dangerous, but they do respond aggressively to the perceived threat from humans. Under certain conditions, as a defensive response, they attack humans. The results of this study suggest that the circumstances that lead to sudden encounters can be avoided and thereby the frequency of attacks can be reduced. The day to day survival of sloth bears hinges on their defensive attacks and attempts to modify this behaviour are not appropriate, nor likely to be successful. Rather, the problem solving required here involves management of human behaviour in bear habitats. Most sloth bear attacks in the forests in India are probably caused by defensive attacks in sudden encounters. Therefore, the focus on human management would be more appropriate for managing most sloth bear attack problems in India. Even in North America, the management has been urged to shift its focus on avoiding problem bear behaviour by modifying human behaviour (Gniadek and Kendall 1998). Three types of human activity in wildlife habitats: wildlife viewing, camping and hiking have been identified as the main activities during bear attacks in North America (Herrero 1970, 1985). These types of activities are easier to regulate than activities such as cattle grazing or MFP collection that are the primary human activities in the forests of India.

With regard to Panna NP, certain modifications of human activities in forests need to be implemented by the management in order to reduce the frequency of encounters with bears. This would benefit both humans and the unknown number of bears probably being injured or stressed in such encounters. Suggested measures include: stopping night time usage of forests, such as grazing buffaloes, restricting people from using footpaths in the escarpment habitat, making paths wider in *Lantana* patches, relocating forest blocks that are open for grazing and the forest villages away from escarpments, and extending the Park boundary to include most of the neighbouring escarpment habitat. These measures complement the ones suggested earlier for humans to avoid encounters. Educating humans who use the forests about the behaviour and ecology of bears and the ways to avoid encounters are essential. Education about how to safeguard and minimise injuries during attacks is also needed. Also, better communication, transport and medical facilities would help the attack victims to get treatment for injuries in time. Appalling medical facilities in the rural areas around Panna is one of the main reasons the injuries left severe impacts on humans and this is probably true for many rural areas in India.

The bear attacks that occur in forests, caused by sudden encounters could be managed by modification of human behaviour. However, attacks that happen in crop fields or village vicinities (Iswariah 1984, Bargali *et al.* 1999, Rajpurohit and Krausman 2000) need to be dealt with by other means. For one such area, Rajpurohit and Krausman (2000) suggested alteration of bear behaviour: to destroy sloth bear dens located close to villages and to scare bears away when they entered crop fields. Bargali *et al.* (1999) advocated modification of human behaviour: to curtail human activities in the mornings, to ask that humans use the bear habitats do so in groups and to carry weapons such as a fire-stick or axe. Other resolutions to this kind of problem may include fencing the crop fields or villages, improvement of habitats to sustain bears within forest boundaries, removal of problem animals, or negative conditioning of bears. A rule of thumb could be, if attacks occur in bear habitat, then human behaviour should be modified and if the attacks happen in human habitats, then the focus should be on managing bear behaviour.

Negative conditioning has been suggested for minimising damage to both bears and humans in North America (McCullough 1982, Mace and Waller 1996). Negative conditioning of bears may be a potential method to reduce offensive attacks, but it has never been tried in India. However, negative conditioning may have been occurring indirectly in the past due to the then prevalent hunting or persecution of bears. As the conditioning factor reduced in frequency, the effect of past negative conditioning might have waned and the fear response might have been lost in bears. In some cases, habituation of bears to frequent encounters with humans, but without any reinforcement of fear through punishment may have happened. In such cases, negative conditioning may be effective. The techniques of negative conditioning, however, need to be adapted based on behaviour theory and local conditions. For example, negative conditioning techniques that mimic stimuli that a species finds naturally aversive would be more effective than those that depend on the behaviour learned during the lifetimes of individual bears (Whittaker and Knight 1998). Bears learn rapidly (Bacon and Burghardt 1976) and the role of learning in producing the various responses to humans has great potential in conflict resolution (McCullough 1982, Whittaker and Knight 1998).

It is doubtful if any active management of bear attacks is practiced or has even been planned in India. In some places, compensation to the attack victims is given and the management action ends with that. On the other hand, there has not been a study in India that assessed the problem objectively and suggested management measures. Improved management will come only with a good understanding of the ecology of the species, but this has not been the focus as yet in India. Herrero (1970) noted that the human injury due to bear attacks could be reduced to a minimum through improved management. Since long, research studies and management practices in North America have addressed the problem objectively and worked on effectively resolving conflicts, based on positive feedback from each other. Frequency of attacks and property damage have been controlled in North America by controlling situations that attracted bears to human-generated food (garbage), by relocating problem bears, by segregating human use areas from bear habitats or in essence, by basing management of bear – human conflict on proper plans (Herrero 1985, Blanchard and Knight 1995, Gniadek and Kendall 1998, Hood and Parker 2001).

Conclusions

I investigated the behavioural and ecological conditions that lead to attacks on humans by sloth bears in Panna NP and identified certain measures that could reduce the frequency of attacks. There has not been a study on the sloth bear before this one that has analysed the conflict in relation to its behavioural ecology. Further, there is possibly no other study that investigated the ecological conditions that lead to sudden encounters and the resultant defensive attacks by bears, in such detail. The results of this study would apply to most places where the bear attacks are defensive. The results can also serve as a model for evaluating causes of attacks in other areas and for predicting situations that may lead to attacks. Further, based on the results of this study, spatial models to predict the encounter probabilities from habitat attributes can be developed for larger landscapes. A large part of the sloth bear range consists of dry deciduous forests and the habitat characteristics of these forests are heavily influenced by the monsoon. Day temperatures and seasonal changes in temperature would also be similar in these habitats. Therefore, the results of sloth bear activity and habitat use studies can be extrapolated to many areas in the sloth bear range. An assessment of attack history from an area could provide data on time and habitat parameters associated with attacks. Associating that information with sloth bear behaviour, the probable causes of attacks can be identified and certain immediate measures can be taken to contain the problem. Further, the actual causes of attacks can be investigated by using the results of this study as a basis to form testable hypotheses.

8.5. SUMMARY

- I investigated the ecological and behavioural conditions that led to attacks on humans by sloth bears in Panna NP, and identified certain measures that could reduce the frequency of attacks.

- Thirty five villages around Panna NP were surveyed, and official records were examined to gather information on sloth bear attack incidents. I interviewed over 200 people, who had close encounters with sloth bears and who use forest areas intensively for various purposes, and gathered information on various parameters associated with attack incidents and encounters. Most recent encounter locations were visited and location coordinates, terrain type, vegetation cover, visibility, and other parameters were recorded.

- I used the information that I gathered on other aspects of behavioural ecology of sloth bears, namely, diel activity, space and habitat use, and feeding behaviour, to identify the possible factors underlying the attacks. I also assessed the diel activity, habitat use, and intensity of human use of forest. Observations on sloth bear interactions with conspecifics, predators and humans were made.

- 30 villages had reports of bear attacks, totalling 80 incidents. All attacks were defensive in nature and none appeared to be deliberate. The general bear response to an encounter with humans was to flee, bluff charge and retreat, or to attack. Human response to an encounter with a bear was to flee, confront or yield.

- Humans and sloth bears in Panna NP avoided direct encounters and only a small proportion of encounters resulted in attacks. Bears attacked primarily when the encounter was sudden, and this was probably a defensive response.

- Most attacks occurred during cold (41%) or wet (39%) seasons. More than 70% of the attacks happened in the crepuscular period, and about half were in the evenings alone. 43% of the attacks occurred in the escarpment habitat, 30% in *Lantana* shrub patches and another 15% in other habitats having dense vegetation cover. Overall, the majority of the attacks took place in escarpment or other habitats with dense vegetation cover, in the crepuscular period of wet and cold seasons.

- About 40% of the humans that were attacked were tending cattle, 30% were collecting minor forest products (MFP) and 24% were travelling along footpaths in the forests. Attacks on humans tending cattle were disproportionately more in the wet season and less in the dry season, whereas attacks on humans collecting MFP were disproportionately more in the dry season and less in the wet season.
- Attacks involving bears resting or foraging was related to season and time of day. Of the foraging bears, disproportionately more were involved in attacks during the crepuscular period in the wet season, whereas, of the resting bears disproportionately more were involved in attacks during the day in the cold season.
- The various major occupations of humans in different seasons took them to different habitats and this determined their relative use of habitats across seasons. Overall, the intensity of human use of forest was highest in some wet and cold season months and remained at a moderate level during the rest of the year.
- Human and bear activity were both high in the mornings and evenings. The overlap period was longer in the evenings than in the mornings in all seasons. Also, there was a longer period of activity overlap in the wet and cold seasons as compared to the dry season.
- Bears that were either resting or foraging mostly used escarpments or other habitats of dense vegetation cover (mainly *Lantana*) in the crepuscular and day times, when their activity overlapped with humans. In these times, humans also used the same habitats. Most attacks happened during these periods of high overlap in habitat use or activity and in the habitats where the simultaneous use was greater.
- As with the partial overlap in activity, only some of the human use of forest habitats overlapped with that of bears. The overlap in activity and habitat use was nevertheless substantial.

- More the use of forest by humans, more the daytime activity of bears, earlier the bears started activity before sunset, longer the day and crepuscular activity period of bears, and more the usage of *Lantana* habitat (or conversely, less the usage of escarpment) for day-resting by bears, the higher were the frequency of attacks. Further, relative use of *Lantana* habitat for day-resting, time of bear activity start before sunset, and intensity of human use of forest were the chief variables that were related to frequency of attacks.
- It seems that the visibility level in a habitat determines whether a human or a bear sense each other's presence in advance, or meet suddenly. That is, the habitat conditions often made the encounters sudden and the behavioural response of bears during such encounters caused the attacks.
- Sudden encounters can be avoided best by avoiding habitats with poor visibility. While sudden encounters might be a proximate influence on probability of attacks, an ultimate factor might be the defensive response of sloth bear to humans that manifests as an aggressive disposition. The evolutionary pressures of sympatric predators might have influenced the development of aggression in sloth bears.
- **Conservation Implications.** As suggested by the results of this study, the circumstances that lead to sudden encounters can be avoided and thereby the frequency of attacks can be reduced. The problem solving required here involves management of human behaviour in bear habitats, rather than management of bear behaviour. Suggested measures for reducing the frequency of encounters in Panna NP include: stopping night time usage of forests, such as grazing livestock, restricting people from using footpaths in the escarpment habitat, making paths wider in Lantana patches, relocating forest blocks that are open for grazing and the forest villages away from escarpments, and extending the Park boundary to include most of the neighbouring escarpment habitat.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology, 74: 1313-1325.

Aitchison, J. 1986. The statistical analysis of compositional data. Chapman and Hall, London, U. K. 416p.

Amstrup, S. C., and J. Beecham. 1976. Activity patterns of radio collared black bears in Idaho. Journal of Wildlife Management, 40: 340-348.

Anderson, D. R., K. P. Burnham, W. R. Gould, and S. Cherry. 2001. Concerns about finding effects that are actually spurious. Wildlife Society Bulletin, 29: 311-316.

Armstrong, D. V. 1994. Heat stress interaction with shade and cooling. Journal of Dairy Science, 77: 2044-50.

Aschoff, J. 1966. Circadian activity pattern with two peaks. Ecology, 47: 657-662.

Aubensberg-traun, M., and E. S. De Boer. 1990. Species abundance and habitat differences in biomass of subterranean termites (Isoptera) in the wheat belt of Western Australia. Australian Journal of Ecology, 15: 219-226.

Aune, K. E. 1994. Comparative ecology of black and grizzly bears on the rocky mountain front, Montana. International Conference on Bear Research and Management, 9: 365-374.

Ayres, L. A., L. S. Chow, and D. M. Graber. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park.

Pages 151-154, in P. Zager, editor. Bears – Their Biology and Management: Proceedings of the 6th International Conference on Bear Research and Management, Grand Canyon, AZ, U.S.A.

Bacon, E. S. and G. M. Burghardt. 1976. Learning and color discrimination in the American black bear. Pages 27-36 in M. R. Pelton, J. W. Lentfer, and G. E. Folk, Jr., editors. Bears – Their Biology and Management. IUCN New Ser. Publ. 40.

Baptiste, M. E., J. B. Whelan, and R. B. Frary. 1979. Visitor perception of black bear problems at Shenandoah National Park. Wildlife Society Bulletin, 7: 25-29.

Bargali, H. S., N. Akhtar, and N. P. S. Chauhan. 1999. Human mauling behaviour of sloth bears in North Bilaspur Forest Division, Madhya Pradesh, India. Presented in the 12th International Conference on Bear Research and Management, Romania. Unpublished MS.

Bargali, H. S., N. Akhtar, and N. P. S. Chauhan. 2002. Feeding ecology of sloth bears (*Melursus ursinus*) in a degraded and high conflict area in central India. 14th International Conference on Bear Research and Management, Steinkjer, Norway. Unpublished Poster.

Bartholomew, G. A. 1977. Body temperature and energy metabolism. Pages 364-449, in M. S. Gordon, editor. Animal physiology: Principles and adaptations. Macmillan, New York, U.S.A.

Baskaran, N. 1990. An ecological investigation on the dietary composition and habitat utilisation of sloth bear at Mudumalai Wildlife Sanctuary, Tamil Nadu (South India). M.Sc. Thesis, A. V. C. College (Bharathidasan University), Mannampandal, India. 57p.

Baskaran, N., N. Sivaganesan, and J. Krishnamoorthy. 1997. Food habits of sloth bear in Mudumalai Wildife Sanctuary, Tamil Nadu, Southern India. Journal of Bombay Natural History Society, 94: 1-9

Basu, P. 1997. Seasonal and spatial patterns in ground foraging ants in a rain forest in the Western Ghats, India. Biotropica, 29: 489-500.

Beale, C. M., and P. Monaghan. 2004. Human disturbance: people as predation-free predators? Journal of Applied Ecology, 41: 335-343.

Beckmann, J. P., and J. Berger. 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. Journal of Zoology, 261: 207-212.

Belshaw, R. and B. Bolton. 1993. The effect of forest disturbance on the leaf litter ant fauna in Ghana. Biodiversity and Conservation, 2: 656-666.

Bennett, A. F., and J. A. Ruben. 1979. Endothermy and activity in vertebrates. Science, 206: 649-654.

Beyer, Jr. D. E. and J. B. Haufler. 1994. Diurnal versus 24-hour sampling. Journal of Wildlife Management, 58: 178-180.

Bianca, W. 1962. Relative importance of dry and wet bulb temperatures in causing heat stress in cattle. Nature, 195: 251-252.

Blanchard, B. M. and R. R. Knight. 1995. Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. Journal of Wildlife Management, 59: 560-565.

Brandt, D. Ch. 1980. Is the mound of *Formica polyctena* Foerst,. in origin a simulation of a rock. Oecologia, 44: 281-282.

Briese, D. T. and B. J. Maucaulay. 1980. Temporal structure of an ant community in semi-arid Australia. Australian Journal of Ecology, 5: 121-134.

Brody, A. J., and M. R. Pelton. 1988. Seasonal changes in digestion in black bears. Canadian Journal of Zoology, 66: 1482-1484.

Bunnell, F. L., and A. S. Harestad. 1989. Activity budgets and body weight in mammals: How sloppy can mammals be? Current Mammalogy, 2: 245-305.

Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears – implications. Pages 75-98 in C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, U.S.A.

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

Caldwell, G. S. 1986. Predation as a selective force on foraging herons: effects of plumage colour and flocking. Auk, 103: 494-505.

Champion, F. W. 1934. The jungle in sunlight and shadow. Chatto and Windus, London, U. K.

Chamrad, A. D. and T. W. Box. 1964. A point frame for sampling rumen contents. Journal of Wildlife Management, 28: 473-477.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theoretical and Population Biology, 9: 129-136.

Chauhan, N. P. S., H. S. Bargali, and N. Akhtar. 1999. Human – sloth bear conflicts in the State of Madhya Pradesh, India. Presented in the 12th

International Conference on Bear Research and Management, Romania. Unpublished MS.

Chauhan, N. P. S., H. S. Bargali, and N. Akhtar. 2004. Activity patterns of sloth bear in fragmented and disturbed areas of Bilaspur Forest Division, Chattisgarh, India. Presented in the 15th International Conference on Bear Research and Management, San Diego, CA, U.S.A. Unpublished MS.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology, 64: 1297-1304.

Chiarello, A. G. 1998. Activity budgets and ranging patterns of Atlantic forest maned sloth *Bradypus torquatus* (Xenarthra: Bradypodidae). Journal of Zoology, 246: 1-10.

Clarke, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). Behavioural Ecology and Sociobiology, 13: 205-209.

Clevenger, A. P., F. J. Purroy, and M. R. Pelton. 1990. Movement and activity patterns of a European brown bear in the Cantabrian Mountains, Spain. Pages 205-211, in L. M. Darling, W. R. Archibald, editors. Bears – Their Biology and Management: Proceedings of the Eighth International Conference on Bear Research and Management, Victoria, B.C., Canada.

Clevenger, A. P., F. J. Purroy, and M. R. Pelton. 1992. Food habits of brown bears (*Ursus arctos*) in the Cantabrian Mountains, Spain. Journal of Mammalogy, 73: 415-421.

Corbet, G. B. and J. E. Hill. 1991. A world list of mammalian species. Oxford University Press, New York.

Craighead, F. C., Jr., and J. J. Craighead. 1965. Tracking grizzly bears. Bioscience, 15: 88-92.

Craighead, F. C., Jr., and J. J. Craighead. 1972. Grizzly bear pre-hibernation and denning activities as determined by radio-tracking. Wildlife Monographs, 32.

Craighead, J. J., J. S. Sumner, and J. A. Mitchell. 1995. The grizzly bears of Yellowstone: Their ecology in Yellowstone ecosystem, 1959-1992. Island Press, Washington D.C. 535p.

Crompton, A. W., C. R. Taylor, and J. A. Jagger. 1978. Evolution of homeothermy in mammals. Nature, 272: 33-336.

Dahle, B. and J. E. Swenson. 2003. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. Journal of Zoology, 260: 329-335.

Davidar, P., and E. S. Morton. 1986. The relationship between fruit crop sizes and fruit removal by birds. Ecology, 67: 262-265.

De Blainville, H. 1817. Sur le Paresseux a cinq doigts (*Bradypus ursinus* de Shaw). Pages 74-76, in Bulletin des Sciences par la Societe Phlomatique de Paris, Paris.

Desai, A. A., N. Baskaran, and S. Venkatesh. 1997. Behavioural ecology of the sloth bear in Mudumalai Wildlife Sanctuary and National Park, Tamil Nadu. Bombay Natural History Society and Tamil Nadu Forest Department. Unpublished Report. 29p.

Dominy, N. J. and P. W. Lucas. 2001. Ecological importance of trichromatic vision to primates. Nature, 410: 363-366.

Dunbar-Brander, A. A. 1923. Wild animals in central India. First Indian Edition (1982), Natraj Publishers, Dehra Dun, India.

Eagle, T. C., and M. R. Pelton. 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management, 5: 94-101.

Egbert, A. L., and A. W. Stokes. 1976. The social behaviour of brown bears on an Alaskan salmon stream. Pages 41-56, in M. R. Pelton, J. W. Lentfer, and G. E. Folk, editors. Bears – Their Biology and Management: Proceedings of the third International Conference on Bear Research and Management, Binghamton, N. Y., U. S. A.

Eggleton, P., D. E. Bignell, W. A. Sands, N. A. Mawdsley, J. H. Lawton, T. G. Wood, and N. C. Bignell. 1996. The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, Southern Cameroon. Philosophical transactions of the Royal Society of London, Series B, 351: 51-68.

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

Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management, 53: 962-968.

Enright, J. T. 1970. Ecological aspects of endogenous rhythmicity. Annual Review of Ecology and Systematics, 1: 221-238.

Erdbrink, D. P. 1953. A review of fossil and recent bears of the world. Pages 89-122, in Deventer – Drukkerij Jan De Lange.

ESRI, 1996. Environmental Systems Research Institute, Inc. Redlands, CA, U. S. A.

Ferguson, S. H., A. T. Bergerud, and R. Ferguson. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. Oecologia, 76: 236-245.

Fletcher, F. W. F. 1911. Sport on the Nilgiris and in Wynaad. MacMillan and Co, Ltd., London, U. K.

Franzmann, A. W., and C. C. Schwartz. 1988. Evaluating condition of Alaskan black bears with blood profiles. Journal of Wildlife Management, 52: 63-70.

Frid, A. and L. M. Dill. 2002. Human caused disturbance stimuli as a form of predation risk. Conservation Ecology, 6, 11 (online http//http://www. consecol.org/vol6/iss1/art11).

Ganesh, T. and P. Davidar. 1999. Fruit biomass and relative abundance of frugivores in a rain forest of southern Western Ghats, India. Journal of Tropical Ecology, 15: 399-413.

Garner, G. W., S. T. Knick, and D. C. Douglas. 1990. Seasonal movements of adult female polar bears in the Bering and Chukchi seas. International Conference on Bear Research and Management, 8: 219-226.

Garshelis, D. L. 2000. Delusions in habitat evaluation: Measuring use, selection and importance. Pages 111-164, in L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: Controversies and consequences. Columbia University Press, New York.

Garshelis, D. L., A. R. Joshi, J. L. D. Smith, and C. G. Rice. 1999. Sloth bear conservation action plan. In C. Servheen and B. Peyton, editors.

Bears: Status survey and conservation action plan. IUCN/SSC Bear and Polar Bear Specialist Groups. IUCN, Gland, Switzerland. 309p.

Garshelis, D. L., and M. R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. Journal of Mammalogy, 61: 8-19.

Garshelis, D. L., and M. R. Pelton. 1981. Movements of black bears in the Great Smoky Mountains National Park. Journal of Wildlife Management, 45: 912-925.

Garshelis, D. L., H. B. Quigley, C. R. Villarrubia, and M. R. Pelton. 1982. Assessment of telemetric motion sensors for studies of activity. Canadian Journal of Zoology, 60: 1800-1805.

Garton, E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radio-telemetry studies. Pages 16-42, in J. J. Millspaugh and J. M. Marzluff, editors. Radio-tracking and animal populations. Academic Press, San Diego, CA, U.S.A.

Gautier-Hion, A., J.-M. Duplantier, R. Quris, F. Feer, C. Sourd, J.-P. Decoux, G. Dubost, L. Emmons, C. Erard, P. Hecketsweiler, A. Moungazi, C. Roussilhon, and J.-M. Thiollay. 1985. Fruit characteristics as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia, 65: 324-337.

Gee, E. P. 1964. The wildlife of India. Collins, London, U. K. 192p.

Gende, S. M., T. P. Quinn, and M. F. Willson. 2001. Consumption choice by bears feeding on salmon. Oecologia, 127: 372-382.

Gibeau, M. L., A. P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. Biological Conservation, 103: 227-236.

Gill, J. A., and W. J. Sutherland. 2000. Predicting the consequences of human disturbance from behavioural decisions. Pages 51-64, in L. M. Gosling and W. J. Sutherland, editors, Behaviour and Conservation. Cambridge University Press, Cambridge.

Gittleman, J. L. 1993. Carnivore life histories: a re-analysis in the light of new models. Symposium of Zoological Society of London, 65: 65-86.

Gittleman, J. L. and P. H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. Behavioural Ecology and Sociobiology, 10: 57-63.

Gniadek, S. J., and K. C. Kendall. 1998. A summary of bear management in Glacier National Park, Montana, 1960-1994. Ursus, 10: 155-159.

Gokula, V., N. Sivaganesan, and M. Varadarajan. 1995. Food of the sloth bear (*Melursus ursinus*) in Mundanthurai plateau, Tamil Nadu. Journal of Bombay Natural History Society, 92: 408-410.

Goldman, P., P. R. Giri and S. J. O’Brien. 1989. Molecular genetic-distance estimates among the ursidae as indicated by one- and two-dimensional protein electrophoresis. Evolution, 43: 282-295.

Gomper, M. E. and J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia, 87: 343-348.

Gopal, R. 1991. Ethological observations on the sloth bear (*Melursus ursinus*). Indian Forester, 117: 915-920.

Groff, C. A., E. Caliari, E. Dorigatti, and A. Gozzi. 1998. Selection of denning caves by brown bears in Terentino, Italy. Ursus, 10: 275-279.

Gross, L. 2005. Why not the best? How science failed the Florida panther. PLoS Biology, 3(9): e333.

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

Harris, M. A. and Steudel, K. 1997. Ecological correlates of hind limb length in carnivora. Journal of Zoology, 241: 381-408.

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.

Harvey, P. H. and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Heinrich, B. 1977. Why have some animals evolved to regulate a high body temperature? The American Naturalist, 111: 623-640.

Heller, H. 1988. Sleep and metabolism. Canadian Journal of Zoology, 66: 61-69.

Hellgren, E. C., and M. R. Vaughan. 1988. Seasonal food habits of black bears in Great Dismal Swamp, Virginia – North Carolina. Proceedings of the Annual Conference of South-eastern Association of Fish and Wildlife Agencies, 42: 295-305.

Hellgren, E. C., M. R. Vaughan and R. L. Kirkpatrick. 1989. Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia – North Carolina. Canadian Journal of Zoology, 67: 1837-1850.

Herrera, C. M. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos, 55: 250-262.

Herrero, S. 1970. Human injury inflicted by grizzly bears. Science, 170: 593-598.

Herrero, S. 1985. Bear attacks – their causes and avoidance. Winchester Press, Piscataway, New Jersey, U. S. A. 287p.

Herrero, S., and S. Fleck. 1990. Injury to people inflicted by black, grizzly or polar bears: recent trends and new insights. International Conference on Bear Research and Management, 8: 25-32.

Hewitt, D. G. and C. T. Robbins. 1996. Estimating grizzly bear food habits from fecal analysis. Wildlife Society Bulletin, 24: 547-550.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology, 77: 132-138.

Holldobler, B., and E. O. Wilson. 1990. The Ants. Harvard University Press, Cambridge, MA, U. S. A.

Holloway, J. D., A. H. Kirk-Spriggs, and V. K. Chey. 1992. The response of some rain forest insect groups to logging and conversion to plantation. Philosophical transactions of the Royal Society of London, Series B, 335: 425-436.

Holm, G. W., F. G. Lindzey, and D. S. Moody. 1999. Interactions of sympatric black and grizzly bears in northwest Wyoming. Ursus, 11: 99-108.

Hood, G. A., and K. L. Parker. 2001. Impact of human activities on grizzly bear habitat in Jasper National Park. Wildlife Society Bulletin, 29: 624 - 638.

Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The Animal Movement Program, Version 2.04 Beta. USGS Alaska Biological Science Centre, Anchorage, AK, U. S. A.

Horner, M. A. and R. A. Powell. 1990. Internal structure of home ranges of black bears and analyses of home range overlap. Journal of Mammalogy, 71: 402-410.

Howe, H. F., and D. De Steven. 1979. Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. Oecologia, 39: 185-196.

Howe, H. F., and G. F. Estabrook. 1977. On interspecific competition for avian dispersers in tropical trees. The American Naturalist, 111: 817-832.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics, 13: 201-228.

Howe, H. F., and L. C. Westley. 1986. Ecology of pollination and seed dispersal. Pages 185-215, in M. J. Crawley, editor. Plant ecology. Blackwell Scientific Publications, Oxford.

Iswariah, V. 1984. Status survey report and recommendations for conservation of the sloth bear in Ramnagaram Taluk, Karnataka. WWF-India, unpublished report, Bangalore. 34p.

IUCN. 1996. 1996 IUCN red list of threatened animals. IUCN, Gland, Switzerland.

Iverson, S. J., J. E. McDonald, Jr., and L. K. Smith. 2001. Changes in the diet of free-ranging black bears in years of contrasting food availability revealed through milk fatty acids. Canadian Journal of Zoology, 79: 2268-2279.

Izhaki, I. 2002. The role of fruit traits in determining fruit removal in East Mediterranean ecosystems. Pages 161-175 in D. J. Levey, W. R. Selva, and M. Galetti, editors. Seed dispersal and frugivory: Ecology, evolution and conservation. CABI Publishing, Oxon, U.K.

Izhaki, I., and U. N. Safriel. 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. Oikos, 54: 23-32.

Jacobi, E. F. 1975. Breeding sloth bears in Amsterdam Zoo. Pages 351-356, in R. D. Martin, editor. Breeding endangered species in captivity. Academic Press, London.

Jacoby, M. E., G. V. Hilderbrand, C. Servheen, C. C. Schwartz, S. M. Arthur, T. A. Hanley, C. T. Robbins, and R. Michener. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management, 63: 921-929.

Johnsingh, A. J. T. 1981. Ecology and behaviour of the Dhole (*Cuon alpinus*), with special reference to prey-predator relations in Bandipur. Ph. D. Dissertation, Madurai University, Madurai, India. 306p.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, 61: 65-71.

Johnson, D. H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management, 63: 763-772.

Johnson, L. A. 1996. Black bear myrmecophagy in the central Upper Peninsula of Michigan. M. S. Thesis, Northern Michigan University, Marquette, MI, U. S. A.

Johnson, S. J., and D. E. Griffel. 1982. Sheep losses on grizzly bear range. Journal of Wildlife Management, 46: 786-790.

Jonkel, C., and I. McT. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs, 27: 1-57.

Jope, K. L. 1985. Implications of grizzly bear habituation to hikers. Wildlife Society Bulletin, 13: 32-37.

Josens, G. 1983. The soil fauna of tropical savannas: III. The termites. Pages 505-524, in F. Bourliere, editor. Ecosystems of the World 13: Tropical Savannas. Elsevier Science Publishers, Amsterdam.

Joshi, A. R. 1996. The home range, feeding habits and social organization of sloth bears (*Melursus ursinus*) in Royal Chitwan National Park, Nepal. Ph.D. Dissertation, University of Minnesota, Minneapolis.

Joshi, A. R., D. L. Garshelis and J. L. D. Smith. 1995. Home ranges of sloth bears in Nepal: Implications for conservation. Journal of Wildlife Management, 59: 204-214.

Joshi, A. R., D. L. Garshelis and J. L. D. Smith. 1997. Seasonal and habitat-related diets of sloth bears in Nepal. Journal of Mammalogy, 78: 584-597.

Joshi, A. R., J. L. D. Smith and D. L. Garshelis. 1999. Sociobiology of the myrmecophagus sloth bear in Nepal. Canadian Journal of Zoology, 77: 1690-1704.

Judd, S. L., R. R. Knight, and B. M. Blanchard. 1986. Denning of grizzly bear in the Yellowstone National Park area. International Conference on Bear Research and Management, 6: 111-117.

Kaczensky, P., D. Huber, F. Knauer, H. Roth, A. Wagner, and J. Kusak. 2001. Activity pattern of brown bears in Slovenia and Croatia. Paper presented in the 12th International Conference on Bear Research and Management, Jackson Hole, Wyoming, U.S.A.

Kavanau, J. L., and J. Ramos. 1972. Twilights and onset and cessation of carnivore activity. Journal of Wildlife Management, 36: 653-657.

Keuhn, L. A., R. A. Stubbs, and R. S. Weaver. 1970. Theory of globe thermometer. Journal of Applied Physiology, 25 (5): 750-757.

Klinka, D. R. and T. E. Reimchen. 2002. Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. Canadian Journal of Zoology, 80: 1317-1322.

Kohler, G. M. and D. J. Pierce. 2003. Black bear home-range sizes in Washington: Climatic, vegetative, and social influences. Journal of Mammalogy, 84: 81-91.

Krebs, C. J. 1989. Ecological methodology. Harper & Row Publishers, New York, N.Y. 654p.

Krebs, J. R. and N. B. Davies. 1993. An introduction to behavioural ecology, 3rd Edition. Blackwell Science, Oxford, UK. 420p.

Krishnaraju, K.S.R., A.V.R.G. Krishna Murthy, C. Subba Reddi, N. A. V. Prasad Reddy, R. Lokaranjan, and K. J. N. G. Shankar. 1987. Status of wildlife and habitat conservation in Andhra Pradesh. Journal of Bombay Natural History Society, 84: 605-619.

Kurten, B. 1968. Pleistocene mammals of Europe. Aldine, Chicago.

Landers, J. L., R. J. Hamilton, A. S. Johnson and R. L. Marchinton. 1979. Foods and habitats of black bears in south-eastern North Carolina. Journal of Wildlife Management, 43: 143-153.

Lariviere, S., J. Huot, and C. Samson. 1994. Daily activity patterns of female black bears in a northern mixed-forest environment. Journal of Mammalogy, 75: 613-620.

Laurie, A. and J. Seidensticker. 1977. Behavioural ecology of the sloth bear (*Melursus ursinus*). Journal of Zoology, 182: 187-204.

Leban, F. A. 1999. Resource Selection for Windows. Version 1.00 Beta 8.4. University of Idaho, Moscow, ID, U. S. A.

Lee, K. E., and T. G. Wood. 1971. Termites and soils. Academic Press, New York. 251 p.

Leigh, E. G. and Windsor, D. M. 1982. Forest production and regulation of primary consumers on Barro Colorado Island. Pages 111-122, in E. G. Leigh, A. S. Rand and D. M. Windsor, editors. The ecology of a neotropical forest: seasonal rhythms and long term changes. Smithsonian Institution Press, Washington, D.C.

Lenth, R. V. 1981. On finding the source of a signal. Technometrics, 23: 149-154.

Levieux, J. 1983. The soil fauna of tropical savannas. IV. The Ants. Pages 525-540, in F. Bourliere, editor. Ecosystems of the world 13: Tropical savannas. Elsevier Science Publishers, Amsterdam.

Levings, S. C. 1983. Seasonal, annual and among-site variation in the ground ant community of deciduous tropical forest: some causes of patchy species distributions. Ecological Monographs, 53: 435-455.

Lima, S. L. 1988. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. Oikos, 53: 3-11.

Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology, 68: 619-640.

Linnell, J. D. C., J. E. Swenson, R. Andersen, and B. Barnes. 2000. How vulnerable are denning bears to disturbance? Wildlife Society Bulletin, 28: 400-413.

Mace, R. D. and J. S. Waller. 1996. Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. Wildlife Society Bulletin, 24: 461-467.

Mace, R. D., J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. Journal of Applied Ecology, 33: 1395-1404.

MacDonald, D. W. 1983. The ecology of carnivore social behaviour. Nature, 301: 379-394.

Machutchon, G. A., S. Himmer, H. Davis, and M. Gallagher. 1997. Temporal and spatial activity patterns among coastal bear populations. Ursus, 10: 539-546.

MacNally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: The distinction between – and reconciliation of – ‘predictive’ and ‘explanatory’ models. Biodiversity and Conservation, 9: 655-671.

Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals: Statistical design and analysis for field studies. Chapman and Hall, London, U. K.

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

Martorello, D. A., and M. R. Pelton. 2003. Microhabitat characteristics of American black bear nest dens. Ursus, 14: 21-26.

Mattson, D. J. 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management, 8: 33-56.

Mattson, D. J. 1998. Diet and morphology of extant and recently extinct northern bears. Ursus, 10: 479-496.

Mattson, D. J. 2001. Myrmecophagy by Yellowstone grizzly bears. Canadian Journal of Zoology, 79: 779-793.

Mattson, D. J. 2002. Consumption of wasps and bees by Yellowstone grizzly bears. Northwest Science, 76(2): 166 - 172.

Mattson, D. J., and Merrill. 2002. Extirpations of grizzly bears in the contiguous United States, 1850-2000. Conservation Biology, 16: 1123-1136.

Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977-1987. Canadian Journal of Zoology, 69: 1619-1629.

Mattson, D. J., S. Herrero, R. G. Wright, and C. M. Pease. 1996. Science and management of the Rocky Mountain grizzly bears. Conservation Biology, 10: 1013-1025.

McCullough, D. R. 1982. Behaviour, bears, and humans. Wildlife Society Bulletin, 10: 27-33.

McDonald, P., R. A. Edwards, J. F. D. Greenhalgh. 1981. Animal nutrition. 3rd edition, Longman, New York.

McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. Journal of Applied Ecology, 25: 451-460.

McLellan, B. N., and D. M. Shackleton. 1989. Immediate reactions of grizzly bears to human activities. Wildlife Society Bulletin, 17: 269-274.

McLellan, B. N., F. W. Hovey, R. D. Mace, J. G. Woods, D. W. Carney, M. L. Gibeau, W. L. Wakkinen, and W. F. Kasworm. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. Journal of Wildlife Management, 63: 911-920.

McLoughlin, P. D., S. H. Ferguson and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. Evolutionary Ecology, 14: 39-60.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. The American Naturalist, 97: 133-140.

McNab, B. K. 1978. The evolution of homeothermy in the phylogeny of mammals. The American Naturalist, 112: 1-21.

McNab, B. K. 1983. Ecological and behavioural consequences of adaptation to various food resources. Pages 664-697, in J. F. Eisenberg, and D. G. Kleiman, editors. Advances in the study of mammalian behaviour. American Society of Mammalogists, Special Publication, No. 7.

McNab, B. K. 1984. Physiological convergence amongst ant-eating and termite eating mammals. Journal of Zoology, 203: 485-510.

McNab, B. K. 1992. Rate of metabolism in the termite-eating sloth bear (*Ursus ursinus*). Journal of Mammalogy, 73: 168-172.

Mech, L. D., K. L. Heezen, and D. B. Sniff. 1966. Onset and cessation of activity in cottontail rabbits and snowshoe hares in relation to sunset and sunrise. Animal Behaviour, 14: 410-413.

Mills, J., and C. Servheen. 1994. The Asian trade in bears and bear parts: impacts and conservation recommendations. International Conference on Bear Research and Management, 9: 161-167.

Murthy, R. S. and K. Sankar. 1995. Assessment of bear-man conflict in North Bilaspur. Madhya Pradesh Forest Department, Bhopal and Wildlife Institute of India, Dehradun, India. Unpublished Report.

Nams, V. O. 1989. Effects of radio-telemetry error on sample size and bias when testing habitat selection. Canadian Journal of Zoology, 67: 1631-1636.

Nelson, R. A., G. E. Folk, Jr., E. W. Pfeiffer, J. J. Craighead, C. J. Jonkel, and D. M. Wellik. 1983. Behaviour, biochemistry and hibernation in black, grizzly and polar bears. Pages 284-290, in E. C. Meslow, editor. Bears – Their Biology and Management. 5th International Conference on Bear Research and Management, Madison, WI, U.S.A.

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.

Noyce, K. V., P. B. Kannowski, and M. R. Riggs. 1997. Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Canadian Journal of Zoology, 75: 1671-1686.

Ohdachi, S., and T. Aoi. 1987. Food habits of brown bears in Hokkaido, Japan. International Conference on Bear Research and Management, 7: 215-220.

Olson, T. L., B. K. Gilbert and R. C. Squibb. 1997. The effects of increasing human activity on brown bear use of an Alaskan river. Biological Conservation, 82: 95-99.

Palomares, E., and M. Delibes. 1992. Data analysis and potential bias in radio tracking studies of animal habitat use. Acta Œcologica, 13: 221-226.

Palomares, E., and M. Delibes. 1994. Spatio – temporal ecology and behaviour of European genets in south-western Spain. Journal of Mammalogy, 75: 714-724.

Peek, J. M., M. R. Pelton, H. D. Picton, J. W. Schoen, and P. Zager. 1987. Grizzly bear conservation and management: a review. Wildlife Society Bulletin, 15: 160-169.

Pelton, M. R., C. D. Scott, and G. M. Burghardt. 1976. Attitudes and opinions of persons experiencing property damage and/or injury by black bears in the Great Smoky Mountains National Park. Pages 157-167, in M. R. Pelton, J. W. Lentfer, and G. E. Folk, Jr., editors. Bears – their biology and management. IUCN New Ser. Publ. 40.

Pengelley, E. T., and S. J. Asmundson. 1974. Circannual rhythmicity in hibernating mammals. Pages 95-160, in E. T. Pengelley, editor. Circannual clocks: animal biological rhythm. Academic Press, New York, U.S.A.

Peyton, B. 1980. Ecology, distribution and food habits of spectacled bears, *Tremarctos ornatus*, in Peru. Journal of Mammalogy, 61: 639-652.

Phythian-Adams, E. G. 1950. Jungle memories: Part V – Bears. Journal of Bombay Natural History Society, 49: 1-8.

Pocock, R. I. 1933. The black and brown bears of Europe and Asia. Part II. Journal of Bombay Natural History Society, 36: 101-138.

Porter, S. D. 1988. Impact of temperature on colony growth and development rates of the ant, *Solenopsis invicta*. Journal of Insect Physiology, 34: 1127-1133.

Powell, R. A., and D. E. Seaman. 1990. Production of important black bear foods in the southern Appalachians. International Conference on Bear Research and Management, 8: 183-187.

Powell, R. A., J. W. Zimmerman, and D. E. Seaman. 1997. Ecology and behaviour of North American black bears: home ranges, habitat and social organization. Chapman & Hall, London, U.K.

Prater, S. H. 1965. The book of Indian animals. 3rd edition, Bombay Natural History Society, Bombay. 324p.

Pritchard, G. T. and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology, 68: 1645-1651.

Prus, T. 1975. Measurement of calorific value using Phillipson microbomb calorimeter. Pages 149-159, in W. Grodzinski, R. Z. Klekowski, and A. Duncan, editors. Methods for ecological bioenergetics. Blackwell Science Publishers, Oxford.

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

Rajpurohit, K. S. and P. R. Krausman. 2000. Human - sloth-bear conflicts in Madhya Pradesh, India. Wildlife Society Bulletin, 28: 393-399.

Rangarajan, M. 1996. Fencing the forest: Conservation and ecological change in India’s Central Provinces 1860 - 1914. Oxford University Press, Delhi. 245p.

Rangarajan, M. 2001. India’s wildlife History. Permanent Black, Delhi. 135p.

Redford, K. H. 1985. Feeding and food preference in captive and wild giant anteaters (*Myrmecophaga tridactyla*). J. Zool. Ser. A., 205: 559-572.

Reid, D., M. Jiang, Q. Teng, Z. Qin, and J. Hu. 1991. Ecology of the Asiatic black bear (*Ursus thibetanus*) in Sichuan, China. Mammalia, 55: 221-237.

Robbins, C. T. 1993. Wildlife feeding and nutrition. 2nd edition, Academic Press, New York, U.S.A.

Roces, F., and J. A. Nunez. 1995. Thermal sensitivity during brood care in workers of two *Camponotus* ant species: Circadian variation and its ecological correlates. Journal of Insect Physiology, 41(8): 659-669.

Rode, K. D. and C. T. Robbins. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology, 78: 1640-1645.

Rodgers, A. R. and A. P. Carr. 2002. HRE: The Home Range Extension for Arcview. Version 1.1c. Ontario Ministry of Natural Resources, Thunder Bay, ON, Canada.

Rogers, L. L. 1987. Effects of food supply and kinship on social behaviour, movements, and population growth of black bears in north-eastern Minnesota. Wildlife Monographs, 97: 1-72.

Roth, D. H. 1983. Diel activity of a remnant population of European brown bears. In Bears – Their biology and Management. Proceedings of the Fifth International Conference on Bear Research and Management, Madison, WI, U. S. A.

Samson, C., and J. Huot. 1995. Reproductive biology of female black bears in relation to body mass in early winter. Journal of Mammalogy, 76: 68-77.

Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology, 54: 711-719.

Samy, P. L. 1970. "*Sanga Ilakkiyathil Vilangina Vilakkam*". Thirunelveli Thenninthiya Saiva Sithantha Noorpathippu Kazhagam, Chennai, India. (Tamil).

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164-182, in J. L. Gittleman, editor. Carnivore behaviour, ecology and evolution. Cornell University Press, Ithaca, NY, U. S. A.

Santiapillai, A. and C. Santiapillai. 1990. Status, distribution and conservation of the sloth bear (*Melursus ursinus*) in Sri Lanka. Tiger Paper, 17: 13-15.

Sanders, C. J. 1972. Seasonal and daily activity patterns of carpenter ants (*Camponotus* spp.) in north-western Ontario (Hymenoptera: Formicidae). The Canadian Entomologist, 104: 1681-1687.

Schaller, G. B. 1967. The deer and tiger: a study of wildlife in India. The University of Chicago Press, Chicago. 370p.

Schaller, G. B. 1970. Food habits of the Himalayan black bear (*Selenarctos thibetanus*) in the Dachigam Sanctuary, Kashmir. Journal of Bombay Natural History Society, 66: 156-159.

Schaller, G. B., Q. Teng, K. G. Johnson, X. Wang, H. Shen, and J. Hu. 1989. The feeding ecology of the giant pandas and Asiatic black bears in the Tangjiahe Reserve, China. Pages 212-241, in J. Gittleman, editor. Carnivore behaviour, ecology and evolution. Comstock Publishing Associates, Ithaca, New York.

Schmidt-Nielsen, K., F. R. Hainsworth, and D. E. Murrish. 1970. Counter current heat exchange in the respiratory passages: Effects on water and heat balance. Respiration Physiology, 9: 263-276.

Schmidt-Nielsen, K. 1972. How animals work. Cambridge University Press, London, U. K. 113p.

Schmidt-Nielsen, K. 1990. Animal physiology: Adaptation and environment, 4th edition, Cambridge University Press, Cambridge, U. K.

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

Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. Journal of Wildlife Management, 58: 367-374.

Schwartz, C. C., and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs, 113: 1-58.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology, 77: 2075-2085.

Shaw, G. and F. P. Nodder. 1791. *Vivarium Naturae*, or The Naturalist's Miscellany, Vol. II, Pl. 58 & 59, with description (5 p). London.

Siegel, S., and N. J. Castellan, Jr. 1988. Nonparametric statistics for the behavioural sciences. 2nd edition, McGraw-Hill Book Company, New York, NY, U.S.A.

Sih, A. 1993. Effects of ecological interactions on forager diets: Competition, predation risk, parasitism and prey behaviour. Pages 182-211, in R. N. Hughes, editor. Diet selection: An interdisciplinary approach to foraging behaviour. Blackwell Scientific Publications, Oxford.

Snow, D. W. 1971. Evolutionary aspects of fruit eating by birds. Ibis, 113: 194-202.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: The principles and practice of statistics in biological research. 3rd edition, W. H. Freeman and Company, New York, U.S.A. 887p.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University, Princeton, NJ, U.S.A. 247p.

Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society, 108: 344-352.

Sunquist, M. E. 1982. Movements and habitat use of a sloth bear. Mammalia, 46: 545-547.

Surridge, A. K., D. Osorio, and N. I. Mundy. 2003. Evolution and selection of trichromatic vision in primates. Trends in Ecology and Evolution, 18: 198-205.

Swenson, J. E., A. Jansson, R. Riig, and F. Sandegren. 1999a. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Canadian Journal of Zoology, 77: 551-561.

Swenson, J. E., F. Sandegren, A. Soderberg, M. Heim, O. J. Sorenson, A. Bjarvall, R. Franzen, S. Wikan, and P. Wabakken. 1999b. Interactions between brown bears and humans in Scandinavia. Biosphere Conservation, 2(1): 1-9.

Talbot, S. L. and G. F. Shields. 1996. A phylogeny of the bears (Ursidae) inferred from complete sequences of three mitochondrial genes. Molecular Phylogenetics and Evolution, 5: 567-575.

The Wildlife Society. 1995. Journal News. Journal of Wildlife Management, 59: 196-198.

Torres, J. A. 1984. Diversity and distribution of ant communities in Puerto Rico. Biotropica, 16: 296-303.

Tracy, R. L., and G. E. Walsberg. 2000. Unappreciated tolerance to high ambient temperatures in a widely distributed desert rodent, *Dipodomys merriami*. Physiological and Biochemical Zoology, 73 (6): 809-818.

Tracy, R. L., and G. E. Walsberg. 2002. Kangaroo rats revisited: re-evaluating a classic case of desert survival. Oecologia, 133: 449-457.

Ueckert, D. N., M. C. Bodine, and B. M. Spears. 1976. Population density and biomass of the desert termite *Gnathamitermes tubiformans* (Isoptera: Termitidae) in a short-grass prairie: relationship to temperature and moisture. Ecology, 57: 1273-1280.

Waits, L. P., J. Sullivan, S. J. O'Brien and R. H. Ward. 1999. Rapid radiation events in the family Ursidae indicated by likelihood phylogenetic estimation from multiple fragments of mtDNA. Molecular Phylogenetics and Evolution, 13: 82-92.

Walsberg, G. E. 2000. Small mammals in hot deserts: Some generalizations revisited. Bioscience, 50: 109-120.

Wang, L. C. H. and M. W. Wolowyk. 1988. Torpor in mammals and birds. Canadian Journal of Zoology, 66: 133-137.

Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78: 1105-1119.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA, U.S.A.

White, D., Jr., K. C. Kendall, and H. D. Picton. 1998. Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. Canadian Journal of Zoology, 76: 221-227.

White, D., Jr., K. C. Kendall, and H. D. Picton. 1999. Potential energetic effects of mountain climbers on foraging grizzly bears. Wildlife Society Bulletin, 27: 146-151.

Whittaker, D., and R. L. Knight. 1998. Understanding wildlife responses to humans. Wildlife Society Bulletin, 26: 312-317.

Wielgus, R. B. and F. L. Bunnell. 1994. Sexual segregation and female grizzly avoidance of males. Journal of Wildlife Management, 58: 405-413.

Williamson, E. A., C. E. G. Tutin, M. E. Rogers, and M. Fernandez. 1990. Composition of the diet of lowland gorillas at Lope’ in Gabon. American Journal of Primatology, 21: 265-277.

Wilson, E. O. 1971. The Insect Societies. Harvard University Press, Cambridge, MA, U.S.A.

Witmer, M. C. 1998. Ecological and evolutionary implications of energy and protein requirements of avian frugivores eating sugary diets. Physiological Zoology, 71: 599-610.

Wolda, H. 1988. Insect seasonality: why? Annual Review of Ecology and Systematics, 19: 1-18.

Wolf, B. O., and G. E. Walsberg. 1996. Thermal effects of radiation and wind on a small bird and implications for micro-site selection. Ecology, 77: 2228-2236.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecology modelling 38: 277-298.

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

Wozencraft, W. C. 1989. Classification of the recent carnivora. Pages 569-593, in J. L. Gittleman, editor. Carnivore: Behaviour, Ecology and Evolution. Cornell University Press, Ithaca, NY.

Yoccoz, N. G. 1991. Use, overuse and misuse of significance tests in evolutionary biology and ecology. Bulletin of the Ecological Society of America, 72: 106-111.

Yoganand, K., C. G. Rice, A. J. T. Johnsingh, and J. Seidensticker. (In Press). Is the sloth bear in India secure? A preliminary report on distribution, threats and conservation requirements. Journal of Bombay Natural History Society Centenary Seminar Proceedings, Mumbai, India.

Zhang, Y.-P. and O. A. Ryder. 1993. Mitochondrial DNA sequence evolution in the Arctoidea. Proceedings of the National Academy of Sciences, USA, 90: 9557-9561.