ECOLOGY OF THE LEOPARD (*Panthera pardus*) IN BORI WILDLIFE SANCTUARY AND SATPURA NATIONAL PARK, INDIA

By

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To Aai, Baba and Vinatha.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure page

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

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By

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The ecology of the leopard (*Panthera pardus*) was studied from 2002 to 2006 in the Bori Wildlife Sanctuary and Satpura National Park in Madhya Pradesh, India. Density estimates of the potential prey species of leopards and its sympatric carnivores, the tiger (*Panthera tigris*) and the dhole (*Cuon alpinus*) were made using the line-transect method annually from 2002 to 2005, and for three habitat types. The results obtained by vehicle transects were compared with those of foot transects for obtaining reliable density estimates. The food habits and prey preference of leopards, tigers and dholes were quantified. Leopard density estimates for three sites in Bori-Satpura and one site in Rajasthan, the Sariska Tiger Reserve, were made using camera traps and the mark-recapture method. A predictive habitat suitability map for leopards using Environmental Niche Factor Analysis (ENFA) was made at two scales and its reliability was evaluated. The environmental variables important in describing the habitat for leopards were identified and the extent and location of potential leopard habitat available for conservation action in south-central Madhya Pradesh was quantified.

Chital (*Axis axis*) density was higher in the moist deciduous and teak dominated habitats compared to the dry deciduous habitat. Sambar (*Cervus unicolor*) density was higher in the teak dominated habitat. The densities of nilgai (*Boselaphus tragocamelus*), wild pig (*Sus scrofa*) and

muntjac (*Muntiacus muntjak*) for the three habitat types were not statistically different. Annual density was lower for all prey species in 2005 as compared to 2002. Sambar was the most important prey species in the leopard's diet. It was also the most preferred prey species by leopards, as well as by tigers and dholes. Density of leopards was estimated at 7.3, 7.5, 8.0 and 9.3 per 100 km^2 for the four samples in Satpura Tiger Reserve using the half MMDM method and 4.2, 4.6, 5.3 and 6.2 per 100 km^2 for the full MMDM method. The estimates for the sampled area in Sariska Tiger Reserve using the two methods were 30.9 and 20.7 per 100 km^2, respectively. The results of the ENFA model showed that habitat use by leopards in Satpura was strongly associated with moist and teak forests, as well as with most prey species and was weakly negatively associated with the distance to villages. At the larger scale, in south-central Madhya Pradesh, leopard habitat was positively associated with terrain ruggedness, sambar availability and percentage of forested areas. Approximately 11500 km^2 of habitat in south-central Madhya Pradesh is likely to support leopard populations. The districts with the most optimal habitat were found to be Betul, Hoshangabad and Chhindwara, which have about 2000 km^2 of contiguous habitat for leopard conservation.

CHAPTER 1
INTRODUCTION

Humans have always been fascinated by carnivores, and our responses to them, whether positive or negative, have been strong and emotional. Partly as a result of their food habits, which have placed them in direct competition with us, partly because of their need for large undisturbed areas, and for their valuable body parts, carnivores have been persecuted for many centuries now. As a result the geographic ranges of many species have contracted, and their populations have crashed. There is an urgent need to conserve many carnivore species, and the first step towards this is to obtain knowledge about their basic biology: how many exist, what they eat and where they live. There has been very little research done on most of the 37 extant cat species of the world. This is because cats generally tend to be nocturnal, occur at low densities, and live in remote locations. They are thus difficult and expensive to study.

The leopard has had the reputation of being one of the least studied of the large carnivores despite being the most abundant (Hamilton 1976). The situation is hardly different even now, in the Indian context. Most of the studies on leopards have been done in Africa (Bailey 1993; Bertram 1982; Hamilton 1976; Jenny 1996) The sparse information on leopards in the Indian subcontinent has mostly come from studies that focussed on the tiger (Karanth & Sunquist 1995, 2000; Sunquist 1981) or the lion (Chellam 1993).

Based on estimates of density and geographic range the leopard's total effective global population size has been estimated at greater than 50000 breeding individuals, and is listed as a species of least concern by the IUCN red list. In India, however, it is listed in Schedule I of the Indian Wildlife (Protection) Act, 1972, under the highest level of protection. This is because habitat destruction, loss of wild prey, poaching for skins, bones and claws, and poisoning carcasses of livestock killed by leopards are a significant threat to the species.

The leopard is a large sized cat, weighing on an average 58 kg for males and 37.5 kg for females (Bailey 1993). It is the most widely distributed of the wild cats (Nowell & Jackson 1996), and is found in almost every kind of habitat, from the rainforests of the tropics to desert and temperate regions (Kitchener 1991). It occurs from Africa through most of Asia up to the Amur valley in Russia. The Indian subspecies, *Panthera pardus fusca*, is found in all forested habitats in the country, absent only in the arid deserts and above the timber line in the Himalayas (Prater 1980). The leopard is quite adaptable with respect to habitat and food requirements, being found in intensively cultivated and inhabited areas as well as near urban development (Nowell & Jackson 1996). There is a wide variation in the ecology of the species across its range and in different ecosystems.

Leopards have been found to be essentially solitary and territorial animals. They are most likely to socialize at the carcass of large prey (Hamilton 1976). In Wilpattu, Sri Lanka, the only social groupings seen were mother with cubs and courting pairs (Eisenberg & Lockhart 1972). In Ruhuna National Park, also in Sri Lanka the majority of leopards observed were solitary (Santiapillai et al. 1982). Schaller (1976) observed pairs only in three instances out of a total of 155 observations, the rest of which were of solitary leopards.

Scent marking has been conjectured as the primary mode of communication. This includes scraping, marking with feces and spraying of urine, which have been found in tigers to be used most often along trails and trail intersections that serve as common boundaries between territories (Smith et al. 1989). Communication has been speculated to serve several functions, chief among which are to allow leopards to separate themselves in space and time, to attract the opposite sex during courtship, and to distinguish each other by age, sex and individual status (Bailey 1993).

Home ranges in leopards have been found to vary from being exclusive or slightly overlapping to completely overlapping between the sexes. In Nepal, for example, the home range of a male leopard enclosed the home ranges of several females (Seidensticker 1976), while in Wilpattu, areas were being used exclusively by a single male and a single female (Muckenhirn & Eisenberg 1973). Male leopards had slightly overlapping home-ranges in Thailand (Rabinowitz 1989). In Kruger National Park, South Africa, little spatial overlap between home ranges of adult male leopards in summer has been observed and this decreased even further during the wet season (Bailey 1993). Female home ranges also overlapped a little, while male home ranges completely overlapped many female home ranges, as in the Nepal study (Seidensticker 1976). Female home ranges appeared to be related to availability of prey needed to successfully raise young ones. The juveniles share female home ranges until maturity after which they disperse and become transient until they can find a suitable undefended portion of habitat. They can then establish and defend a home range (Eisenberg 1986). In Asia, leopard home ranges have been reported from Sri Lanka, Nepal and Thailand. In Wilpattu, home ranges of four leopards were recorded as between 8 and 10.5 km^2 (Muckenhirn & Eisenberg 1973), while female home ranges between 6 and 13 km^2 in Nepal (Seidensticker 1976) Thailand male leopards had ranges of 27-37 km^2 and female ranges were between 11-17 km^2 (Rabinowitz 1989). The low densities of terrestrial herbivores found in rainforests may not be able to support high leopard densities. Home range of a male leopard in wet evergreen forest in Ivory Coast was found to be 86 km^2, with partially overlapping female ranges that were up to three times smaller than the male home range (Jenny 1996). The highest densities recorded in Kruger were 1 per 3.3 km^2 where prey biomass varied from 2932 to 6186 kg/km^2 (Bailey 1993) while a crude density of 1 per 29 km^2 for the entire park has been suggested (Pienaar 1969). For the Serengeti the density of leopards was estimated at about 1 per 22 to 26.5 km^2 (Schaller 1976). In Wilpattu National Park the estimated density was 1 per 29 km^2 (Muckenhirn & Eisenberg 1973). There are no published density estimates for India.

Leopards have been shown to kill medium-sized prey, mainly impala (*Aepyceros melampus*), but also take a very wide variety of small animals including hyrax, civet and mongoose in Kruger National Park in South Africa (Bailey 1993). A wide spectrum of the potential prey available in the Tai National Park, Ivory Coast, with about thirty species recorded (Hoppe-Dominik 1984). In the Kalahari desert leopards have been known to take small prey like Bat-eared foxes (*Otocyon megalotis*), jackals (*Canis spp*), genets (*Genetta spp*), hares (*Lepus spp*), duiker (*Cephalopus spp*) and porcupines (*Hystrix spp*) (Bothma & Le Riche 1984).

In Wilpattu leopards took chital, wild pig (*Sus scrofa*), sambar, langur, hare, porcupine and domestic buffalo calves (Muckenhirn & Eisenberg 1973). In Nepal, wild pig , sambar, chital, hog deer (*Axis porcinus*), muntjac and domestic cattle were part of their diet (Seidensticker et al. 1990). In the Pakistan Himalayas, leopards took mainly wild goats (*Capra aegagrus*) but also preyed on livestock, hare and porcupine (Schaller 1977). In India too dietary studies have found that leopards take a range of prey. In the Shivalik hills of Rajaji National Park analysis of scats has shown that leopards eat chital, sambar, muntjac, goral and livestock (Johnsingh *pers comm*). In Sariska Tiger Reserve leopard scats contained rodents (Sankar & Johnsingh 2002). The leopards on the Mundanthurai plateau have been preying mainly on sambar (Sathyakumar 1992) while in Bandipur the leopard kills were mainly chital (Andheria et al. 2007; Johnsingh 1983). In Gir, 40 percent of leopard scats contained chital remains while langur remains were found in 25% of the scats (Chellam 1993). Near Mumbai, leopards living near urban areas survive to a large extent on domestic dogs and rodents (Edgaonkar & Chellam 1998). In Chapter 2, I estimate the density of wild prey in the Satpura Tiger Reserve using the line transect method, while in Chapter 3 I quantify the diet of leopards and its sympatric carnivore species, the dhole (*Cuon alpinus*) and the tiger, and also estimate selection for the major prey species.

The dramatic reduction in tiger populations (Jhala et al. 2008) in India has also meant that there is increasing poaching pressure on the leopard to meet the demands of the skin and bone trade. This has been borne out by seizures of thousands of skins in recent years. In spite of this, we do not have any reliable estimate of leopard populations in India, neither do we know whether the population is really declining. An important first step is to estimate the densities at which leopards are found in Indian forests. In Chapter 4, I use camera trapping and the mark-recapture method to estimate leopard densities in three sites in the Satpura Tiger Reserve and and one site in the Sariska Tiger Reserve.

To conserve leopards, it is necessary to first identify areas that have good leopard habitat. In Chapter 5, I present a model that identifies leopard habitat using presence-only data for Satpura Tiger Reserve and for the larger south- central Madhya Pradesh. The model also identifies the habitat attributes that contribute to the likelihood of leopard presence.

The aim of this dissertation is to generate further information on the basic ecology of a large carnivore, the leopard (*Panthera pardus*), which has been little studied in India. My objectives are: 1) to estimate leopard prey density over four years in Satpura Tiger Reserve.

2) Quantify prey species selection by the leopard and its sympatric carnivores, dhole and tiger. 3) Obtain density estimates for leopards using the mark-recapture framework, and 4) to generate a leopard habitat suitability model for Satpura Tiger Reserve and for south-central Madhya Pradesh.

CHAPTER 2
DENSITY ESTIMATION OF POTENTIAL PREY SPECIES OF LARGE CARNIVORES IN SATPURA TIGER RESERVE USING LINE-TRANSECT SAMPLING.

Introduction

Accurate and precise estimation of animal abundance is a necessary first step to detect and mitigate unacceptable levels of population change. Until recently there was a paucity of reliable information on population densities of wild ungulates and other vertebrate species in India. This paucity was attributed to funding difficulties, the politics of research and the relatively small number of scientists engaged in long-term research (Eisenberg & Seidensticker 1976). However, conditions in India have changed, and in the last 10-15 years the number of ungulate studies employing rigorous methods has markedly increased and we now have population density estimates of large herbivores from at least 10 protected areas. Density estimates of large herbivores are available for Nagarhole (Karanth & Nichols 2000; Karanth & Sunquist 1992), Bandipur (Johnsingh 1983; Karanth & Nichols 2000), Bhadra (Jathanna et al. 2003), Mudumalai (Varman & Sukumar 1995), Gir (Khan et al. 1996), Melghat (Karanth & Nichols 2000), Pench (Acharya 2008; Biswas & Sankar 2002; Karanth & Nichols 2000), Kaziranga (Karanth & Nichols 2000), Ranthambore (Bagchi et al. 2004; Karanth & Nichols 2000) and Sariska (Avinandan 2003; David et al. 2005).

While these efforts are laudable, India is undergoing a rapid change and by some estimates the economy has been projected to grow annually at a rate of 5 percent or more for the next 30 years (Wilson & Purushothaman 2003). There is increasing pressure on natural areas and there are reports of decline in forest quality (Lele et al. 2000). A recently released report has estimated a population of between 1165 and 1657 tigers in India (Jhala et al. 2008), which is much lower than estimates from just a decade earlier. A critical component for conservation of tigers and other carnivores is the availability of wild prey (Karanth et al. 2004b). There is thus an urgent need to establish baseline densities of prey in all protected areas in India and put in place a monitoring program that would detect changes in their populations.

Ideally the monitoring scheme should use a method that minimizes bias and error while maximizing precision, and has sufficient power to be able to detect population changes. Distance-based methods have the advantage of not requiring animals to be handled, are relatively easy to apply and give robust results if underlying assumptions are met. Violations of these assumptions bias the resulting estimates in various ways, the details of which can be found in Buckland et al. (2001).

A disadvantage of line transects is that a large number of observations are needed to calculate the detection function precisely, and obtaining these is a labor intensive process. Vehicle transects have been run along road networks as a substitute to foot transects (Ogutu et al. 2006; Ward et al. 2004). These yield a larger effort in the same time. However, the resulting estimate may be biased as roads are not usually randomly laid with respect to the animals (Varman & Sukumar 1995). Some species are attracted to the edge habitat created by roads while other species may avoid the disturbance. This is likely to be area-specific depending on the configuration of the road network and the species being monitored. It is nevertheless worth investigating whether vehicle transects can be used to monitor populations in a given area.

The objectives of the present study are to 1) Estimate the density of potential prey species of tigers, leopards and dholes using the line-transect method. 2) Evaluate changes in density over 4 years of sampling to enable monitoring of the population, and 3) Determine if vehicle transects yield density estimates equivalent to those obtained by foot transects.

Methods

Study Area

The Satpura Tiger Reserve (22°19' to 22° 30' N and 77° 56' to 78° 20' E) is a 1428 km^2 protected area located in the Hoshangabad district of Madhya Pradesh state in India. It comprises of the Pachmarhi and Bori Wildlife Sanctuaries, and Satpura National Park. An intensive study area of approximately 200 km^2 was located in Bori Wildlife Sanctuary and Satpura National Park (Figure 2-1). The intensive study area is a mosaic of dry and moist deciduous mixed forest. Teak (*Tectona grandis*) plantations replaced mixed forests in some areas, though many of these plantations are not pure teak, but are mixed with other species. Common tree species found there include Palas, *Butea monosperma;* Mahua, *Madhuca latifolia*; Landia, *Lagerstroemia parviflora;* Kari, *Schleicheria oleosa*; Saj, *Terminalia arjuna* and Tendu, *Diospyros melanoxylon* .

The tiger (*Panthera tigris*), leopard (*Panthera pardus*) and the dhole (*Cuon alpinus*) are carnivores of management interest in the study area. Other carnivores include jackal (*Canis aureus*), striped hyena (*Hyaena hyaena*), sloth bear (*Melursus ursinus*), jungle cat (*Felis chaus*), palm civet (*Paradoxurus hermaphroditus*), small Indian civet (*Viverricula indica*), ruddy mongoose (*Herpestes smithii*), common mongoose (*Herpestes edwardsi*) and ratel (*Mellivora capensis*). A diverse community of ungulates and ground birds are preyed upon by the carnivores. Potential prey for tigers, leopards and dholes include the wild pig (*Sus scrofa*), chousingha (*Tetracerus quadricornis*), chital (*Axis axis*), Indian muntjac (*Muntiacus muntjak*), sambar (*Cervus unicolor*), nilgai (*Bosephalus tragocamelus*) gaur (*Bos gaurus*), the common langur (*Semnopithecus entellus*), black-naped hare (*Lepus nigricollis*) and Indian porcupine (*Hystrix indica).*

Estimation of Habitat Types

A georeferenced and orthorectified cloud-free Landsat ETM+ image for the study area was obtained from the Global Landcover Facility (www.landcover.org). Spectral signatures for the classification supervision were obtained by using information from vegetation plots. A sample of 473 circular plots of 10 m radius were laid along transects and dirt trails in the study area. The number and composition of woody tree species larger than saplings was noted inside the plot. Five cover types were delineated. These were: moist forest, dry forest, bare ground/village, teak dominated forest and water. Supervised classification was performed using FISHER classifier for the study site using Idrisi Kilimanjaro (Eastman 2004). The transects were then stratified *post hoc* as belonging to one of 3 different habitats: dry deciduous, moist deciduous and teak dominated. Any transect traversing more than one habitat was allocated to the habitat type that it most represented. A fourth habitat type, the riverine forest habitat, is found along streams. It was considered part of the moist deciduous habitat for the purposes of stratification since it formed a small proportion of the overall area. Density of trees along the transects was estimated from the vegetation plots, and a Sorenson's index (Krebs 1989) was calculated to quantify the tree species similarity between the three habitats.

Estimation of Prey Density

Density of the major prey species was estimated by the line-transect sampling method. Twenty permanent transects were laid in the study area. The area was divided into approximately 5 km^2 grids and ten grids were randomly chosen. A 2 km transect was laid in a random direction in each grid to make a total of 10 transects. The vegetation on the transect was minimally cut so as to allow observers to move through the forest, but not so much as to change the nature of the habitat close to the transect. These ten transects were then supplemented in the second year by ten more transects of 3 km length. These were laid systematically so that gaps in coverage between the first ten transects were filled as much as possible. The location of transects is shown in Figure 2-1. The total length of the transects was 50 km. The twenty transects were walked repeatedly for a total effort of 1272 km. Transects were walked early in the morning and evening in summer and winter at a speed of about 3 kmph, so that it took 40 minutes to walk a 2 km transect and one hour for the 3 km transect. The species, group size, angle and angular distance to the center of the group or to the individual was noted. Distance measurements were taken with a laser rangefinder (Bushnell Yardage Pro 400) and angles were measured with a magnetic compass. Program Distance v5 release 2 (Thomas et al. 2006) was used to estimate the density of prey species. Two estimates of density were made: 1) A pooled density was estimated over all habitats for each year. 2) Density was estimated pooled over all years for each habitat type. This was calculated as a mean of the densities in each habitat type weighted by the area of each habitat.

An exploratory analysis of the distribution of the distances was done by grouping them in small intervals and plotting the resulting histograms as recommended by Buckland et al. (2001). Depending on the resulting histogram, data were truncated at an appropriate distance for each species. Evidence of heaping, spikes near the line and avoidance movements or a sharp drop-off away from the line was investigated. The data were then grouped into appropriate intervals for each species so that the detection function gave a good fit.

A detection-probability function was estimated from pooled data across years and habitats for each species to maximize the number of sightings. Since all three habitats had similar tree densities, there was no reason to believe that detections differed between habitats and years. The data were modeled with the uniform, half normal and hazard rate models fitted with the cosine and simple polynomial series for each species. The negative exponential model, recommended only as a last resort, was used for the Indian peafowl since the other models did not fit well. The model with the smallest Akaike Information Criterion (AIC) value was selected as the best-fit model provided that the p-value for the chi-square goodness of fit for the model was greater than 0.05 (Burnham & Anderson 2003). The cluster size was calculated as a mean of observed clusters, and variance was calculated by bootstrapping observations within transects for most species. In the case of grey jungle fowl, muntjac and gaur the bootstrap estimates failed to converge. Variance was estimated empirically for these species.

Vehicle Transects

Sixty-five drives were made using a 4-wheel drive vehicle on the dirt trails in the study area, with a total effort of 388 km. Two observers were used and the vehicle was driven at between 10 and 15 km per hour. Perpendicular distance to the sighting was estimated by stopping in front of the animal cluster and taking a distance measurement with a laser rangefinder to the center of the cluster. The drives overlapped with each other in spatial coverage, and were made on one trail network. The data were analyzed as if it was from one drive to avoid inflating degrees of freedom, and the variance was estimated using the Poisson assumption.

Results

Description of Habitat

The teak dominated habitat had the highest stem density (798 trees/ha) and number of tree species (42) of which 20 percent was teak (163 stems/ha). The dry deciduous habitat had 35 tree species and a density of 673 stems/ha, of which the most common species was *Diospyros melanoxylon* (134 stems/ha). The moist deciduous habitat had 40 tree species (541 stems/ha) and was dominated by bamboo (83 clumps/ha). The ten most dominant species in each habitat type are presented in Table 2-1. The Sorensen's index of similarity between teak dominated and dry deciduous was 0.86, between teak dominated and moist deciduous was 0.83, and between dry deciduous and moist deciduous was 0.80.

Estimation of Density

Density estimates of potential prey species in the moist deciduous, dry deciduous and teak dominated habitats are presented in Tables 2-2, 2-3 and 2-4. Amongst the ungulates, chital were found in significantly higher densities in the moist deciduous and teak dominated habitat compared to the dry deciduous habitat. Sambar was found in significantly higher densities in the teak dominated habitat. The densities of nilgai, wild pig and muntjac for the three habitat types were not statistically different. The densities of black-naped hare, grey jungle fowl, red spurfowl and Indian peafowl were also not significantly different among the three habitats. Common langur density was highest in moist deciduous, followed by teak dominated habitat and then the dry deciduous habitat.

When pooled over all the habitats, the number of observations of chital, sambar, nilgai, muntjac, wild pig and peafowl were sufficient to estimate density for each year from 2002 to 2005. Densites were lower for all species in 2005, the last year of sampling (Figure 2-2 and 2-3) when compared to the first year, 2002. The estimates for 2002 and 2005 were statistically different for sambar, nilgai and common langur.

Average density, weighted by area of each habitat for 11 species pooled over four years is presented in Table 2-5. Common langur is the most abundant species. Amongst ungulates, chital numbers were highest, followed by sambar, nilgai, wild pig, gaur and muntjac. Ungulate densities in Satpura Tiger Reserve are among the lower estimates when compared to other protected areas in India (Table 2-6).

Density estimates derived from vehicle transects are given in Table 2-7. A comparison of density estimates from vehicle transects with those from foot transects for the same year are presented in Figure 2-3, and detection function curves for the two methods are presented in Figure 2-4. Density estimates of chital, sambar and nilgai by foot transects were higher than those estimated by vehicle transects, but the difference is not statistically significant. Density of muntjac, langur, peafowl and wild pig is greater when estimated by vehicle transects but the difference is significant only for peafowl and langur.

Discussion

The accuracy of density estimates depends on how well the underlying assumptions are met. The data were gathered by trained observers using a laser rangefinder and compass to estimate the bearing and distance to the animal group. Detections near the line, as shown by the low chi-square values for the first distance interval, were as expected for each model for all species. There was no evidence of heaping or a sharp drop-off indicating evasive movement in response to the observer for most species. Estimated strip width, as could be expected if distance played a major role in detectability, was wider for the large sized species than for the small sized species. A notable exception was the common langur, which was detected at larger distances.

Overall wild ungulate density in Satpura Tiger Reserve is lower than that reported for protected areas such as Nagarhole and Bandipur in southern India and Kanha and Pench tiger reserves in Madhya Pradesh, but is comparable to other protected areas in central India like Tadoba, Melhghat and the Maharshtra side of Pench tiger reserve (Karanth & Nichols 2000).

In the study area, the densities of most species were lowest in the dry deciduous habitat though some of these differences were not significant. There were fewer water sources in this habitat and it also tended to be closer to the villages found interspersed within the study area. These factors could be responsible for the lower densities. Nilgai, which is known to tolerate disturbance and lack of water (Bagchi et al. 2003a), was not found in lower density in this habitat. The teak dominant habitat had the highest density of sambar, but this area was close to rugged terrain and also had a number of artificial waterholes. Sambar is known to prefer hilly areas (Bhatnagar 1991) and this could have caused the higher density seen here.

Estimation of annual density shows up a pattern of density reduction for all species for the last year. Visual inspection of the data does not show a continuous declining trend for any species except for common langur. However, four years of data are too short a time period to statistically estimate a trend or rate of change using methods like generalized additive modeling (GAM) as has been done for Nagarhole (Gangadharan 2005). One study has speculated about long-term cyclic changes associated with 3 to 10 year lagged rainfall patterns (Ogutu & Owen-Smith 2005) in Africa, but there is little information to indicate the reason for this decline. Possible reasons could be pressure due to over-grazing, illegal poaching or part of a natural cyclic tendency. Personal observation did not indicate a higher degree of poaching for the last year, nor was there a change in the number of domestic cattle over the years. It can only be speculated that the below average rainfall in 2001 and 2002 (Mooley et al. 2007) may be responsible for the reduction in ungulate density in 2005.

Estimates of variance of density were lowest for langur and sambar for which a large number of observations were made, and highest for gaur, of which only 35 groups of which were observed. The variance estimate is a combination of variances in the detection probability, cluster size and encounter rate, with the encounter rate variance being the major component. Encounter rate variance remained the major component for all the years for each species, except for jungle fowl in 2005, where detection probability was the major component.

A larger effort can be achieved in a short amount of time with vehicle transects. Except for langur and peafowl, confidence intervals for the two density estimates overlapped. The state forest department clears viewing lanes along some dirt trails for tourism purposes. This probably attracts peafowl, muntjac, langur and wild pig to the cleared areas for foraging leading to an increased estimate of density. There may some tendency for larger ungulates such as chital, sambar and nilgai to stay away from the disturbance caused by roads, leading to reduced density estimates, though the difference is not significant.

Even though densities of most species are moderately low in the study area, the ungulate community is still intact and should be protected. The Bori-Satpura area is large enough to be potentially able to support a relatively large tiger population, but to do this the ungulate prey base will have to be enhanced. The baseline estimates generated in this study can be used to monitor future changes in population. The last year of sampling showed lower density for all species, and that is a matter of concern. It is therefore recommended that a monitoring program be initiated and protection measures strengthened to arrest the putative decline in wildlife populations in the study area. Vehicle transects can be used as the network of dirt trails is sufficiently extensive to be able to obtain reasonably accurate results.

Table 2-1. Density of dominant tree species (individuals per hectare) in the three habitat types along transects.

Rank order	Teak dominated plantation (N= 73 plots)	Dry deciduous teak (N = 73 plots)	Moist deciduous teak (N = 61 plots)
1	*Tectona grandis* (163)	*Diospyros melanoxylon* (134)	Bamboo species (83)
2	*Diospyros melanoxylon* (85)	*Choloroxylon swietania* (95)	*Diospyros melanoxylon* (79)
3	*Terminalia arjuna* (78)	*Terminalia arjuna* (60)	*Tectona grandis* (70)
4	*Lagerstroemia parviflora* (71)	*Tectona grandis* (53)	*Terminalia arjuna* (32)
5	*Aegle marmelos* (41)	Bamboo species (50)	*Saccopetalum tomentosum* (29)
6	*Anogeissus latifolia* (40)	*Acacia catechu* (42)	*Madhuca indica* (28)
7	*Zizyphus xylopara* (37)	*Buchanania lanzan* (35)	*Lagerstroemia parviflora* (27)
8	*Saccopetalum tomentosum* (34)	*Madhuca indica* (29)	*Emblica officinalis* (22)
9	*Buchanania lanzan* (34)	*Lagerstroemia parviflora* (22)	*Choloroxylon swietania* (20)
10	*Choloroxylon swietania* (30)	*Emblica officinalis* (21)	*Zizyphus xylopara* (20)

Table 2-2. Estimation of density parameters of potential prey by the line-transect method in the moist deciduous habitat.

Species	n	D	CV D	CI D	Ds	Cv Ds	CI Ds	Model
Chital	92	8.0	14.0	6.2-10.5	2.4	12.5	2.0-3.1	Hazard Polynomial
Sambar	68	3.8	10.6	3.0-4.4	1.8	10.1	1.4-2.0	Half-Normal Cosine
Nilgai	26	1.4	17.3	1.1-2.1	0.7	15.2	0.5-1.0	Half-Normal Cosine
Muntjak	34	1.2	21.9	0.8-2.0	1.1	21.6	0.6-1.7	Half-Normal Cosine
Wild pig	29	2.5	26.6	1.4-3.9	0.8	14.8	0.6-1.0	Half-Normal Cosine
Black-naped hare	21	2.7	16.2	2.1-3.7	2.6	15.6	2.0-3.5	Half-Normal Cosine
Common langur	313	39.9	10.3	34.0-51.0	9.1	9.5	8.0-11.7	Half-Normal Cosine
Indian peafowl	29	2.0	21.1	1.3-2.9	1.3	18.7	0.8-1.7	Neg exp Cosine
Red spurfowl	20	2.7	20.4	1.7-3.6	1.5	18.8	1.0-2.0	Half-Normal Cosine
Grey jungle fowl	34	2.9	26.9	1.5-5.6	1.6	26.2	0.8-3.0	Uniform Polynomial

n: number of observations, D: density of individuals/km^2, Ds: Density of groups/km^2, CV: coefficient of variation, CI: 95% Confidence. Sample size: 6 transects, effort: 408 km.

Table 2-3. Estimation of density parameters of potential prey by the line-transect method in the dry deciduous habitat.

Species	n	D	CV D	CI D	Ds	Cv Ds	CI Ds	Model
Chital	27	1.9	14.5	1.4-2.4	0.6	13.4	0.5-0.4	Hazard Polynomial
Sambar	70	3.1	10.2	2.4-3.6	1.5	9.6	1.1-1.7	Half-Normal Cosine
Nilgai	37	1.6	17.0	1.2-2.3	0.8	14.5	0.6-1.1	Half-Normal Cosine
Muntjak	17	0.5	36.7	0.2-1.1	0.4	36.5	0.2-0.9	Half-Normal Cosine
Wild pig	15	1.0	25.9	0.6-1.6	0.3	14.2	0.2-0.4	Half-Normal Cosine
Black-naped hare	42	4.3	15.6	3.4-6.1	4.1	15.1	3.2-5.7	Half-Normal Cosine
Common langur	155	15.7	10.4	13.4-20.2	3.6	9.6	3.1-4.6	Half-Normal Cosine
Indian peafowl	29	1.6	21.1	1.0-2.3	1.0	18.8	0.7-1.4	Neg exp Cosine
Red spurfowl	23	2.5	20.4	1.5-3.3	1.4	18.8	0.9-1.9	Half-Normal Cosine
Grey jungle fowl	42	2.9	18.9	1.9-4.4	1.5	17.9	1.0-2.3	Uniform Polynomial

n: number of observations, D: density of individuals/km^2, Ds: Density of groups/km^2, CV: coefficient of variation, CI: 95% Confidence. Sample size: 8 transects, effort: 513 km.

Table 2-4. Estimation of density parameters of potential prey by the line-transect method in the teak dominated habitat.

Species	n	D	CV D	CI D	Ds	Cv Ds	CI Ds	Model
Chital	70	7.1	13.9	5.6-9.2	2.1	12.5	1.7-2.7	Hazard Polynomial
Sambar	124	8.0	10.3	6.3-9.3	3.7	9.7	3.0-4.3	Half-Normal Cosine
Nilgai	32	2.0	17.6	1.5-3.0	1.0	15.1	0.8-1.4	Half-Normal Cosine
Muntjak	12	0.5	24.6	0.3-0.9	0.4	24.3	0.2-0.8	Half-Normal Cosine
Wild pig	19	1.9	26.2	1.1-2.9	0.6	15.6	0.4-0.8	Half-Normal Cosine
Black-naped hare	20	3.0	15.2	2.4-4.	2.8	14.6	2.3-3.9	Half-Normal Cosine
Common langur	169	25.1	10.4	21.4-32.2	5.7	9.6	5.0-7.4	Half-Normal Cosine
Indian peafowl	40	3.3	20.3	2.1-4.5	2.0	18.6	1.4-2.7	Neg exp Cosine
Red spurfowl	16	2.5	20.4	1.5-3.4	1.4	18.8	0.9-1.9	Half-Normal Cosine
Grey jungle fowl	10	1.0	36.9	0.4-2.5	0.5	36.4	0.2-1.3	Uniform Polynomial

n: number of observations, D: density of individuals/km^2, Ds: Density of groups/km^2, CV: coefficient of variation, CI: 95% Confidence. Sample size: 6 transects,effort: 351 km.

Table 2-5. Estimation of overall density and its associated parameters by the line-transect method over 4 years in the study area.

Species	n	D	CV D	CI D	Ds	Cv Ds	CI Ds	Model
Chital	189	5.4	13.8	4.2-7.1	1.6	12.4	1.3-2.1	Hazard Polynomial
Sambar	262	4.0	10.3	3.2-4.7	1.9	9.7	1.5-2.2	Half-Normal Cosine
Nilgai	95	1.6	17.0	1.2-2.3	0.8	14.7	0.6-1.1	Half-Normal Cosine
Muntjac	63	0.8	19.0	0.6-1.2	0.7	17.3	0.5-1.1	Half-Normal Cosine
Wild pig	63	1.8	26.2	1.1-2.9	0.6	14.5	0.4-0.7	Half-Normal Cosine
Black-naped hare	83	3.4	15.6	2.7-4.7	3.2	15.0	2.6-4.4	Half-Normal Cosine
Gaur	35	0.8	37.4	0.4-1.8	0.2	33.4	0.1-0.4	Half-Normal Cosine
Common langur	637	28.3	10.3	24.1-36.3	6.4	9.5	5.7-8.3	Half-Normal Cosine
Indian peafowl	98	2.0	20.0	1.3-2.9	1.3	17.7	0.9-1.7	Neg exp Cosine
Red spurfowl	59	2.6	20.4	1.6-3.5	1.5	18.8	1.0-1.9	Half-Normal Cosine
Grey jungle fowl	86	2.7	17.1	1.8-3.8	1.4	16.0	1.0-2.0	Uniform Polynomial

n: number of observations, D: density of individuals/km^2, Ds: Density of groups/km^2, CV: coefficient of variation, CI: 95% Confidence. Sample size: 20 transects, effort: 1272 km.

Table 2-6. Density of wild ungulates (individuals per km^2) at various study sites in India.

Place	Chital	Sambar	Nilgai	Muntjac	Wild pig	Gaur
Bandipur[1]	20.1	5.6	-	0.7	0.7	7.0
Nagarhole[2]	49.1	3.4	-	4.3	3.4	5.6
Pench-M.P.[3]	80.7	6.1	0.4	-	2.6	0.3
Kanha[1]	49.7	1.5	-	0.6	2.5	-
Ranthambore[5]	31.0	17.1	11.4	-	9.8	-
Sariska[6]	27.6	8.4	5.2	-	17.5	-
Gir[7]	25.2	1.8	0.4	-	2.1	-
Bhadra[4]	2.3	5.8	-	5.4	2.6	0.7
Melghat[1]	-	2.7	-	0.6	0.5	1.0
Tadoba[1]	3.2	3.3	0.7	0.9	2.6	1.8
Pench-Maharshtra[1]	5.8	5.9	0.5	-	2.0	0.8
Bori-Satpura[8]	5.4	4.0	1.6	0.8	1.8	0.8

[1]Karanth and Nichols (2000) [2]Karanth and Sunquist (1992), [3]Biswas and Sankar (2002), [4]Jathanna et al. (2003), [5]Bagchi et al. (2003) [6]Avinandan, D (2003) [7]Khan et al (1996) [8]This study.

Table 2-7. Estimation of density parameters of potential prey by the vehicle transects assuming Poisson variance.

Species	n	D	CV D	CI D	Ds	Cv Ds	CI Ds	Model
Chital	51	3.7	17.0	2.6-5.2	1.1	14.6	0.8-1.4	Uniform cosine
Sambar	61	2.3	17.7	1.7-3.3	1.1	15.1	0.8-1.5	Uniform cosine
Nilgai	21	0.5	31.4	0.3-0.9	0.3	28.0	0.2-0.6	Half-Normal Cosine
Muntjac	35	1.3	21.9	0.8-1.9	1.0	19.6	0.7-1.5	Uniform cosine
Wild pig	18	3.3	44.9	1.4-7.9	0.8	36.8	0.4-1.7	Neg exp cosine
Common langur	148	36.0	13.7	27.5-47.0	5.1	12.0	4.1-6.5	Hazard rate
Indian peafowl	74	4.9	18.0	3.4-7.0	2.6	15.1	1.9-3.5	Half normal

n: number of observations, D: density of individuals/km^2, Ds: Density of groups/km^2, CV: coefficient of variation, CI: 95% Confidence. Sample size: 1 transect, effort: 388 km.

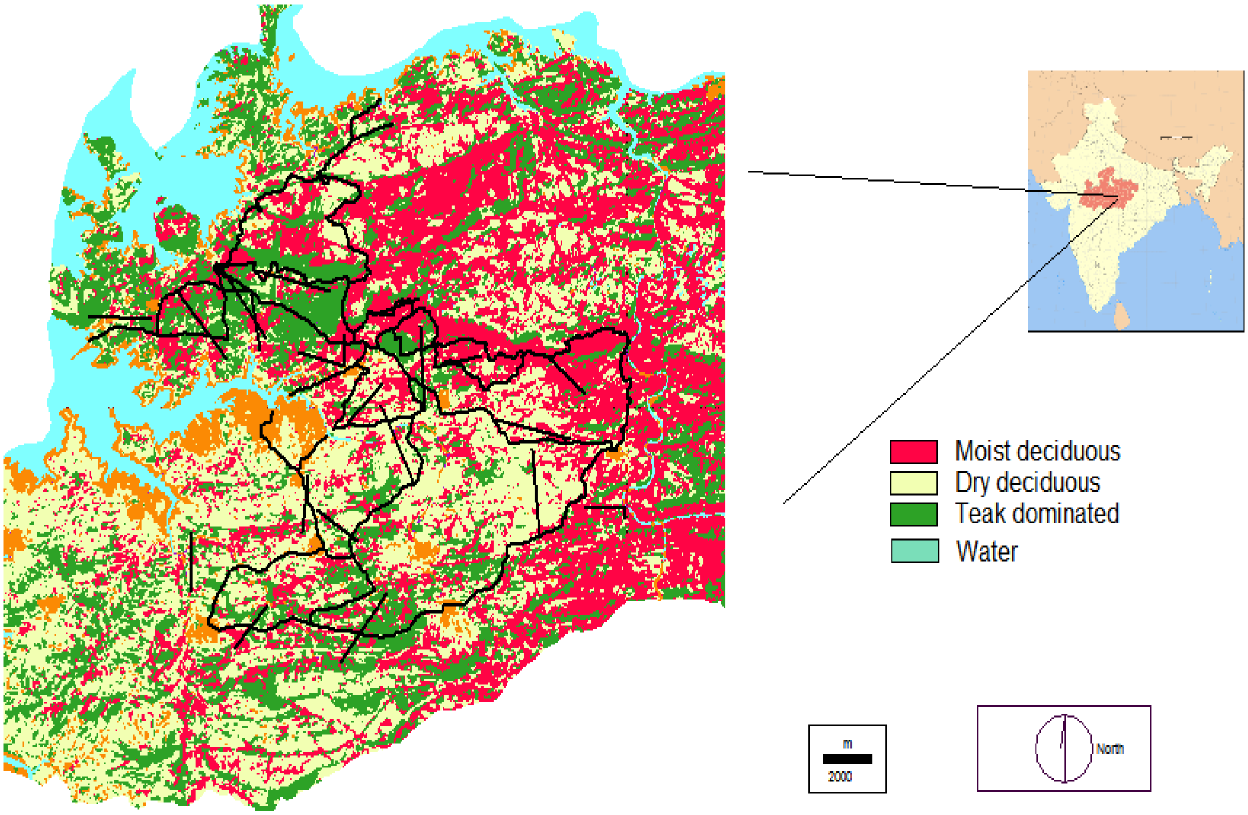

Figure 2-1. Map of the study area, showing the habitat types, transects and vehicle transects trails.

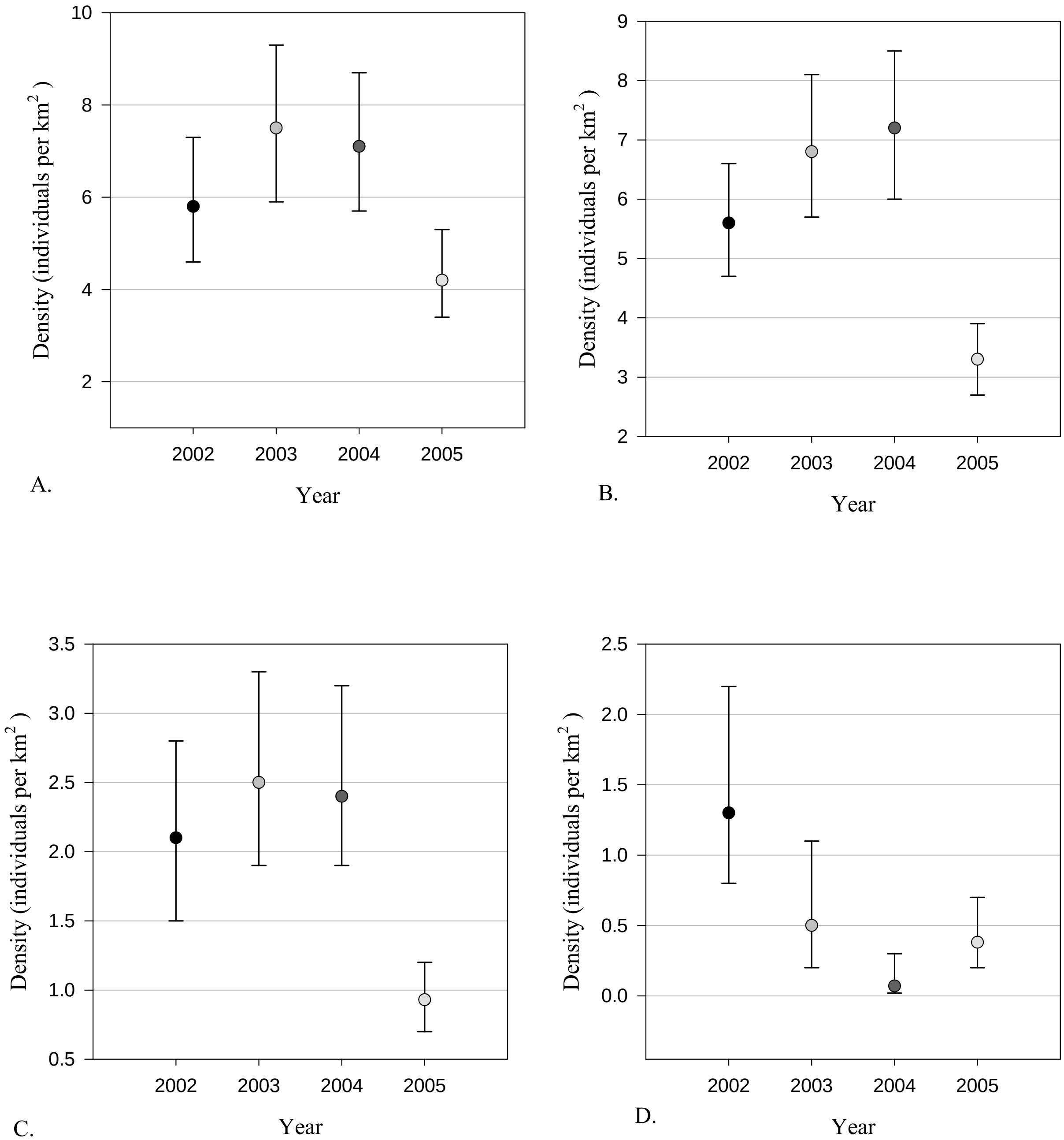

Figure 2-2. Annual densities of selected species (individuals/km^2) in the study area. A) Chital. B) Sambar. C) Nilgai. D) Muntjac. E) Common langur. F) Indian peafowl. G) Wild pig. Error bars are bootstrapped 95% confidence limits.

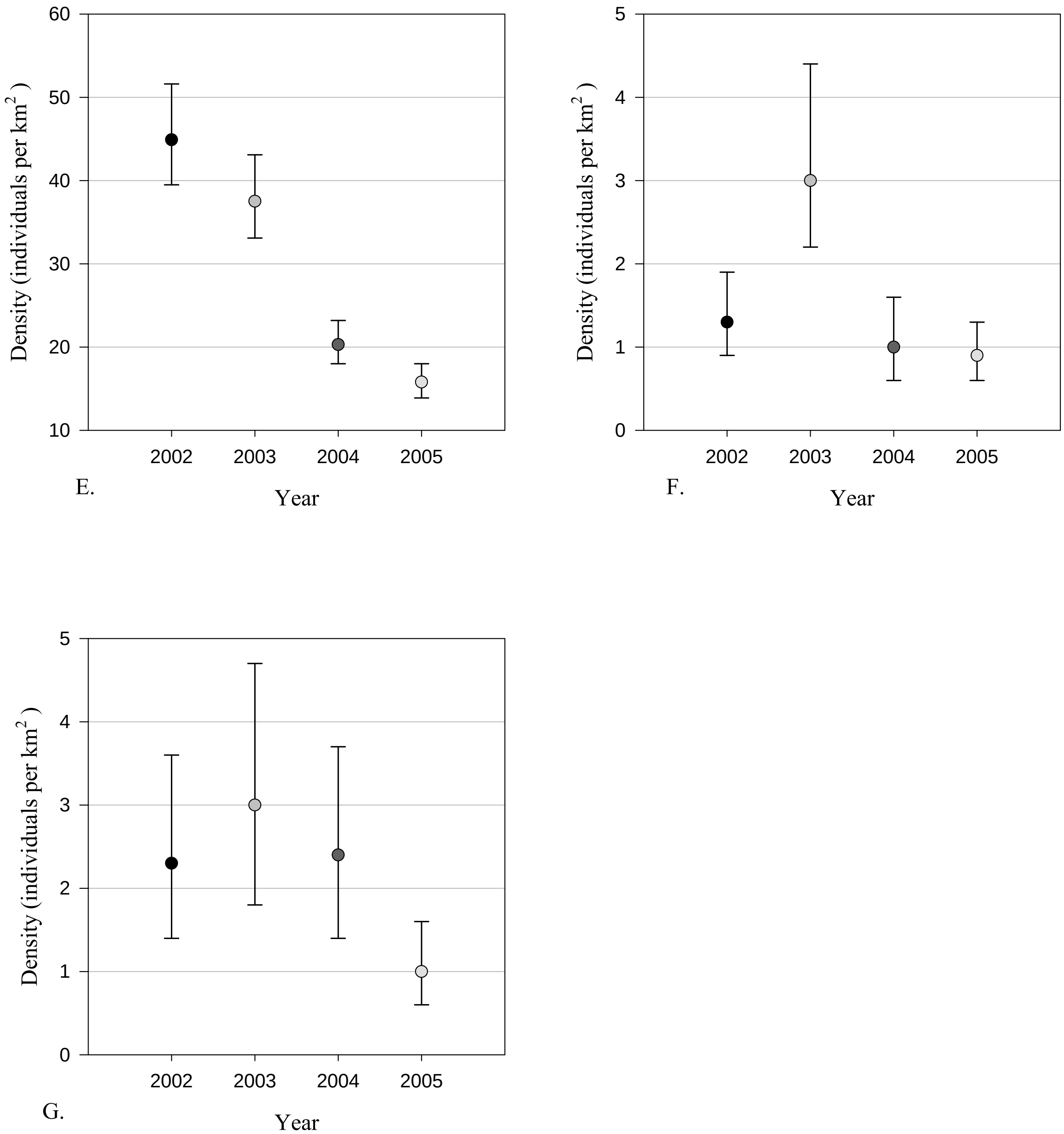

Figure 2-2: Continued.

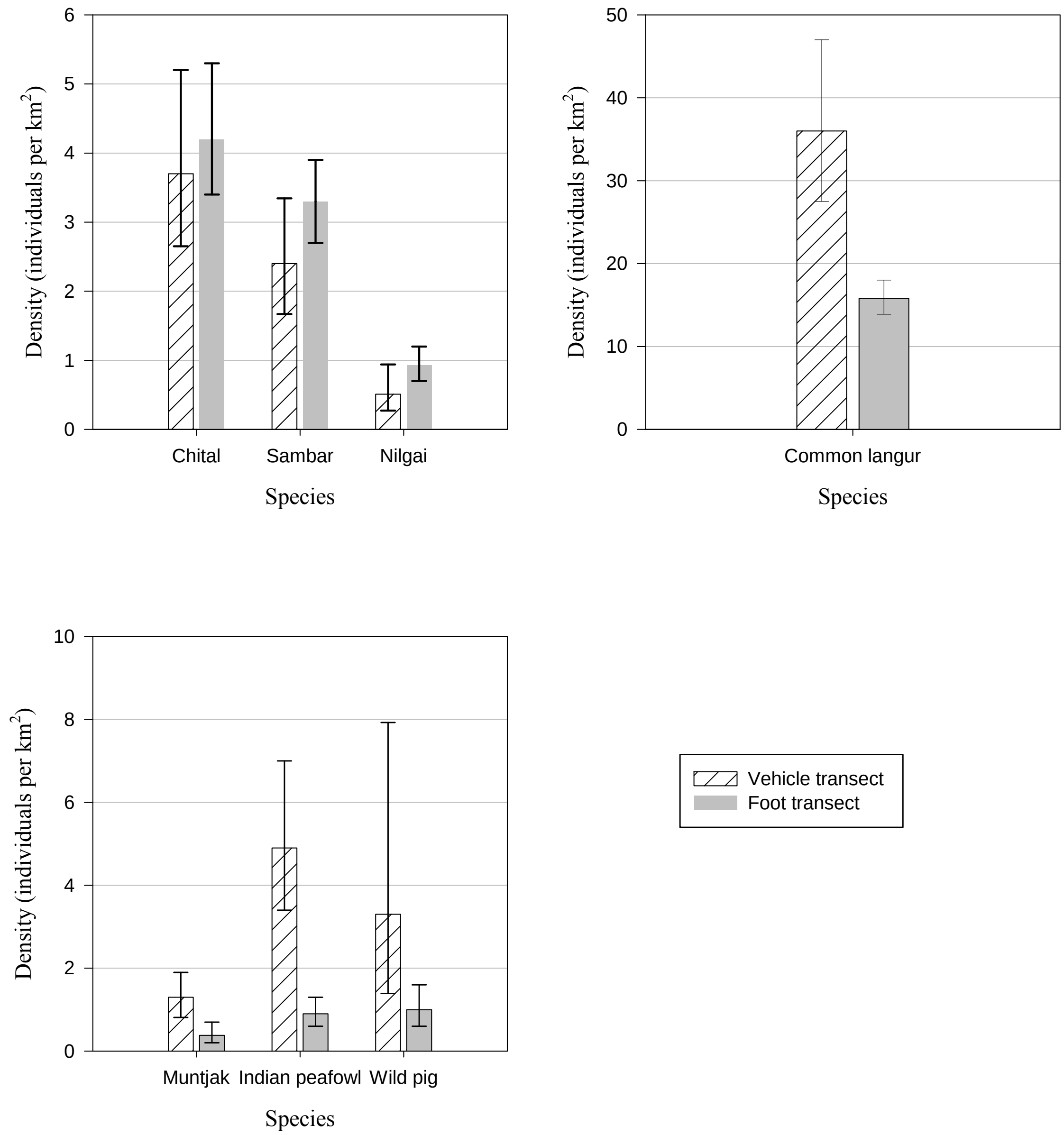

Figure 2-3. Comparison of density estimates (individuals/km^2) between foot transects and vehicle transects in 2005 for potential prey species of large carnivores in Satpura Tiger Reserve. Error bars are bootstrapped 95% confidence limits.

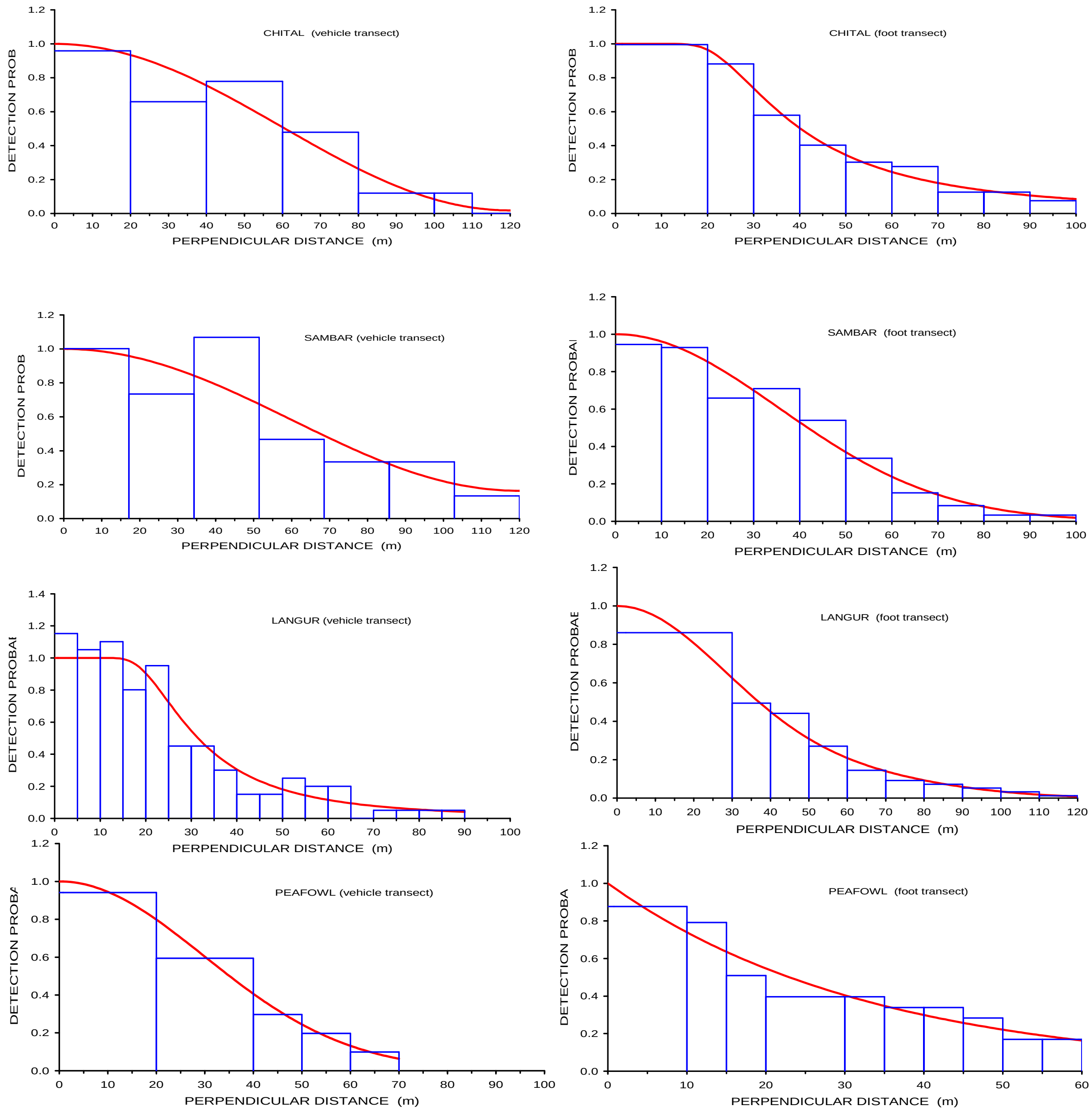

Figure 2-4. Detection function curves for vehicle and foot transects for chital, sambar, langur and peafowl.

CHAPTER 3
PREY SELECTION AND THE FOOD HABITS OF TIGER, LEOPARD AND DHOLE IN SATPURA TIGER RESERVE.

Introduction

Information about interactions between tropical large carnivore species is scarce. Some food habits studies have been conducted on single species (Bagchi et al. 2003b; Biswas & Sankar 2002; Edgaonkar & Chellam 2002; Reddy et al. 2004), and there is information on diet selection and overlap between multiple species including tigers, leopards and dholes from southern India (Johnsingh 1983; Karanth & Sunquist 1995), and on leopards and tigers (Sankar & Johnsingh 2002) and lions and leopards (Chellam 1993) in western India. Differential spatial use by tigers and leopards was reported by one study in Nepal (Seidensticker 1976), but not in another (Karanth & Sunquist 1995). In the neotropics, spatial avoidance of jaguars (*Panthera onca*) by pumas (*Puma concolor*) (Scognamillo et al. 2003) was seen at fine scales, but another (Taber et al. 1997) did not find a similar pattern. Some degree of dietary separation between pumas and jaguars has been noted, with jaguars tending to take slightly larger prey and more peccaries (Emmons 1987). Tigers and leopards are opportunistic stalking predators and are expected to kill more randomly as opposed to dhole, which is a coursing predator (Schaller 1967). Dholes, or Asiatic wild dogs, are also more diurnal than tigers and leopards (Johnsingh 1983). They are group living, coursing predators weighing about 20 kg. Anecdotal evidence exists of aggressive interactions between the three carnivores, especially between leopards and dholes. There is need for more data on the potential for competition and resource overlap among these major predators in tropical forest assemblages over a range of resource availabilities. The present study describes the prey taken, quantifies the dietary overlap and measures the prey selectivity of tigers, leopards and dholes at a site where the abundance of prey is lower than other at places where food habits of these carnivores have been studied.

Methods

Study Area

The study was conducted in the Satpura Tiger Reserve (STR). STR covers 1428 km^2 in area, and is located in the Hoshangabad district of the central Indian state of Madhya Pradesh in India. It includes three administrative units, the Pachmarhi and Bori Wildlife Sanctuaries, and Satpura National Park. An intensive study area of approximately 200 km^2 was located in Bori Wildlife Sanctuary and Satpura National Park (Figure 3-1).

The forest in STR (22°19' to 22 ° 30' N and 77 ° 56' to 78 ° 20' E) is mainly of the moist deciduous type (Champion & Seth 1968). The intensive study area is a mosaic of dry and moist deciduous forest dominated in many places by teak. Teak plantations replaced mixed forests in some areas, though now even these are not pure teak, but have secondary growth of species. Common species found there include Palas, *Butea monosperma;* Mahua, *Madhuca latifolia*; Landia, *Lagerstroemia parviflora;* Kari, *Schleicheria oleosa*; Saj, *Terminalia arjuna* and Tendu, *Diospyros melanoxylon* .

A diverse assemblage of fauna is found including wild pig (*Sus scrofa*), chousingha (*Tetracerus quadricornis*), chital (*Axis axis*), Indian muntjac (*Muntiacus muntjak*), sambar (*Cervus unicolor*), chinkara (*Gazella gazella*), nilgai (*Bosephalus tragocamelus*) and gaur (*Bos gaurus*). The common langur (*Semnopithecus entellus*) and rhesus macaque (*Macaca mulatta*) are the primates found here. Carnivores are represented by tiger (*Panthera tigris*), leopard (*Panthera pardus*), wild dog (*Cuon alpinus*), jackal (*Canis aureus*), striped hyena (*Hyaena hyaena*), sloth bear (*Melursus ursinus*), jungle cat (*Felis chaus*), palm civet (*Paradoxurus hermaphroditus*), small Indian civet (*Viverricula indica*), ruddy mongoose (*Herpestes smithii*), common mongoose (*Herpestes edwardsi*) and ratel (*Mellivora capensis*). Black-naped hare (*Lepus nigricollis*), Indian porcupine (*Hystrix indica*), Indian giant squirrel (*Ratufa indica*) and the large Indian flying squirrel (*Petaurista petaurista*) are some of the smaller mammals found here.

Reconstruction of Carnivore Diets

Scats were collected opportunistically as well as systematically along animal and man-made trails and dirt roads in the study area (Figure 3-1). Identification of tiger and leopard scats was based on associated tracks or sign. Scat size or diameter was not used as the criterion for discriminating between species as there is suspected to be overlap in scat size amongst the three species and this may lead to significant misidentification of scats (Farrell et al. 2000). Only scats of tigers and leopards that had associated tracks or sign near them were collected to ensure correct identification. Scats of dholes were easy to identify as they were deposited at communal defecation sites (Johnsingh 1983). Scats were washed and undigested remains of hair were mounted on a slide and compared under a microscope with a reference collection of hair at the Wildlife Institute of India following a standard protocol (Mukherjee et al. 1994). Bird and rodent taxa were not identified to species level. In total 193 leopard scats, 93 tiger scats and 81 dhole scats were analyzed. The percentage frequency of occurrence of all the major species was calculated along with their bootstrap confidence intervals.

Sample Size Adequacy

To check for the stability of percent frequency of occurrence in the diet, all scats for each carnivore were randomized and the percentage frequency of occurrence of each prey item in the diet was plotted cumulatively, at an interval of 10 scats. The number of scats required for the frequencies to reach an asymptote was considered sufficient to quantify that prey item in the diet reliably.

Prey Biomass and Number

The frequency of occurrence is biased towards smaller sized prey, since relatively more scats are produced for smaller prey than larger prey. To correct for this bias, relative frequencies of prey were converted to relative biomass consumed for tigers and leopards using an equation estimated for cougars (Ackerman et al. 1984), and for dholes using an equation estimated for wolves (Floyd et al. 1978). This regression equation estimates the number of field collectable scats for a given weight of prey biomass.

These are

$y = 0.38 + 0.020x$ (for dhole) and
$y = 1.98 + 0.035x$ (for tigers and leopards)

where the independent variable x is the average weight of the prey and the dependant variable y is the number of field collectable scats for that weight of prey. The dependant variable can then be converted into the relative biomass of prey consumed by multiplying it by the relative frequency of each prey species found in the scats. The relative number of each species consumed is obtained by dividing relative biomass by the average weight of the prey species. The weight of various prey species killed by tiger, leopard and dhole was assumed to be similar to that used in previous research (Karanth & Sunquist 1995).

Estimation of Prey Selection

Selectivity can be defined as taking a prey at frequencies different from that expected given its availability (Chesson 1978). If there is no selection one would expect a prey item to be taken at relative frequencies similar to the relative frequency of its availability. Any statistically significant deviation, whether positive or negative, would indicate, preference or avoidance of that prey type.

Availability of a prey species is likely to be a function of its abundance, anti-predatory behavior, habitat selection at a fine scale and time of activity. It is assumed, as in other studies (Bagchi et al. 2003b; Biswas & Sankar 2002; Karanth 1995), that abundance is the major component of availability. Abundance was therefore estimated as the density of groups of the major prey species, since the probability of encountering prey is likely to be proportional to the density of groups, rather than of individuals (Karanth & Sunquist 1995). The prey density was estimated by the line-transect method. Twenty permanent transects were laid in the study area. The first ten transects were laid randomly. The area was gridded into approximately 5 km^2 grids and ten grids were randomly chosen. A 2 km transect was laid in a random direction in each grid. The next ten transects were then laid as 3 km lines so that gaps in coverage between the first ten transects were filled as much as possible. The location of transects is shown in Figure 3-1. Transects were walked repeatedly for a total effort of 1272 km. The species, group size, angle and angular distance to the individual or center of group was noted. Distance measurements were taken with a laser rangefinder (Bushnell Yardage Pro 400) and angles were measured with a magnetic compass. Program Distance v5 release 2 (Thomas et al. 2006) was used to estimate the density of prey species.

Selectivity was quantified by comparing the observed frequency of each prey species in the scats to expected frequencies (Link & Karanth 1994). Expected frequencies were derived from the densities estimated by line transects. If a kill of $species_i$ with a density d_i , produces λ_i scats, then the proportion of scats produced when the carnivore takes prey in proportion to their density is given by

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

The program SCATMAN v2.0 (Hines 2002) was used to estimate prey selection by comparing the Πi to the the observed proportion based on random samples of predator scats. The program uses the estimated d_i and λ_i, and the variation associated with these parameters. It implements a parametric bootstrap designed to handle the problem of excessive Type I error caused by comparison of estimated frequencies as opposed to exact frequencies (Link & Karanth 1994). Inputs to the program are the estimated availability and standard error of each prey species, and the number of collectable scats that are produced by an average kill of each prey species, along with their standard errors. High chi-square values in the output indicate that observed frequencies are significantly different from expected, and the presence of selectivity of prey. The contribution of each species to the total chi-square indicates whether the prey species is taken more or less than expected.

The Jacobs' index (Jacobs 1974) has been used to estimate dietary preference in carnivores (Hayward 2006; Hayward et al. 2006a; Hayward & Kerley 2005; Hayward et al. 2006b). It has the advantage of being simple to compute and can be used to compare across studies easily. Availability and utilization of prey species in other study sites in India were obtained from the published literature. The index was computed for all the study sites using the using the formula

$$D = \frac{r - p}{r + p - 2rp}$$

where, r is the proportion of total kills of a prey species, and p is the proportion of the total abundance of that species. The values of the index range from +1 to -1, indicating maximum preference and maximum avoidance respectively.

The relative number of each prey species killed was obtained by dividing the relative biomass by the average weight of the species taken by tiger, leopard and dhole, respectively. The mean weight of prey killed was calculated as the sum of the weight of prey species multiplied by the proportional number taken.

Dietary Overlap

The extent of dietary overlap between all three species pairs was calculated by Pianka's index (Pianka 1973) . The program EcoSim version 7.72 (Gotelli & Entsminger 2007) was used on the percent frequency matrix assuming all availabilities to be equal, as well as on an electivity matrix (Lawlor 1980), which is a matrix of frequencies of prey taken weighted by their densities. The calculated index can take values from 0 to 1, where 1 stands for identical diets or complete ovelap and 0 indicates completely different diets, or no overlap. The formula used for calculating the overlap of $species_1$ with $species_2$, O_{12} is

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^{n} (p_{2i}^2)(p_{1i}^2)}}$$

where p_{ij} is the percentage frequency of species $_j$ taken by carnivore $species_i$.The index was also calculated on the electivity matrix comprising of electivity e_{ij} where R_j is the availability of prey species $_j$.

$$e_{ij} = p_{ij} / R_j$$

The program randomizes the electivity for each combination of predator and prey species to generate a null model to compare with the observed mean index. If the mean overlap index value is at either tail of the distribution of simulated values then it can be judged to be significantly different than expected by chance. The density of the major prey species was derived from the results of the line transects. Porcupine density was assumed to be similar to that reported in the literature (Sever & Mendelssohn 1991).

Results

Density of Potential Prey Species

The mean density of groups and individuals of the potential prey species over four years is presented in Table 3-1. Amongst ungulates, chital were the most common, while the Indian muntjac had the lowest density. Ground birds likely to be found in the carnivore diet are represented by the Indian peafowl (*Pavo cristatus*), grey jungle fowl (*Gallus sonneratii*) and red spurfowl (*Galloperdix spadicea*). Their densities were similar. Overall, the common langur was the most abundant prey species.

Sample Size Adequacy

The results of the scat analyses for various prey species in the diet of the three carnivores show stability (Figure 3-2). For chital, sambar and langur, about 50 scats provides a stable estimate of the percentage frequency of that prey in the diet. The sample size of scats used in the analysis can therefore be considered adequate for quantifying the major species found in the diet of these carnivores.

Composition of Diet

Leopard preyed on 10 species, the tiger took 7 species and 4 species were found in dhole scats. It was necessary to analyze about 55 scats to detect all these species (Figure 3-3). The percentage frequency and relative biomass of the major prey species in the scats of the leopard, tiger and dhole are given in Tables 3-3, 3-4 and 3-5. It can be seen that sambar is the major prey in the diet of all three predators. Chital is taken by dhole and to a lesser extent by leopard, but is not an important component of the diet of the tiger in this study. Livestock is also not an important constituent of the diet, especially for leopards and dholes. Rodents, birds, porcupines, and wild pigs also do not figure in the diet of dholes. Porcupine was only taken by leopards, while hare was taken by both leopards and dholes but not by tigers. Relative biomass and number were not estimated for the categories of bird and rodent species because of uncertainty about their weights. However, since they are a minor component of the diet, it would have little effect on the results.

Tigers take the highest mean weight of prey (129 kg), followed by dholes (46 kg) and leopard (27 kg). The percentage of prey taken by tiger, leopard and dhole in various prey size classes is presented in Figure 3-4. Leopards take prey from each size class, though they take medium-sized prey the most. Tigers and dholes seem to specialize on large and medium-sized prey, respectively. A small percentage of smaller sized prey is taken by both species, but dholes do not take larger prey.

Prey Selection

Tigers ($\chi2 = 61.5$, d. f = 4, $p < 0.01$), leopards ($\chi2 = 52.2$, d.f. = 4, $p<0.01$) and dholes ($\chi2 = 54.3$, d.f. = 3, $p< 0.01$) all exhibited overall selectivity in their diet. Figure 3-5 shows the observed and expected frequencies of the major prey species in scats. Tigers significantly preferred sambar ($\chi2 = 60.9$, $p<0.01$) while avoiding chital ($\chi2= 16.1$, $p<0.01$), langur ($\chi2= 10.3$, $p<0.01$) and hare ($\chi2= 4.1$, $p=0.04$). Wild pig was neither preferred nor avoided ($\chi2= 2.8$, $p=0.1$). Leopards also significantly preferred sambar ($\chi2 = 43.4$, $p<0.01$), while avoiding langur ($\chi2 = 20.6$, $p<0.01$) and wild pig ($\chi2 = 8.2$, $p=0.005$). Chital ($\chi2 = 0.98$, $p=0.4$) and hare ($\chi2 = 0.23$, $p=0.64$) were neither preferred nor avoided. Dholes significantly preferred both chital ($\chi2 = 18.4$, $p<0.01$) and sambar ($\chi2 = 16.7$, $p<0.01$) avoiding hare ($\chi2 = 7.2$, $p <0.01$) and langur ($\chi2 = 30.9$, $p<0.01$). Wild pig ($\chi2 = 2.1$, $p=0.15$) was taken in proportion to its availability.

The preference for major prey species by tigers, leopards and dholes in various protected areas in India using the Jacobs' index is presented in Tables 3-5, 3-6 and 3-7. Overall, tigers seem to take chital (mean Jacobs' index -0.05, SE 0.19, n=6 sites) and wild pig (mean Jacobs' index 0.06, SE 0.27, n= 6 sites) approximately in proportion to their availability, though the variance on these estimates is high. Tigers prefer sambar (mean Jacobs' index 0.38, SE 0.14, n = 6 sites) and avoid nilgai (mean Jacobs' index -0.9, SE 0.08, n = 4 sites), gaur (mean Jacobs' index -0.45, SE 0.37, n = 4 sites) and langur (mean Jacobs' index -0.2, SE 0.16, n= 5 sites). Leopards take chital in proportion to their availability (mean Jacobs' index 0.07, SE 0.1, n = 4 sites), prefer sambar (mean Jacobs' index 0.18, SE 0.27, n = 4 sites) and avoid gaur (mean Jacobs' index -0.46, SE 0.37, n =3 sites), langur (mean Jacobs' index -0.21, SE 0.3, n = 3 sites) and wild pig (mean Jacobs' index -0.12, SE 0.45, n= 4 sites). Dholes prefer chital (mean Jacobs' index 0.20, SE 0.2, n = 4 sites) and sambar (mean Jacobs' index 0.41, SE 0.28, n = 4 sites), and avoid gaur (mean Jacobs' index -0.80, SE 0.18, n = 4 sites), wild pig (mean Jacobs' index -0.12, SE 0.45, n = 4 sites) and langur (mean Jacobs' index -0.80, SE 0.13, n = 3 sites).

Diet Overlap

The diet overlap (Table 3-8) exhibited a similar pattern when calculated with percent frequency or electivity. The diets of all 3 species overlapped considerably. Tiger-leopard and leopard-dhole diets overlapped more extensively than tiger-dhole diets, though this overlap increased when electivity was used to calculate the index.

Discussion

Surprisingly, sambar is the preferred prey of all three species, and forms a large proportion of the diet of the tiger in this study. Sambar has been found to be a preferred prey of tigers in other studies also (Bagchi et al. 2003b; Biswas & Sankar 2002; Karanth & Sunquist 1995). It is a large sized deer (about 200 kg), found in moderate densities, and is known to choose dense forest areas (Varman & Sukumar 1995). This probably makes it more vulnerable to tiger predation, unlike the chital. The minor role of chital in the tiger's diet probably has to do with its habitat selection and density. In STR, chital are found in open plain areas near villages, where there is a lot of human disturbance. Their abundance is also not as high as that found in other national parks in India. Their habit of congregating near human inhabitation at night has been speculated to be the reason why they are not found in tiger diet in Bandipur (Johnsingh 1983). In Pench National Park (Biswas & Sankar 2002) in central India and in Nepal's Royal Bardia tiger reserve (Stoen & Wegge 1996), chital congregate in large numbers along low-lying areas. They comprise a larger proportion of the tiger's diet there, though they are still not highly preferred. Wild pig are also taken less than expected, and this may be because of their low densities. In Bardia and Nagarjunasagar (Reddy et al. 2004), wild pig were more commonly taken, and they were found to be preferred prey of tigers in Pench (Biswas & Sankar 2002). Common langur is also taken less than expected. In STR, langur is less important in the diet of the tiger than of the leopard with respect to biomass and percentage frequency in scats, though relatively more langur is taken by the tiger than by the leopard. This is because the diet of the leopard is more evenly distributed amongst its prey species than that of the tiger. A similar pattern was seen in the Sariska Tiger Reserve (Sankar & Johnsingh 2002), while only marginally more langur were taken by leopards in Nagarhole (Karanth & Sunquist 1995).

Although one tiger kill of gaur was seen, gaur, nilgai and muntjac were not found to be a part of the diet of the tiger as measured by scat analysis. This could be because of the low density of these species in the study area. The nilgai also prefers disturbed and open areas which are not used by the tiger (Bagchi et al. 2003a). Livestock were also not an important component of the diet, being found in about 5% of scats. This figure is comparable with some other studies, being about 7% in Srisailam Tiger Reserve (Reddy et al. 2004), and 4.3% in Pench Tiger Reserve. Leopards take chital in proportion to its availability, though it comprises about 20 % of its biomass intake. Unlike the tiger, the leopard is also found close to human inhabitation, where chital congregate at night. In STR, its relative lack of importance in the leopards diet may be due to the larger mean group size of chital (6.3 per group, n=469 groups) as compared to the sambar (2.2 per group, n=419 groups), which increases vigilance and helps avoid stalking predators. In studies where chital is a major part of the diet, the chital density is quite high as compared to sambar density (Johnsingh 1983; Karanth & Sunquist 1995). This is not the case in this study, where densities of the two ungulates are roughly similar. Hayward et al. (2006) reviewed leopard prey across many studies and concluded that preferred prey were likely to be in smaller groups and in denser vegetation than avoided prey. Chital are likely to be in larger groups and in more open vegetation than sambar, and are probably not selected because of this. In Chitwan National Park it was observed that predation on sambar by tigers increased when chital congregated in large herds on newly burned grasslands (Sunquist 1981). Perhaps the reason for a lack of preference by leopards is an anti-predatory strategy of larger herd formation. Wild pig were not an important component of the leopard's diet in Gir National Park (Mukherjee et al. 1994), in Sariska National Park (Sankar & Johnsingh 2002) and in Bandipur (Johnsingh 1992) or Nagarhole (Karanth & Sunquist 1995). In this study wild pigs were avoided, the adults are probably dangerous prey for the leopard which likely only prey upon subadults and young. Hares were taken in proportion to their availability by leopards and by dholes.

Along with sambar, chital is a preferred prey for the dhole. The herding behavior and congregation by chital is not an effective strategy against a diurnal, coursing predator. Many chases were observed, usually in the morning. The anti-predatory strategy of the chital sometimes included running towards the village, where the dhole would not follow (Johnsingh 1983).

The diets of the three predators overlap to a great extent. The tiger diet overlaps more with that of the leopard than the dhole because of shared inclusion of wild pig, cattle, rodents and birds. The dhole-leopard overlap is more than the dhole-tiger overlap because the former species-pair hunts in open areas also and both thus take a significant amount of chital, unlike the tiger.

Tigers seem to prefer large prey species that are more easily available, the mean size of prey being 129 kg. The leopard and dhole tend to take medium sized prey. The leopard takes a mean prey size of 27 kg, while the pack living dhole takes larger prey of 46 kg. The leopard also takes the largest range of prey size, taking small prey like hare, birds, rodents and porcupines that dhole did not kill in this study.

Table 3-1. Estimation of overall density and its associated parameters by the line-transect method over 4 years in the study area.

Species	n	D	CV D	CI D	Ds	Cv Ds	CI Ds	Model
Chital	189	5.4	13.8	4.2-7.1	1.6	12.4	1.3-2.1	Hazard Polynomial
Sambar	262	4.0	10.3	3.2-4.7	1.9	9.7	1.5-2.2	Half-Normal Cosine
Nilgai	95	1.6	17.0	1.2-2.3	0.8	14.7	0.6-1.1	Half-Normal Cosine
Muntjak	63	0.8	19.0	0.6-1.2	0.7	17.3	0.5-1.1	Half-Normal Cosine
Wild pig	63	1.8	26.2	1.1-2.9	0.6	14.5	0.4-0.7	Half-Normal Cosine
Black-naped hare	83	3.4	15.6	2.7-4.7	3.2	15.0	2.6-4.4	Half-Normal Cosine
Gaur	35	0.8	37.4	0.4-1.8	0.2	33.4	0.1-0.4	Half-Normal Cosine
Common langur	637	28.3	10.3	24.1-36.3	6.4	9.5	5.7-8.3	Half-Normal Cosine
Indian peafowl	98	2.0	20.0	1.3-2.9	1.3	17.7	0.9-1.7	Neg exp Cosine
Red spurfowl	59	2.6	20.4	1.6-3.5	1.5	18.8	1.0-1.9	Half-Normal Cosine
Grey jungle fowl	86	2.7	17.1	1.8-3.8	1.4	16.0	1.0-2.0	Uniform Polynomial

n: number of observations, D: density of individuals/km^2, Ds: Density of groups/km^2, CV: coefficient of variation, CI: 95% Confidence. Sample size: 20 transects, effort: 1272 km.

Table 3-2. Food habits of the leopard obtained by scat analyses (N =193 scats).

Species	Weight Of prey	Scats	Collectable scats per kill	% in Scat	Bootstrapped CI (95%)	Percent Biomass	Relative number
Sambar	62	102	14.9	52.8	46.1-59.6	62.2	27.1
Chital	48	39	13.1	20.2	15.0-25.9	20.7	11.6
Langur	8	21	3.5	10.9	6.7-15.5	7.0	23.7
Hare	3	11	1.4	5.7	2.6-9.3	3.2	29.2
Wild pig	37	4	11.3	2.1	0.5-4.1	1.8	1.3
Cattle	150	3	20.7	1.6	0.0-3.6	3.1	0.5
Porcupine	8	6	3.5	3.1	0.0-3.6	1.9	6.5
Rodents	0.1	6	0.05	3.1	1.0-3.6	-	-
Bird spp	5	7	2.3	3.6	1.0-6.2	-	-

Table 3-3. Food habits of the tiger obtained by scat analyses (N = 93 scats).

Species	Weight Of Prey	Scats	Collectable scats per kill	% in Scat	Bootstrapped CI (95%)	Percent Biomass	Relative number
Sambar	212	73	22.5	78.5	69.9-86.0	89.6	54.8
Chital	55	4	14.1	4.3	1.1-8.6	2.0	4.8
Langur	8	7	3.5	7.5	2.2-12.9	2.1	33.6
Hare	3	0	1.4	0	-	0	0
Wild pig	38	2	11.5	2.2	0.0-5.4	0.9	2.9
Cattle	180	5	21.7	5.3	1.1-10.8	5.4	3.9
Porcupine	8	0	3.5	0	-	0	0
Rodents	0.1	2	0.05	2.0	0.0-5.4	-	-
Bird spp	5	2	2.3	2.0	0.0-5.4	-	-

Table 3-4. Food habits of the dhole obtained by scat analyses (N = 81 scats).

Species	Weight Of Prey	Scats	Collectable scats per kill	% in scat	Bootstrapped CI (95%)	Percent Biomass	Relative number
Sambar	70	39	39.3	48.1	37.0-59.3	56.0	36.8
Chital	55	34	37.2	41.9	31.5-51.9	40.7	34.1
Langur	8	5	14.8	6.2	1.2-12.3	2.2	12.6
Hare	3	3	6.8	3.7	0.00-8.6	1.1	16.4
Wild pig	38	3	33.3	0	-	0	0

Table 3-5. Jacobs' index values of preference for prey species in tiger diets at study sites in India.

Place	Chital	Sambar	Nilgai	Wild pig	Gaur	Langur
Bandipur[1]	-0.30	0.07	N.P	0.77	-0.06	N.A.
Nagarhole[2]	-0.45	0.65	N.P.	0.68	0.26	-0.36
Pench[3]	0.11	0.50	-1	0.32	-1	-0.35
Ranthambore[4]	0.32	0.19	-0.71	-0.49	N.P	-0.06
Sariska[5]	0.54	0.07	-0.96	-0.71	N.P	0.30
STR[6]	-0.51	0.81	-1	-0.18	-1	-0.54

[1]Andheria et al.(2007), [2]Karanth and Sunquist (1995), [3]Biswas and Sankar(2002), [4]Bagchi et al. (2003b), [5]Sankar and Johnsingh (2002), [6]this study. NP= not present, NA = not estimated.

Table 3-6. Jacobs' index values of preference for prey species in leopard diets at study sites in India.

Place	Chital	Sambar	Wild pig	Gaur	Langur
Bandipur[1]	0.07	-0.43	0.76	-0.42	NA
Nagarhole[2]	-0.02	0.62	0.27	0.05	0.10
Sariska[3]	0.31	0.05	-1	NP	-0.04
STR[4]	-0.08	0.50	-0.51	-1	-0.69

[1]Andheria et al.(2007), [2]Karanth and Sunquist (1995), [3]Sankar and Johnsingh (2002), [4]this study. NP= not present, NA = not estimated.

Table 3-7. Jacobs' index values of preference for prey species in dhole diets at study sites in India.

Place	Chital	Sambar	Wild pig	Gaur	Langur
Bandipur[1]	0.46	-0.28	0.64	-0.95	NA
Nagarhole[2]	-0.10	0.46	0.42	-0.94	-0.96
Pench[3]	-0.08	0.81	-0.56	-0.33	-0.59
STR[4]	0.53	0.65	-1	-1	-0.84

[1]Andheria et al.(2007), [2]Karanth and Sunquist (1995), [3]Biswas and Sankar(2002), [4]this study. NA = not estimated.

Table 3-8. Diet overlap between tiger, leopard and dhole using Pianka's index.

Species	Dhole Frequency/electivity	Leopard Frequency/electivity
Tiger	0.79/0.88	0.94/0.96
Dhole		0.93/0.95

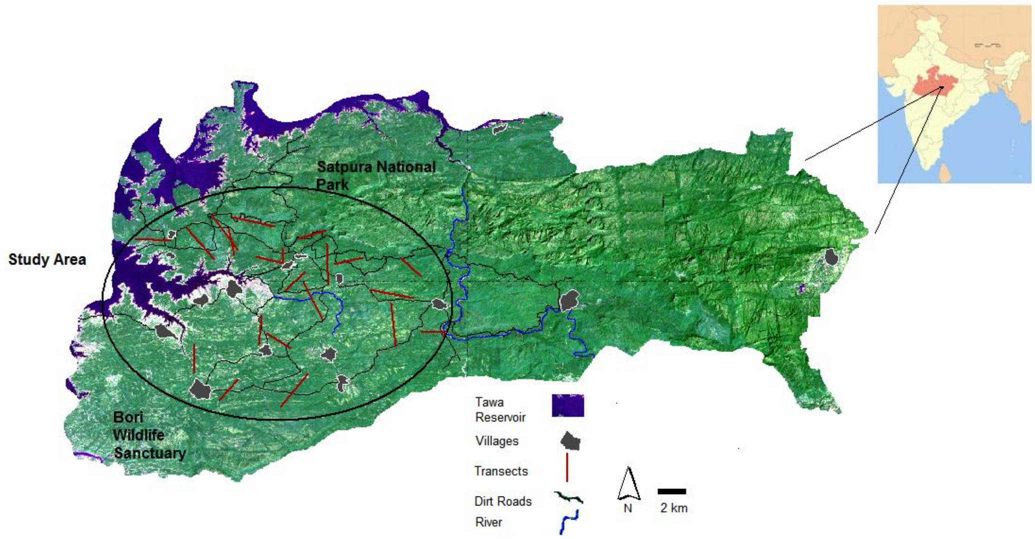

Figure 3-1. Map of Bori Wildlife Sanctuary and Satpura National Park, showing the location of line transects, dirt roads and the study area.

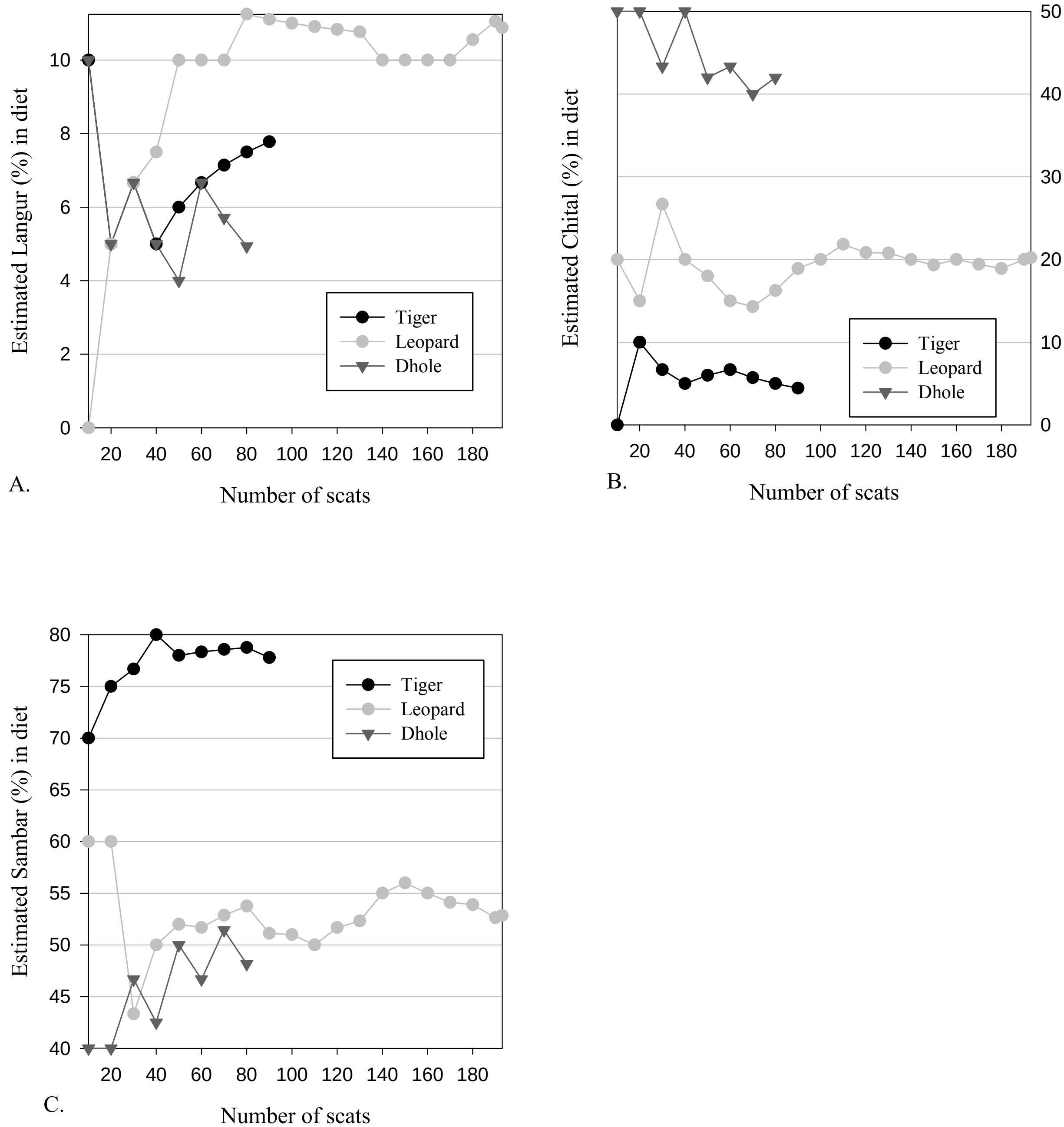

Figure 3-2. Relationship between sample size of scats and the percent frequency of occurrence in tiger, leopard and dhole diet of A) Langur, B) Chital and C) Sambar.

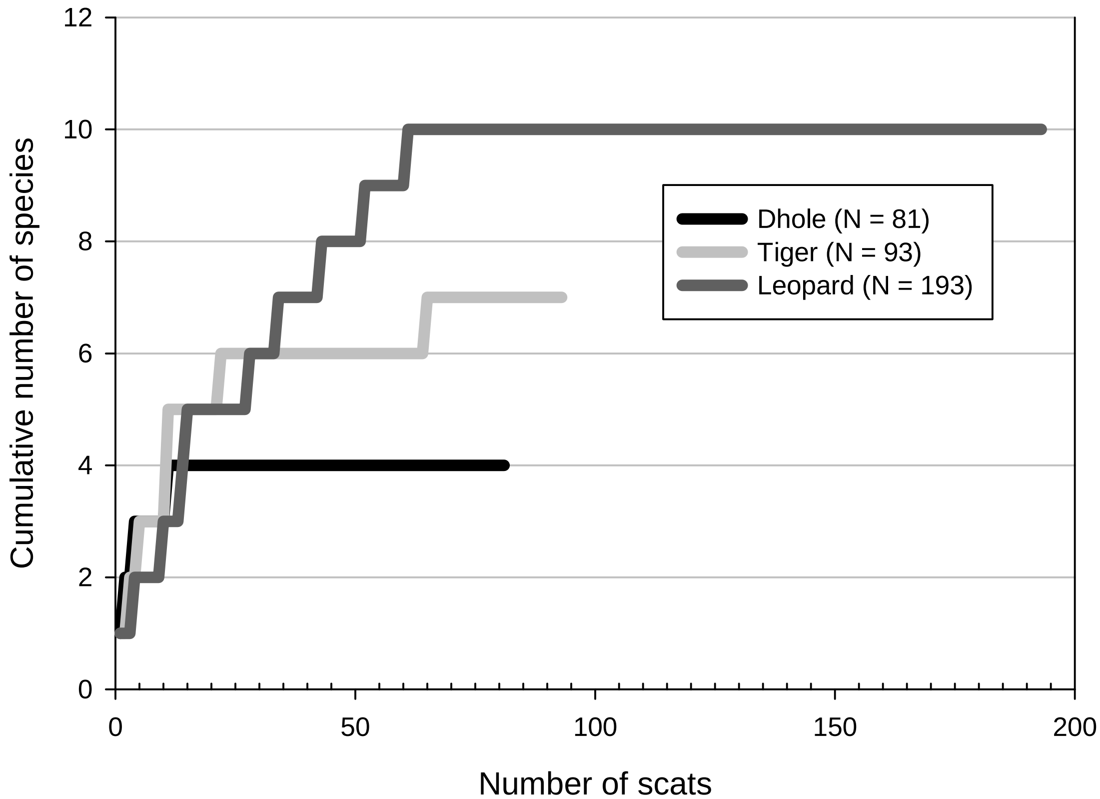

Figure 3-3. Relationship between the number of scats analyzed and the number of prey species found in the diet of tiger, leopard and dhole.

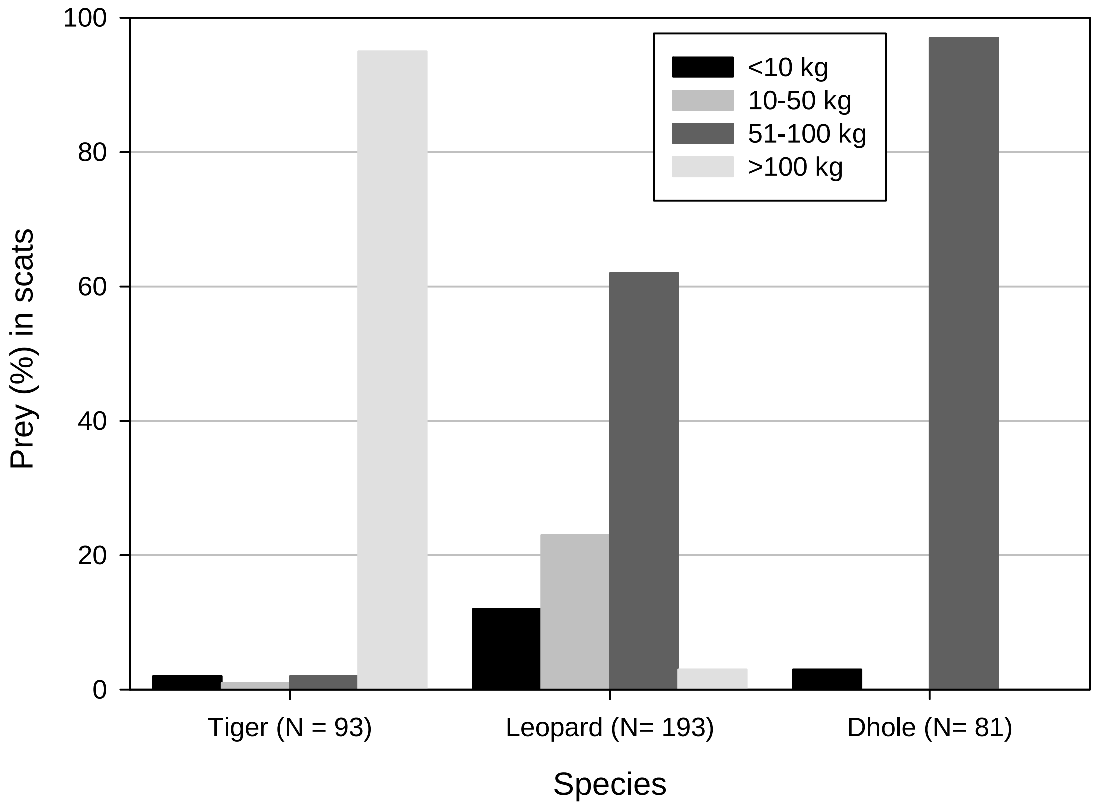

Figure 3-4. Prey taken by tiger, leopard and dhole in various body weight categories.

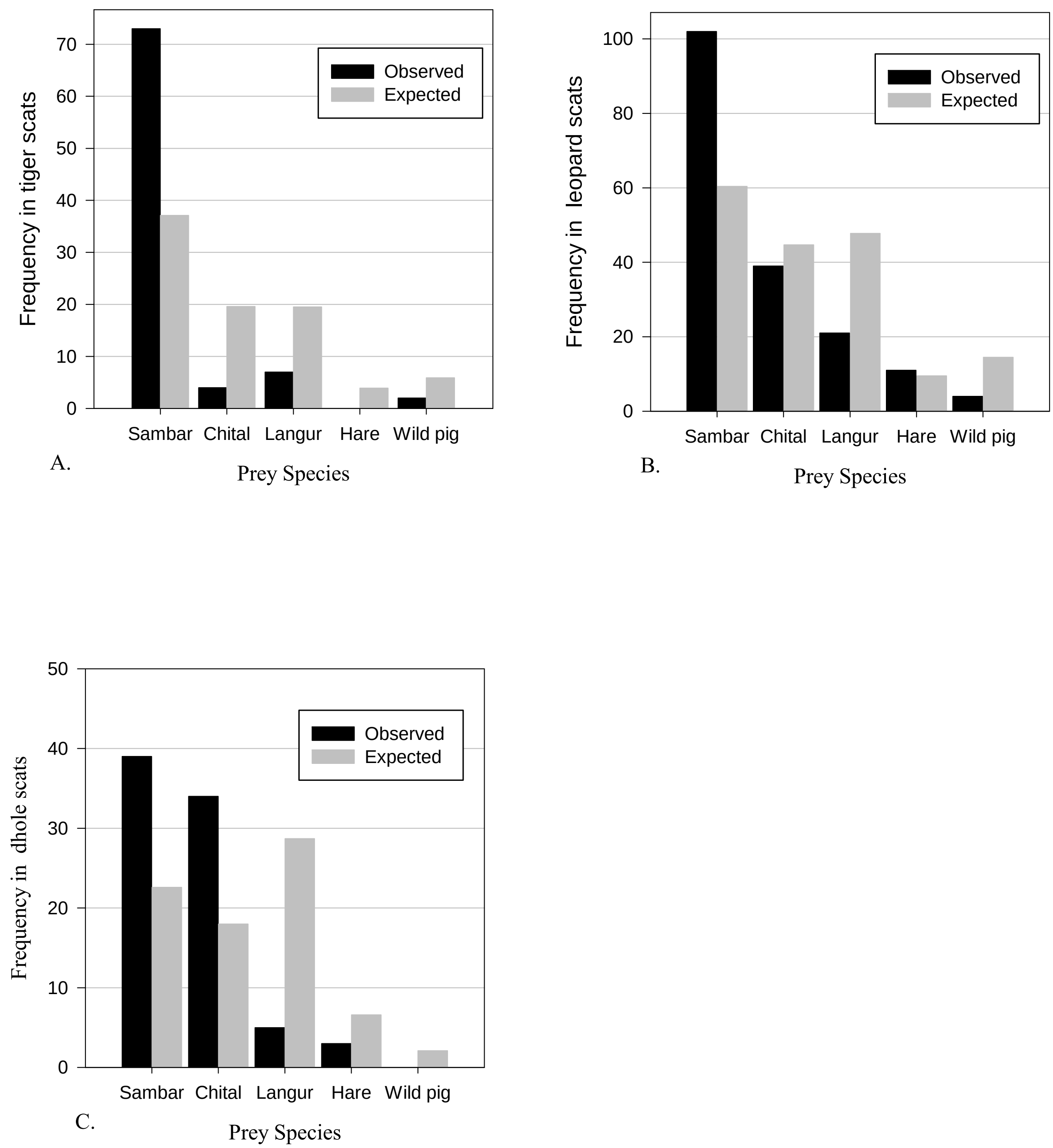

Figure 3-5. Observed and expected frequencies of prey items in scats of A) Tiger, B) Leopard and C) Dhole.

CHAPTER 4
ESTIMATION OF LEOPARD (*Panthera pardus*) ABUNDANCE IN INDIAN FORESTS USING CAMERA TRAPS IN A MARK-RECAPTURE FRAMEWORK.

Introduction

While there has been increased attention to the need for reliable estimates of carnivore densities in India, the work has been largely restricted to tigers, *Panthera tigris* (Harihar 2005; Karanth et al. 2004a; Karanth & Nichols 1998). Even basic information on other large felids is poor, except for food habits. Leopards have been in the popular media in India largely because of an increase in human conflicts. There is a perception that attacks on humans have escalated in recent years, which has been attributed to various causes, including decrease in habitat, decline in leopard prey populations, increase in leopard densities and effects of translocations near populated areas (Athreya et al. 2007). Unfortunately, data on leopard or prey abundances in any of the conflict areas are lacking, and therefore the causes remain speculative.

Estimation of leopard density is, however, logistically feasible even though leopards tend to be nocturnal, inhabit dense cover and occupy large ranges. Camera trapping has been used in conjunction with mark-recapture techniques to estimate the population size of species in which individuals can be uniquely identified based on the coat patterns or other external marks. The primary method of censusing tiger, leopard and lions (*Panthera leo*) by the government agency in India has been the pugmark method (Panwar 1979). This involves taking plaster casts or paper traces of the tracks of the targeted carnivore species in the entire survey area. The assumption is made that the tracks of all individuals are recorded and that all individuals can be identified on the basis of the tracings of their tracks. The method has been criticized for its subjective nature and the lack of incorporation of a correction for detectability (Karanth et al. 2003).

The use of statistically robust indices to monitor populaton trends have been suggested, like track indices (Karanth et al. 2003), camera trapping rates (Carbone et al. 2001; Karanth & Nichols 2002) or occupancy models (MacKenzie & Nichols 2004), but these methods do not provide an estimate of the number of individuals in the protected area.

The mark-recapture method has long been used to estimate biological populations (Otis et al. 1978). Recently the method has been adapted to estimate tiger populations in India using remote camera traps. There are now estimates for tigers (Johnson et al. 2006; Karanth & Nichols 1998; O'Brien et al. 2003), leopards (Spalton et al. 2006), jaguars (*Panthera onca*) (Silver et al. 2004; Soisalo & Cavalcanti 2006) and snow leopards (*Panthera uncia*) (Jackson et al. 2006) using mark recapture for other parts of the world and it is now the accepted method. In India there are few published studies on population estimation for carnivores other than the tiger. It is expected that more studies of leopard abundances will soon be available for this part of the world.

Methods

Study Area

Leopard densities were estimated at three adjacent sites in Satpura Tiger Reserve and one site in Sariska Tiger Reserve. The Satpura Tiger Reserve (22^{o} 19' to 22^{o} 30' N and 77^{o} 56' to 78^{o} 20' E) covers 1428 km^2, and is located in the Hoshangabad district of the central Indian state of Madhya Pradesh. It consists of three administrative units, the Pachmarhi and Bori Wildlife Sanctuaries, and Satpura National Park. The forest is mainly the moist deciduous type (Champion & Seth 1968). The major ungulate fauna includes chital (*Axis axis*), sambar (*Cervus unicolor*), Indian muntjac (*Muntiacus muntjac*) and gaur (*Bos gaurus*). The major carnivores are tiger, leopard, sloth bear (*Melursus ursinus*) and dhole (*Cuon alpinus*). The Sariska Tiger Reserve (25 ^{o} 05' to 25 ^{o} 27' N and 74^{o}17' to 76 ^{o} 74' E) covers 800 km^2 and located in the north-western state of Rajasthan, in the Alwar district in India. The forest is mainly the tropical dry deciduous and thorn type (Champion & Seth 1968). The major ungulates are chital, sambar and nilgai (*Bosephalus tragocamelus*). Gaur and muntjac do not occur there. Major carnivores are leopard, striped hyena (*Hyaena hyaena*), jungle cat (*Felis chaus*) and golden jackal (*Canis aureus*). Sloth bears and dhole are absent while the tiger has recently gone locally extinct due to illegal hunting.

Field Methods

Four sites were chosen for estimation of leopard abundances. Camera-trapping effort at these sites ranged from 33 days (396 trap nights) to 76 days (1216 trap nights). Three of the sites (Churna, Kamti and Lagda) were adjacent to each other in the Satpura Tiger Reserve in central India (Figure 4-3) while the fourth was in Sariska Tiger Reserve (Figure 4-4). Camera trap locations were chosen after reconnaissance to maximize the probability of getting photos of leopards. Locations close to villages or on routes where there was a great deal of human movement were excluded to minimize the possibility of theft. Trailmaster 1550 (Goodson Associates, Lenexa, Kansas) camera traps with Olympus and Canon autofocus cameras were deployed at all sites. At two sites (Churna and Sariska), a one-camera setup was used at most stations, and a two-camera setup was used at a few stations. These two- camera setup locations were changed when both flanks of individuals in that area were obtained. At the other two sites each camera location had a two-camera setup to photograph both flanks at the same time. Camera traps were activated at dusk and deactivated at dawn. The minimum interval between two photos was 6 seconds. Camera sensors were placed at a height that allowed photographs of smaller species like black-naped hare (*Lepus nigricollis*) and grey jungle fowl (*Gallus sonneratii*).

Analytical Methods

All photos were scanned, printed (Fig. 2-1) and the flank of each leopard photographed was compared to every other leopard photo. Printouts of the photos were scrutinized under a magnifying glass to identify patterns of similar looking spots. Photos that were underexposed due to the leopard being farther away from the camera, or where the coat patterns were distorted because the individual was not approximately parallel to the camera, were difficult to identify. Difficult photos were enlarged and matched on the computer after some image processing to enhance contrast and brightness. If a pattern was detected then a separate area of the flank was checked to confirm the identity of the leopard. Leopards whose identities could not be confirmed were discarded and not used in the analysis. Sometimes photos of both flanks were available, usually in cases where two cameras were used. In one case a clear photograph of the face was available to link the two flanks. In these cases the identity of the leopard was unambiguous, and the leopard was included in analyses of both flanks. The number of individuals obtained from the right flank and the left flank were compared and the dataset with the greater number of individuals was used for the analysis.

Estimation of population size

For all sites, capture histories were developed using each day as the sampling occasion. The capture history for each individual leopard consisted of a row vector of t entries where t is the number of trapping occasions for each site. Each entry takes a value of either 1 or 0 depending on whether the individual leopard was photographed on that particular occasion or not. The entire matrix of observations for all the leopards, called the X matrix (Otis et al. 1978) was used to estimate the population, $\hat{N}$, and its standard error. Program CAPTURE2 (Hines 1994) was used for the estimation. CAPTURE2 estimates the population parameters under various assumptions of the sources of variability in capture probabilities. These are: none (M_o), individual heterogeneity (M_h), behavioral heterogeneity (M_b) and time (M_t). The null model, M_o, corresponds to the case which assumes that the capture probability across all individuals is the same. Model M_h assumes that each individual has its own capture probability, and this differs from that of all other individuals. Model M_b assumes that the capture probability varies after the individual is caught for the first time, and becomes either trap shy or trap happy. Model M_t refers to change in capture probability from one occasion to another. Models M_{bh}, M_{th}, M_{tb} and M_{tbh}, assume that variation in capture probability is explained by a combination of these sources of variation. Goodness-of-fit tests and tests of models M_o vs M_h, M_o vs, M_b, M_o vs M_t was calculated using program CAPTURE2 where enough data was available. A model selection procedure which scores the models according to appropriateness using a discriminant function criterion was used (Otis et al. 1978; Rexstad & Burnham 1991). Model M_o, the simplest model, is sensitive to violations of the assumption of similar individual capture probabilities, so when this model was selected, the parameters computed using the next best model have also been presented. The test for population closure computed by program CAPTURE2 was used to detect violation of this assumption. Also, in Churna where trapping was conducted for 150 days, two estimates were obtained for 75 days each to enable the closure assumption to be maintained within these two shorter sessions.

Estimation of leopard density

The Effective Trapping Area (ETA) method: Density, $\hat{D}$, is defined as $\hat{N} / \hat{A}$, where $\hat{N}$ is the estimated number of leopards and $\hat{A}$ is the estimated area in which the sampling was conducted. This area is typically the area encompassed by the trapping grid, plus a strip of buffer around it (Dice 1938), to obtain an ETA (Figure 4-5). The buffering was done using both concave and convex polygons. Boundary width was calculated using the mean maximum distance moved (full-MMDM), and half-MMDM (Parmenter et al. 2003), to get a total of four ETAs (concave-MMDM, convex-MMDM, concave-half MMDM, convex-half MMDM). MMDM and its standard error were approximated by the mean of the maximum distance between two photos of each individual leopard for all leopards photographed at more than one camera trap location. Any portion of the ETA that lay outside the boundaries of the Tiger Reserve was subtracted using a GIS package. A relatively small area (26 km^2) was sampled in Sariska, and so the data from this site were not used in the MMDM estimation.

The Spatially Explicit Maximum Likelihood method: Efford (2004) estimated $\hat{D}$ directly from trapping data by a simulation of the trapping process. This removes the need for a buffer width around the trapping area. The process uses the location of each trap and includes a sub-model for the distribution of individuals and another sub-model for the capture process. The distribution of individuals is modeled by a homogeneous Poisson process. The capture process models the probability of capturing an individual in a particular trap given the location of its unknown home-range center. The capture probability is modeled using the spatial analog of the detection function (Buckland 2001). The half-normal, hazard rate and negative exponential detection functions can be used.

These functions use the independent parameters g(0) for overall efficiency of detection and σ for spatial scale. Incorporation of sources of heterogeneity (individual-based, time-based and behavior-based) is possible in these parameters, as in conventional capture-recapture. However these increase the number of parameters that need to be estimated. Because only a few animals were detected, only the null models for both parameters were used, denoted as g(0)[.] σ[.], the dot denoting lack of heterogeneity. The method assumes that 1) Trap placement is random with respect to location of home ranges, and home ranges are randomly oriented. 2) Home ranges do not change for the duration of the trapping and the population is demographically closed. 3) Home-range centers have a Poisson distribution, and 4) Individuals are independently detected. (Efford et al. in review) provides details of the method. The software Density 4.1 (Efford 2007) was used to calculate the densities and associated variances using all three detection functions. The Akaike Information Criterion (AIC) was used to select between the models, the model with the lowest AIC being selected.

Results

A total of 288 leopard photos were obtained, twenty were unidentifiable and were removed from the analysis. Of the identifiable photos 141 were of the left flank and 127 were of the right flank. Sampling intensity varied between sites, being lowest in Sariska, and highest in Churna (Table 4-1).

Adequacy of Sampling

A measure of the adequacy of sampling is if new individuals are no longer photographed with additional sampling. Figure 4-1 shows the addition of new leopards for the 4 sites using the left flank. The shape of the curves and the number of individuals identified were similar for the right and the left flanks. An asymptote was reached for the sites in Satpura Tiger Reserve by 6 weeks. No asymptote was reached in Sariska suggesting that further sampling would have yielded photographs of additional new individuals.

Sex Ratios

The sex ratios are female biased in all areas except Kamti. The average ratio is 1.7 (SE 0.38) females per male (Table 4-2).

Population Size

The model selection criterion chose M_o for 2 sites and M_h for 3 sites. When M_o was chosen the M_h model selection value was not much lower, though the difference was significant or marginally non-significant (Table 4-3). M_o is not recommended because it is sensitive to departures from the assumption of no individual-based heterogeneity (Karanth & Nichols 1998), though both models have been presented. All M_h were estimated with the jackknife estimator, which is robust and has performed well in simulation studies (Burnham & Overton 1979). Test for population closure was not significant for all the sites, indicating that the assumption of demographic closure was not violated. A high proportion of the estimated population was photographed, ranging from 69 to 89 percent for the M_h model and 69 to 100 percent for the M_o model. Population sizes, capture probability and estimated proportion photographed for both estimators are given in Table 4-4.

Leopard Density

Table 4-5 gives the estimation of density of leopards per 100 km^2 at the different sites using the convex polygon to calculate the Effective Trapping Area method with full-MMDM and half-MMDM. Estimated density is dependant on the method used to calculate the strip width and the polygon. The densities calculated using all combinations of concave and convex polygon with half MMDM and full MMDM are presented in Table 4-6. Concave polygon with half MMDM gave the smallest effective trapping area and consequently the highest density, while the convex polygon with MMDM gave the largest effective trapping area and therefore the lowest density at each site.

Using the maximum-likelihood-spatially-explicit-capture-recapture method, the lowest AIC values for Churna and Kamti were obtained by the four parameter hazard rate model, while for Lagda and Sariska the three parameter half normal model was selected. Densities obtained by this method are given in Table 4-7.

The relative abundance index (Table 4-8) was also highest for Sariska followed by the second session at Churna.

Discussion

Ideally, it is desirable to obtain photos of both flanks of the body so that identification of individuals is unambiguous. When camera numbers are limited, it seems possible to obtain unambiguous photographs of both flanks for a large proportion of the population using two cameras at a few locations, while using one camera at the remaining locations, provided the trapping goes on for a long period. This would maximize coverage of the area with the available number of cameras. The individual identification of leopards from photographs was found to be quite easy except when the animals walked farther away from the cameras, resulting in underexposed photos. This was likely to happen when the distance between the two sensors was more than 10 meters.

Tigers were sometimes observed to avoid camera traps, leaving the trail just before the camera location and getting back on the trail afterwards. Other studies have also observed this behaviour (Wegge et al. 2004). On the evidence of tracks, leopards were never observed to avoid cameras traps, and showed no response to the flash. Leopards of both sexes were photographed while standing or sitting in front of the camera, and did not rapidly move away. Sometimes more than one photograph was taken at the same time, indicating that the leopard stayed in that position for at least 6 seconds after the flash of the first photograph. However, rates of photo-captures for males seemed to be consistently higher than for females. The existence of heterogeneity in capture probabilities with respect to gender is possible. In Kruger National Park for instance, it was easier to capture males as opposed to females in box traps (Bailey 1993).

The calculation of effective area of sampling is a noteworthy issue in the estimation of density using camera traps. There is generally no measurement of the home range of the sample of individuals used in the estimation. It has been recommended that half the mean maximum distance moved (MMDM) be used as the buffer for estimation of densities (Wilson & Anderson 1985). A recent study on jaguars comparing MMDM obtained by telemetry to half MMDM and full MMDM found that the full MMDM results were much closer to densities based on actual movement rates, and that half MMDM seemed to overestimate densities (Soisalo & Cavalcanti 2006). There is still not enough data available for movement in leopards to advocate a shift to full MMDM. Also, as the area of the buffer increases, it is more likely to include habitat that is unsuitable for the species and unrepresentative of the probability of capture at the camera trap location.

In this study densities obtained using the convex polygon-full MMDM gave results that were similar to the MLSECR method at most sites, while densities calculated using half MMDM were much larger (Table 4-8). The density of leopards was highest in Sariska Tiger Reserve, where tigers have been extirpated recently (Sankar et al. 2005), while it was lowest at Lagda, which had the highest activity of tigers amongst all sites (*pers obs*) though it is not a high density tiger area. Variation in density of carnivores is associated with density of prey as shown for tigers (Karanth et al. 2004b), and other carnivores (Carbone et al. 1999). However, other factors, like human disturbance (Woodroffe 2000) and tiger presence (Seidensticker 1976; Sunquist 1981) may also play a role, although there is some evidence that leopard densities may not be unduly depressed by presence of other large carnivores (Marker & Dickman 2005).

Leopard density estimates are available for various parts of the world, but from different methods. For the Serengeti it was about 3.8-4.5 per 100 km^2 (Schaller 1976), for Kruger it was about 3.4 per 100 km^2 (Pienaar 1969). It was estimated at about 7.1 in the rain forest of the Ivory Coast (Jenny 1996), and in Wilpattu National Park in Sri Lanka it was estimated as about 3.4 (Eisenberg & Lockhart 1972). In Namibia, a mean of 10.5 (SE 4.0) inside protected areas (n =6), and 2.1 (SE 1.6) outside protected areas has been reported (Marker & Dickman 2005).

Photocapture rates calculated per 100 trap nights for 4 sites in India ranged from a low of 0.18 for Kaziranga National Park, a medium 2.3 for Pench National Park to a high of 5.44 in Nagarhole National Park (Karanth & Nichols 1998). Estimates of Relative Abundance Index (RAI) for the present study, ranging from 2.2 to 6.8 (Table 4-7) seem to be within the range found in other areas in India.

The second session in Churna, conducted in spring-summer, had higher capture probability than the first session, conducted in winter-spring. Camera traps were mostly placed along topographic contours, where leopard signs were high, and water tended to be found. It is possible that movement of leopards around such places increased in summer when water sources in the hills dried up, leading to the higher capture probability.

RAI has been recommended for tigers when there is not enough data for mark recapture sampling (Carbone et al. 2001). In low leopard density areas it takes a long time to get a sufficient number of captures to use in the mark-recapture framework. If the assumption of population closure is severely violated, then the RAI may be used as a substitute for density estimation. An index can also be used on species that do not have individually identifiable markings. However, the difference between the RAI estimates and density estimates is noteworthy. The second session at Churna and the session at Sariska have similar RAI values, but the density at Sariska is much higher. Similarly, the RAI of the first session at Churna is almost 3 times lower than the RAI of the second session, but density estimates are not significantly different. This indicates that RAI does not seem to index density in a reliable way, as noted elsewhere also (Jennelle et al. 2002; Maffei et al. 2004).

Conclusion

Sariska Tiger Reserve has the highest densities despite having a history of human disturbance and poaching. This may be related to the recent removal of the tiger from Sariska and the occupation of prime habitats by the leopard. Another reason could be the smaller spatial extent of the effective trapping area in Sariska. It may be that the distribution of individuals in Sariska is more patchy and that the lower density areas were not surveyed. In such a scenario, comparing Sariska to another study site will not be useful and the parameter values should be limited to monitoring the same site over time. Leopard RAI values in Bori-Satpura are comparable to other study sites in India. The leopard RAI in Satpura, where tiger density is relatively low, seem to be higher than at Kanha and Pench, which have higher tiger densities.

The estimates provided by the mark-recapture framework give us a relatively robust measure of population size, but the estimation of density is still problematic given the uncertainty involved with estimation of the effective trapping area. The spatially explicit maximum likelihood method offers a solution to that problem, but modeling heterogeneity is more complicated with low population sizes, since the number of parameters to be estimated is high. The precision derived in the present study makes it difficult to detect changes in population density. It is logistically difficult to both sample at an intensity that obtains high precision and at a large enough spatial scale for a species of this size. Given these limitations, serious investigation should be made into the use of indices to monitor population changes with greater precision, though RAI does not seem to be the appropriate index in these study sites.

Table 4-1. Camera-trapping effort (in trap nights) at the study sites.

Site	Number of camera trapping stations	Number of Nights	Effort (trap nights)
Churna (session 1)	16	76	1216
Churna (session 2)	16	75	1200
Kamti	20	52	1040
Lagda	20	33	660
Sariska	12	33	396

Table 4-2. Leopard sex ratios for the different study sites.

Site	Males	Females	Sex ratio (no of females per male)
Churna (session1)	4	6	1.5
Churna (session2)	3	8	2.7
Kamti	7	4	0.6
Lagda	3	5	1.7
Sariska	3	6	2.0

Table 4-3. Model selection criterion and tests for Models M_o, M_h, M_b and M_t in the mark-recapture framework and a test for population closure for the different study sites.

Site	Model selection criterion				M_o vs M_h			M_o vs M_t			M_o vs M_b			M_h Goodness of fit			Closure test	
	M_o	M_h	M_b	M_t	$\chi2$	df	p	$\chi2$	df	p	$\chi2$	df	p	$\chi2$	df	p	z	p
Churna session 1	1.0	0.94	0.51	0.0	Not done			2.5	76	1.00	1.2	1	0.26	85.4	76	0.22	-0.6	0.28
Churna session 2	0.93	1.00	0.46	0.0	5.8	2	0.05	14.5	72	1.0	0.01	1	0.91	106.5	72	0.00	-0.13	0.45
Kamti	0.96	1.00	0.44	0.0	3.6	1	0.06	3.9	82	1.0	0.03	1	0.86	97.4	82	0.11	-1.33	0.09
Lagda	0.93	1.00	0.38	0.0	Not done			8.0	32	0.99	0.00	1	0.97	59.03	32	0.00	-1.36	0.09
Sariska	1.00	0.91	0.42	0.0	Not done			2.2	28	1.0	Test failed			32.91	28	0.24	-1.24	0.11

Table 4-4. Population estimates for leopards at the study sites.

Site	Estimate (M_o)			Estimate (M_h)		
	$\hat{p}$	$Mt+1/\hat{N}$	$\hat{N}$ ±SE	$\hat{p}$	$Mt+1/\hat{N}$	$\hat{N}$ ±SE
Churna session1	0.03	0.92	12±1.5	0.02	0.79	14±3.6
Churna session2	0.08	1.0	11±0.14	0.07	0.79	14±2.6
Kamti	0.03	1.0	10±0.81	0.03	0.83	12±3.7
Lagda	0.08	1.0	8±0.76	0.07	0.89	9±6.9
Sariska	0.04	0.69	13±3.8	0.04	0.69	13±4.4

Table 4-5. Density of leopards and estimates of sampled area using convex polygon and model M_h at the different study sites.

Sites / Estimates	Churna (session1)	Churna (session2)	Kamti	Lagda	Sariska
Effective area (half MMDM) km^2.	152.2	149.2	119.3	122.7	44.4
Density (per 100 km^2)	8.0±2.5	9.3±2.0	7.5±2.8	7.3±5.1	30.9±12.1
Effective area (full MMDM) km^2.	230.8	223.6	195.0	210.9	66.2
Density (per 100 $km^{2)}$	5.3±4.7	6.2±1.6	4.6±2.0	4.2±3.1	20.7±10.0

Table 4-6. Density of leopards with the associated estimated trapping area using models M_o and M_h.

Site	Polygon method	Strip method	ETA (km^2)	Density±SE (per 100 km^2)	
				M_o	M_h
Churna session1	Concave	MMDM	185.6	6.4±2.0	6.6±2.5
	Concave	MMDM/2	77.9	15.4±3.3	15.7±4.8
	Convex	MMDM	230.8	5.2±1.6	5.3±4.7
	Convex	MMDM/2	152.2	7.8±1.7	8.0±2.5
Churna session2	Concave	MMDM	176.8	6.2±1.1	7.9±2.0
	Concave	MMDM/2	73.0	15.0±1.6	19.1±4.1
	Convex	MMDM	223.6	4.9±0.8	6.2±1.6
	Convex	MMDM/2	149.2	7.3±0.8	9.3±2.0
Kamti	Concave	MMDM	179.5	4.5±1.3	5.0±2.1
	Concave	MMDM/2	92.3	8.7±1.8	9.7±3.6
	Convex	MMDM	195.0	4.1±1.2	4.6±2.0
	Convex	MMDM/2	119.3	6.7±1.4	7.5±2.8
Lagda	Concave	MMDM	194.8	4.1±3.4	4.6±3.4
	Concave	MMDM/2	97.7	8.2±1.8	9.1±6.4
	Convex	MMDM	210.9	3.8±1.7	4.2±3.1
	Convex	MMDM/2	122.7	6.5±1.4	7.3±5.1
Sariska	Concave	MMDM	54.6	23.8±11	25.2±12.1
	Concave	MMDM/2	21.1	61.6±25	65.1±25.5
	Convex	MMDM	66.2	19.6±9.1	20.7±10.0
	Convex	MMDM/2	44.4	29.2±10.8	30.9±12.1

Table 4-7. Density estimates for leopards (number/100 km^2) using different capture functions for the null models with the MLSECR method.

Site	Capture function	Model	No of param	Log likelihood	AIC	ΔAIC	Density	SE
Churna session1	Hazard	g0[.]σ[.]	4	-172.29	352.59	0	7.21	3.21
Churna session1	Negative exponential	g0[.]σ [.]	3	-173.52	353.04	0.45	6.62	2.73
Churna session1	Half normal	g0[.]σ [.]	3	-175.03	356.07	3.48	5.92	2.3
Churna session2	Hazard	g0[.]σ [.]	4	-364.57	737.15	0	4.04	1.37
Churna session2	Half normal	g0[.]σ [.]	3	-369.75	745.49	8.34	3.83	1.25
Churna session2	Negative exponential	g0[.]σ [.]	3	-372.9	751.8	14.65	3.51	1.14
Kamti	Hazard	g0[.]σ [.]	4	-179.45	366.9	0	4.67	0.05
Kamti	Half normal	g0[.]σ [.]	3	-183.64	373.28	6.38	4.15	1.61
Kamti	Negative exponential	g0[.]σ [.]	3	-183.81	373.62	6.72	4.08	1.58
Lagda	Half normal	g0[.]σ [.]	3	-149.7	305.4	0	3.27	1.41
Lagda	Negative exponential	g0[.]σ [.]	3	-149.92	305.83	0.43	3.11	1.23
Lagda	Hazard	g0[.]σ [.]	4	-149.09	306.18	0.78	3.44	0.19
Sariska	Half normal	g0[.]σ [.]	3	-73.75	153.49	0	14.58	7.0
Sariska	Hazard	g0[.]σ [.]	4	-73.15	154.3	0.81	20.08	0.4
Sariska	Negative exponential	g0[.]σ [.]	3	-74.17	154.34	0.85	12.65	6.57

Table 4-8. Relative abundance index values for the 5 estimates in Satpura and Sariska Tiger Reserves.

Site	No of camera trap locations	No of independent captures	RAI (per 100 trap nights)	SE of RAI
Churna (session 1)	16	27	2.2	0.65
Churna (session 2)	16	80	6.7	1.85
Kamti	20	39	3.9	0.71
Lagda	20	24	3.8	0.89
Sariska	12	27	6.8	2.21

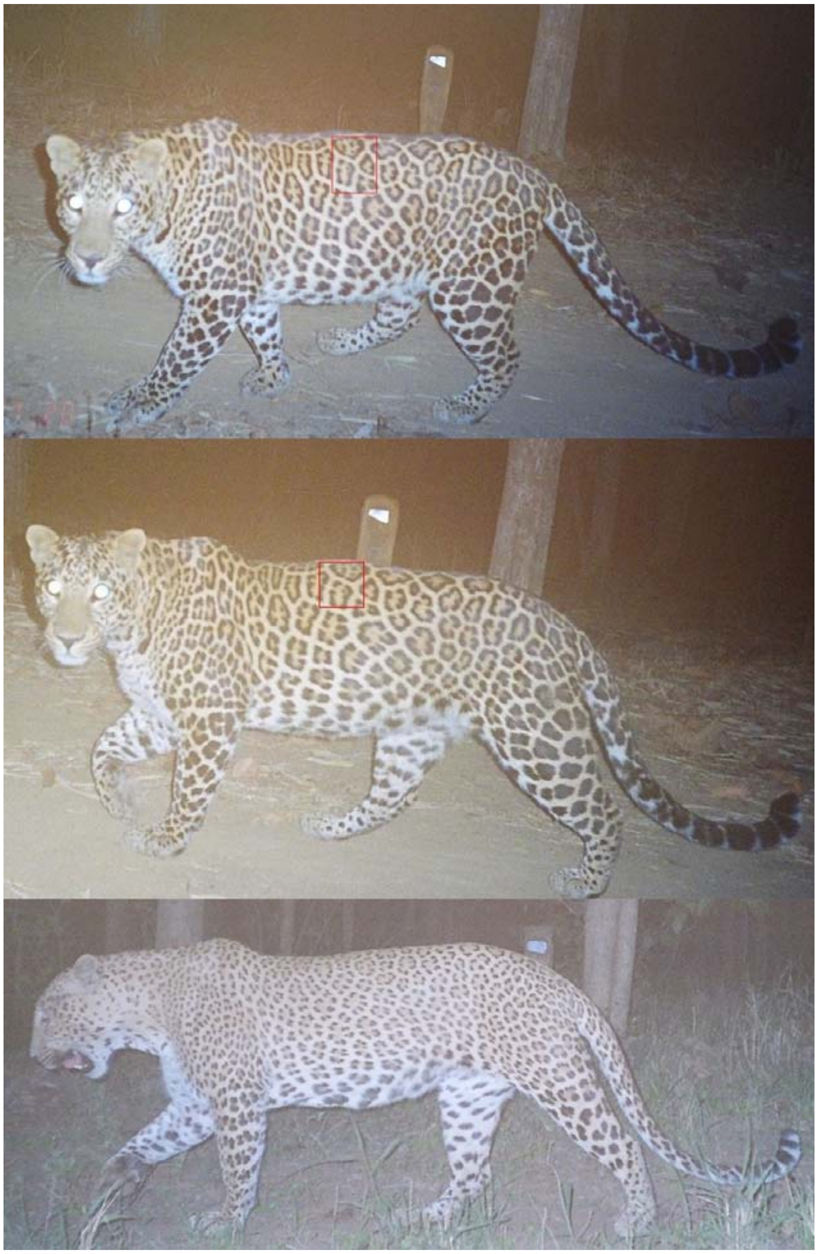

Figure 4-1. Identification of leopards based on spot patterns. The first two photos are of the same leopard, the third photo is of a different leopard.

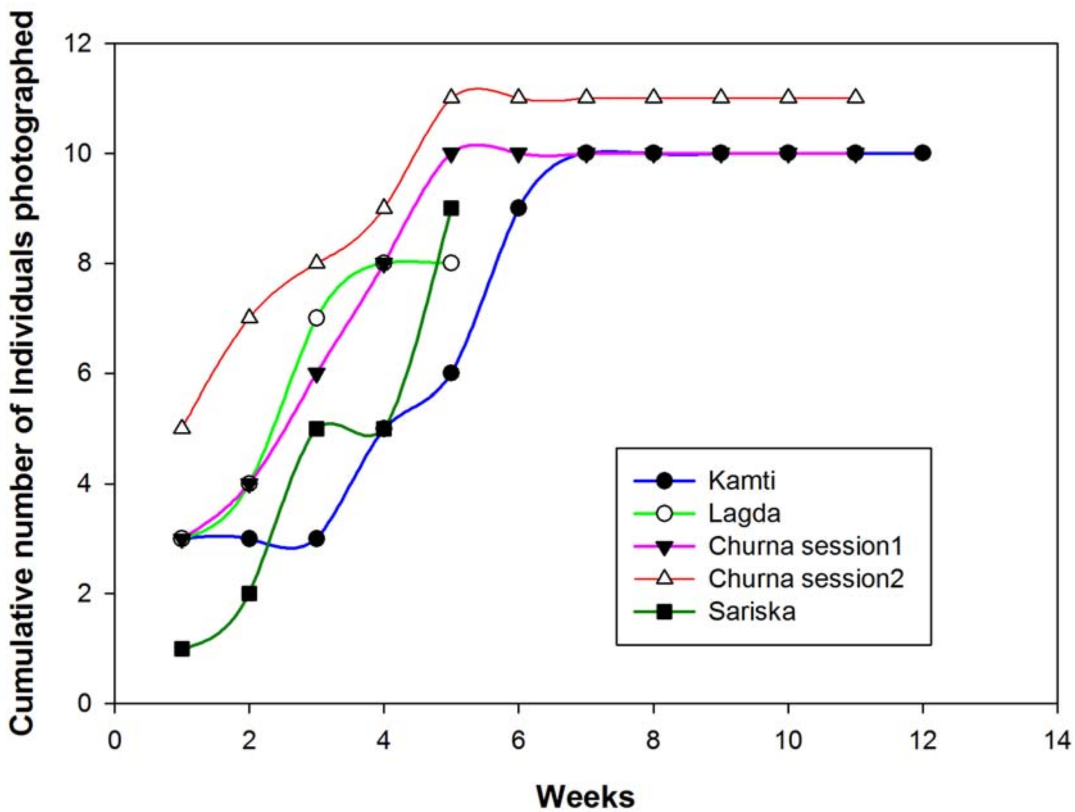

Figure 4-2. Rate of accumulation of new individuals in camera-trap photographs with increase in sampling time at the four sites.

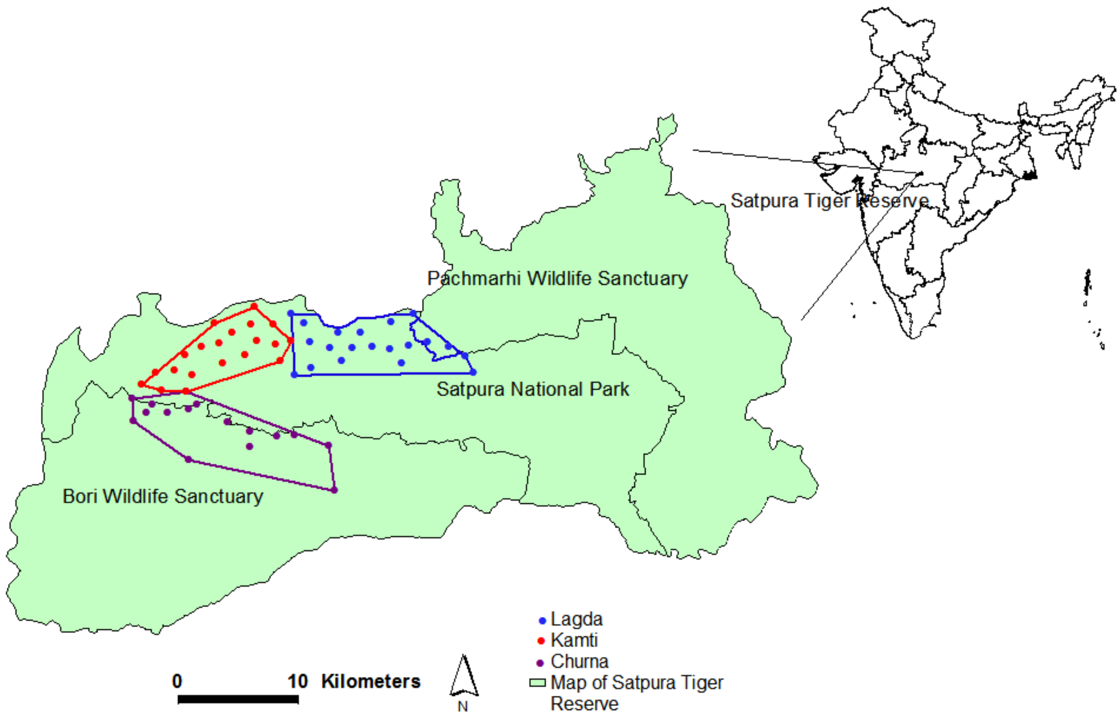

Figure 4-3. Camera trapping in 3 sites (Churna, Kamti and Lagda) in Satpura Tiger Reserve.

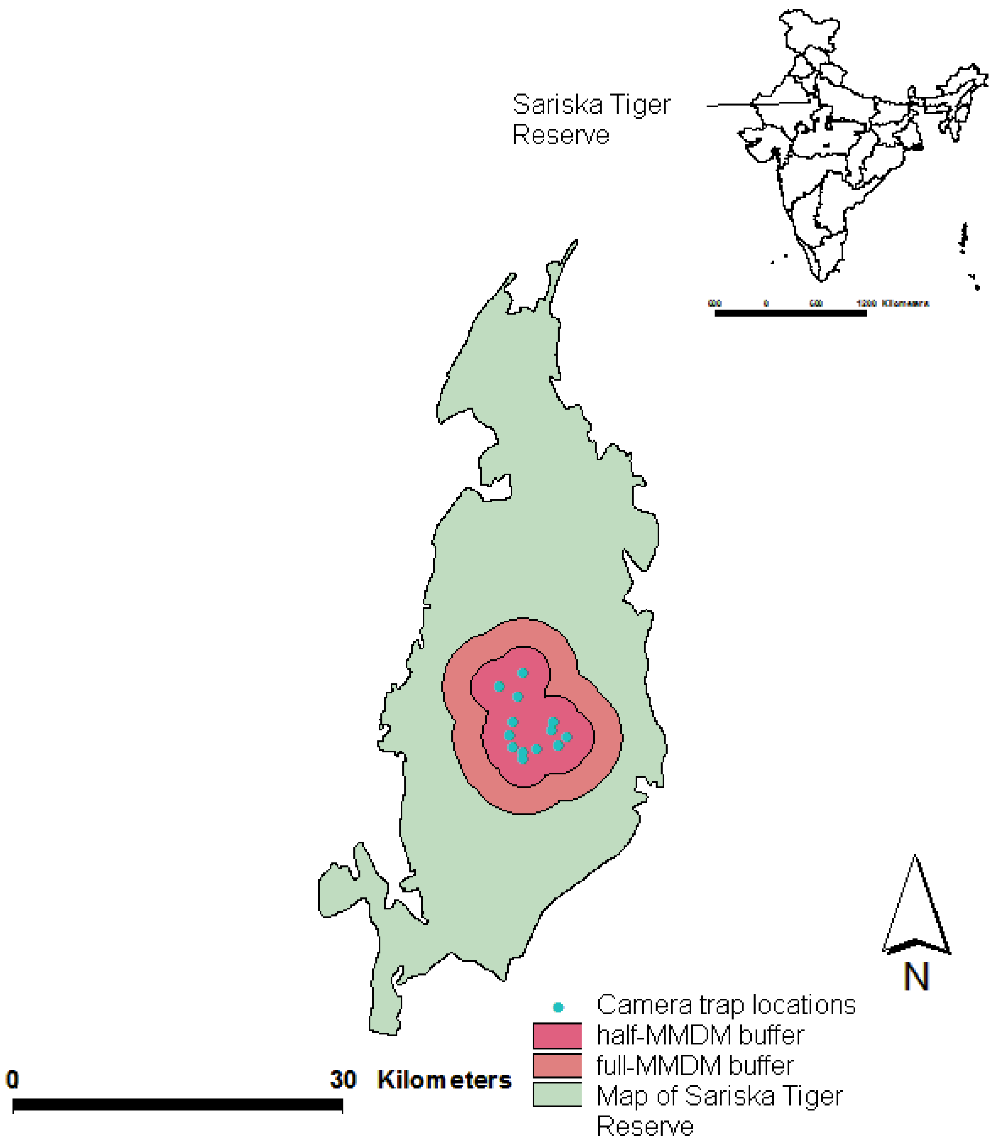

Figure 4-4. Map showing camera trap locations with half MMDM and full MMDM buffers in Sariska Tiger Reserve.

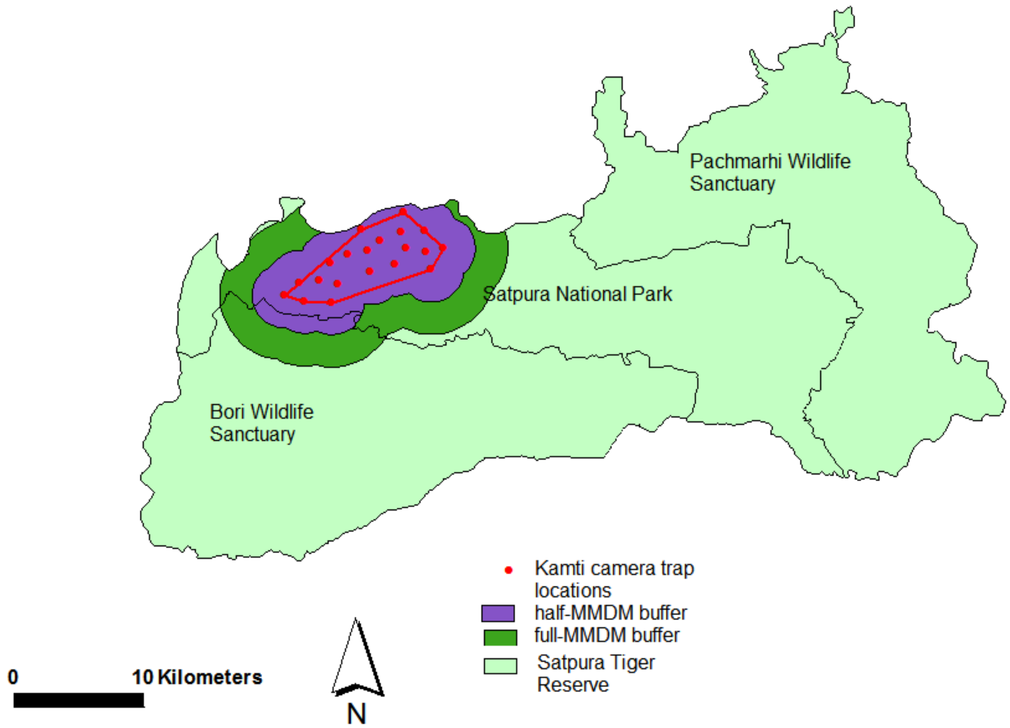

Figure 4-5. Map showing camera trap locations with half MMDM and full MMDM buffers for one site (Kamti).

CHAPTER 5
PRESENCE-ONLY HABITAT SUITABILITY MODELS FOR LEOPARDS (*Panthera pardus*) USING FIELD BASED AND REMOTELY DERIVED VARIABLES AT TWO SPATIAL SCALES IN MADHYA PRADESH, INDIA.

Introduction

Knowledge of the distribution and habitat requirements of a species are essential to formulate conservation strategies. While some species are considered habitat generalists, they are still vulnerable to habitat loss and fragmentation. These factors along with prey depletion and poaching are responsible for the decline of the tiger (*Panthera tigris*) across its geographic distribution (Sunquist et al. 1999). It has been estimated that the tiger exists in only 7 percent of its historical range (Dinerstein et al. 2007). The leopard is a wide-ranging large carnivore that is less susceptible to disturbance, is a generalist with respect to habitat requirements, and can survive on a wide range of prey species (Sunquist & Sunquist 2002). Unlike the tiger, which needs a high biomass of large-sized prey (Karanth & Sunquist 1995), the leopard has been known to survive on domestic dogs and rodents in the absence of wild prey populations (Edgaonkar & Chellam 2002). As tiger populations in India have declined, leopard populations have also come under increased poaching pressure. Conserving leopards in this environment will require a quantification of habitat requirements and identification of potential habitat availability in India. Good habitats for leopards can then be given conservation priority in protection and management strategies.

Categorizing suitable leopard habitat requires information at multiple scales. First-order selection (Johnson 1980) refers to the distribution of a species with respect to geographical space. Large-scale species distribution models can be used to guide conservation strategies (Guisan et al. 2006; Hirzel et al. 2004; Mladenoff & Sickley 1998; Seoane et al. 2006). Techniques like logistic regression (Karlsson et al. 2007; Woolf et al. 2002) and generalized linear models (GLM) (Austin 2007; Bustamante & Seoane 2004) use the information from multivariate measurements of habitat variables at locations with species presence and at locations where the species is absent (Guisan & Zimmermann 2000; Meynard & Quinn 2007). This information is used to derive a probability of species presence at each location. Though these methods are preferred when absence data are reliable (Brotons et al. 2004), logistic regression models are known to be sensitive to even low levels of non-detections (Gu & Swihart 2004). Leopards are not only rare and secretive, they are also crepuscular (Sunquist & Sunquist 2002) and without intensive effort there is a high likelihood of non-detections in areas where leopards are present, contaminating the absence data. Presence-only models are a way of dealing with this problem. This paper uses environmental niche factor analysis (ENFA) (Hirzel et al. 2001), a presence-only environmental habitat-envelope based method to create habitat suitability maps for the leopard in south-central India. ENFA has been used successfully to model the distributions and habitat suitability of a variety of taxa: dung beetles (Chefaoui et al. 2005), corals (Bryan & Metaxas 2007), reptiles (Santos et al. 2006), birds (Braunisch & Suchant 2007; Brotons et al. 2004; Olivier & Wotherspoon 2006; Reutter et al. 2003; Titeux et al. 2007), ungulates (Dettki et al. 2003; Traill & Bigalke 2007) and carnivores (Mestre et al. 2007).

The objectives of this paper are: 1) To develop predictive habitat suitability maps for leopards at two scales and evaluate their reliability; 2) To identify the environmental variables important in describing the habitat for this species, and 3) To quantify the extent and location of potential leopard habitat available for conservation action in south-central Madhya Pradesh.

Study Areas

The extensive study area covers 52971 km^2 (Table 5-1) and includes thirteen districts in south-central Madhya Pradesh; it comprises about 18 percent of the state of Madhya Pradesh. Altitudes in the study area range from 215 to 1312 m. Annual rainfall for the state averages 1143 mm, with rainfall decreasing from the eastern part of the state to the west. The landscape is a mosaic of forests, agriculture, villages and small and large towns (Figure 5-1). The main crops are wheat, soybean, sorghum, sugarcane and pulses. The forests are mainly teak dominated, as well as dry and moist deciduous forests. The climate is cool in winter and very hot in summer, with temperatures ranging from 2-45° C. The largest river in region is the Narmada. The two main protected areas within the landscape are the Satpura and the Pench Tiger Reserves (Figure 5-2).

The intensive study site (Figure 5-3) consists of a 433 km^2 area of moist and dry deciduous forests along with some teak plantations located inside the Satpura Tiger Reserve (STR). It is located in the center of the extensive study site. Topography ranges from relatively flat to very steep slopes and cliffs; altitudes range from 300 to 1315 m. There are 7 small forest villages within its boundaries. Details of the intensive study are given in previous chapters.

Methods

In the STR study site, visual sightings of prey species were obtained from walking 20 straight-line transects (630 km) through the forest, and from driving-transects using a 4-wheel drive vehicle at 10-15 kmph along a network of dirt trails (369.5 km). An encounter rate was calculated as the number of sightings per kilometer using all sightings of potential prey species. Potential prey species include chital (*Axis axis*), sambar (*Cervus unicolor*), langur (*Semnopithecus entellus*), wild pig (*Sus scrofa*), and a small-prey category comprising hare (*Lepus nigricollis*), peafowl (*Pavo cristatus*), red spurfowl (*Galloperdix spadicea*) and grey jungle fowl (*Gallus sonneratii*). This encounter rate was then divided into 5 categories. The first category was 0 encounter rate, and the other 4 were based on equal quantiles (25^{th}, 50^{th}, 75^{th} and 100^{th}). Photos of prey from the camera-trap stations were converted into a rate per trap night, and also similarly divided into 5 increasing categories based on equal quantiles. The two data sources (encounter rates and photo trap rates) were then assumed to be equivalent indices of prey abundance and were subsequently merged. Distance-weighted interpolation of the categorical index was then done using the INTERPOL module of Idrisi Kilimanjaro v14.02 (Eastman 2004) to obtain a prey map.

Sampling for evidence of leopard presence was done using kills, tracks, scrapes and camera-trap photos. All quantitative measures were degraded into presence-absence measures to reduce biases introduced by different sampling efforts. Multiple instances of presence within a one-hectare plot were combined to reduce spatial autocorrelation, which can lead to bias in precision estimates for habitat models (Diniz et al. 2003).

Secondary data were obtained as part of a joint Wildlife Institute of India- Project Tiger initiative to monitor tiger populations in India in 2006. A total of 2582 beats were sampled. A 3 to 4-km-long transect was located in each beat, and each beat was a walked a total of three times by the local forest guard in charge of the beat. The average size of each beat was 20 km^2. Data on presence of livestock signs, encounter rate of prey and sign of leopards were collected. Digitized beat maps were obtained and the centroid of each beat was used to approximate the location of leopard presences in the beat.

Ecogeographical variable (EGV) maps of prey encounter rates for sambar, nilgai (*Bosephalus tragocamelus*) and wild pig using the INTERPOL module of Idrisi were created. The encounter rate of leopard sign was converted to a binary variable of presences and pseudoabsences. A buffer width of 3000 m was applied to create a 9 km^2 patch of leopard-presence pixels around each point. Female leopard home ranges are known to vary from 6 to 30 km^2 in Africa (Bailey 1993) and average 17 km^2 in Nepal (Odden & Wegge 2005), so 9 km^2 was considered a conservative estimate of the area in which presence could be assumed in the forest beat. Only beats where some evidence of leopards was detected were retained for the analysis. All beats where evidence of leopards was not detected were discarded from the dataset.

The elevation layer was obtained from the 90-m resolution DEMs created from the SRTM mission data by the CGIAR-CSI (http://srtm.csi.cgiar.org). Using Idrisi, a slope map and a ruggedness map (using the standard deviation of mean elevation in a 3 x 3 moving window) was created from the DEM. A moving window of 3x3 has been used to create a similar index of terrain ruggedness to model mountain lion habitat in Montana (Riley & Malecki 2001)

The extensive study area encompassed parts of 6 Landsat ETM+ images. Georeferenced and orthorectified cloud-free images dating between 2002 and 2004 were obtained from the Global Landcover Facility (http://glcf.umiacs.umd.edu). Those parts of the extensive study area found in each of these images were classified into four cover types: agriculture, bare ground/urban, forest and water. These were then mosaicked together to obtain the cover map. For the STR area 5 cover types were delineated. These were: moist forest, dry forest, bare ground/village, teak dominated forest and water. Spectral signatures for the classification supervision were obtained by using information from 473 vegetation plots in the Satpura Tiger Reserve, and with visual inspection of satellite imagery using Google Earth (http//:www.earth.google.com) for the extensive study area. Supervised classification was performed using FISHER classifier for both the study sites using the Idrisi GIS package. Using the CircAnn module of Biomapper, the Boolean maps of each land cover type was converted to percent frequency in a 20 km^2 circular moving window for the extensive study area (Figure 5-4) and 1 km^2 for the STR site (Figure 5-5). The models were made at two pixel resolutions: 1000 m for the extensive study area and 100 m for the STR study site. A list of all the EGVs for both study areas is given in Table 5-2 and 5-3.

To observe the effect of pixel resolution on the accuracy of the models, the ENFA analysis was repeated at the 200-m, 300-m and 500-m resolution for the STR area, and at 1000-m without the buffer, at 2000-m, 3000-m and 5000-m for the extensive study area.

The relationship between the distribution of leopard presence patches and a set of mapped ecogeographical variables was analyzed using ENFA. The program Biomapper v3.2 (Hirzel et al. 2006a) was used. Biomapper needs two types of data to calculate habitat suitability. The first is a map of locations where the species has been detected, and the next are a set of quantitative raster maps describing the environment as used by the species under investigation. This presence-only modeling technique describes the ecological niche of a species by computing uncorrelated factors from a comparison of values of ecogeographical variables in the entire study area and their values at the site where the species is known to be present. The first ENFA factor maximizes the absolute value of the marginality, defined as the standardized difference between the species mean and the global mean of each of the EGVs. The first factor explains how the species niche differs most from the available conditions. The first factor also explains all the marginality and some of the specialization. Specialization is defined as the ratio of the overall variance to the species variance for all the EGVs, and describes how restricted is the usage of the species of that variable compared to its availability. Details on the calculation of marginality and specialization are given in Hirzel et al. (2002). The subsequent factors maximize the specialization. A high absolute value of the correlation of the variable with the specialization factor indicates that the species niche breadth is narrow with respect to that variable. There are as many factors as there are variables, but they successively explain a decreasing amount of the specialization. The number of factors used to calculate the habitat suitability was decided using MacArthur's broken-stick criterion (Hirzel et al. 2002) .

The habitat-suitability map was evaluated for its predictive accuracy by internal area adjusted frequency cross-validation (Fielding & Bell 1997). Leopard presences were geographically stratified and randomly partitioned into 10 sets. Nine partitions were used to compute a habitat suitability model and the left-out partition was used to validate it on independent data. This process was repeated 10 times, each time by leaving out a different partition. This process resulted in ten different habitat-suitability maps. Each map was reclassified into 4 bins, where each bin covered some proportion of the total study area (Ai) and contained some proportion of the left-out validation points (Ni).The area-adjusted frequency for each bin was computed as Fi = Ni /Ai. The expected Fi was 1 for all bins if the model was completely random. If the model is good, low values of habitat suitability should have a low F (below 1) and high values a high F (above 1) with a monotonic increase in between. The monotonicity of the curve was measured with a Spearman rank correlation on the Fi in a moving window, termed as the continuous Boyce Index (Boyce et al. 2002; Hirzel et al. 2006b). Validation of the models was also done using the Absolute Validation Index (AVI) and the Contrast Validation Index (CVI). AVI is the proportion of validation points that have a habitat selection of >=50. Possible values the index can take range from 0 to 1. The higher the value the more accurate is the model. CVI is calculated at AVI minus the AVIchance, which is the AVI one would expect from chance alone, and is a measure of departure from randomness of the model. Possible value the index can take range from 0 to AVI. One criticism of the presence models is that they yield too optimistic results (Zaniewski et al. 2002). This problem was mitigated by using breaks in the predicted-to-expected ratio frequency curves to define 4 habitat classes (Hirzel et al. 2006). The map was then reclassified using the new bins into unsuitable, marginal, suitable and optimal habitat.

Results

Model Validation

Overall the habitat suitability models for both STR and the extensive study area were equally accurate. They both showed similar values of AVI, indicating that the proportional accuracy in classifying presence points in the evaluation partition was similar for south-central Madhya Pradesh and for Satpura Tiger Reserve. CVI values showed that the model had some difficulty in discriminating between the suitability map and a purely random model. This is consistent with the generalist nature of the species. Both the continuous Boyce Index values were high, indicating good predictive power for both the models, but the extensive study area model had better predictive power (Table 5-4). The predicted-to-expected frequency curves showed higher variance for good habitat than for bad habitat with both models (Figure 5-8), the inflections in the curves were used to guide the selection of bins to reclassify the habitat suitability maps for the two areas (Figure 5-6 and 5-7).

Extensive Study Area

The marginality value was 1.25 and the tolerance value was 0.92, indicating that leopards were using conditions that were different from the mean environmental values, and that the leopard was more of a generalist in using a wide range from the EGVs. Seven factors were retained. The first factor accounted for 100 % of the marginality, while all 7 factors accounted for 100 % of the marginality and 80% of the specialization. The marginality coefficients show that leopard habitat was more positively correlated with sambar distribution, terrain ruggedness and percentage of forests. It was less strongly correlated with altitude, slope, NDVI and nilgai and wild pig encounter rates. Leopard distribution was negatively correlated with presence of agriculture and urban-bare ground land cover types. Livestock presence, an indicator of human disturbance, was a weak negative correlate. The specialization factor indicated that the leopard used a restricted niche with respect to the availability of percentage frequency of urban-bare ground and agriculture, but not when compared with the availability of elevation, ruggedness and slope measured at the 1 km scale across the big study area (Table 5-5). The amount of suitable, marginal, unsuitable and optimal habitat in each district is given Table 5-7. Maps of the EGVs are shown in Figure 5-4.

Satpura Tiger Reserve

The marginality value was 0.67, indicating that leopards were using conditions not too different from the mean environmental values. Tolerance was also relatively high (0.56), indicating that the leopard was found in areas that had a wide range of values of the EGVs. Four factors were retained, the first factor accounting for 100 % of the marginality. The four factors explained 79 % of the specialization. The marginality factor was strongly positively loaded with the coefficient for tassled-cap ‘greenness’, an index of above ground biomass (Crist & Kauth 1986) and percentage frequency of moist forests and teak dominated forest. It was also positively correlated with distance to water and the encounter rate of cervids (sambar and chital), wild pig and small-sized prey. The positive correlation with langur encounter rate was weak. Leopard presence was negatively correlated with elevation, slope and frequency of bare ground pixels. The negative loading with respect to distance from village was weak. The specialization factor indicated that elevation was used in a more restricted way than was available in the study area, as was the frequency of the moist, dry and teak forests (Table 5-6). Maps of the EGVs are shown in Figure 5-5.

Effect of Changing Resolution

For the extensive study area the best model was at the 1000-m scale with buffer. It gave the highest continuous Boyce Index value. The coarsest resolution model was the most inaccurate. At a resolution of 5 km and a moving window size of 225 km^2, the continuous Boyce Index reduced to 0.55. Changing the resolution did not change the AVI, CVI and the Boyce Index much at all the other resolutions. For the STR area, the best model was the 100-m resolution with a moving window of 1-km^2, followed by the 200-m model. The effect of increasing the moving window scale degraded accuracy slightly. The 300-m and 500-m resolution models had lower Boyce Index values (Table 5-4). The habitat suitability maps for the two areas were made from the best models.

Discussion

The leopard is an adaptable species, being able to live in a wide variety of environmental conditions. This is reflected in the marginality and tolerance values for the model of the STR area, where almost all the area is potential leopard habitat. Habitat use by leopards in Satpura was strongly associated with moist and teak forests, as well as with most prey species, except the langur, with which it was only weakly associated. This is because more langur are seen in open areas, closer to villages, and along roads, rather than in denser forest areas (*pers obs*), perhaps as an anti-predatory strategy, and they do not comprise a large proportion of the leopard’s diet in this area (Chapter 3). Leopard presence had a weak negative association with the distance to villages. That means it was found closer to villages than average, though this tendency was weak. Unlike tigers, which are shy and prone to move away from disturbance, leopards are known to be bold and not uncommonly found in proximity to human habitats, where they prey upon livestock (Odden & Wegge 2005). Though they are tolerant of human presence, they are not unaffected by disturbance, as the extensive study area model showed, with leopard habitat being negatively associated with bare ground/urban land use frequency. In Thailand leopard activity has been shown to be negatively correlated with distance from villages (Ngoprasert et al. 2007). Leopard habitat was negatively correlated with urban-bare ground and agriculture land cover types as also with livestock presence. At the large scale, good leopard habitat was seen to be more associated with terrain ruggedness, sambar availability and percentage of forested areas, and less associated with nilgai and wild pig prey availability. Both the latter species are known to be crop pests and able to live close to human inhabitation (Sekhar 1998), and this probably contributes to the observed pattern. Cougar (*Puma concolor*) abundance has also been shown to be affected by prey availability, terrain ruggedness and forest cover at the landscape scale (Riley & Malecki 2001).

The larger spatial area model had a higher predictive accuracy than the smaller scale as quantified by the higher continuous Boyce Index (Table 5-4). This is possibly because the Satpura Tiger Reserve has relatively little disturbance and is a less heterogeneous area given its smaller size. Given the high density of leopards in the area (Chapter 4) and that they require relatively large tracts of contiguous habitat (Marker & Dickman 2005), they probably move through and spend time in habitats that are not highly preferred, but are still inhabitable. Consequently, very few areas in the Reserve are likely to be completely unsuitable for leopards.

The change in resolution seemed to have a similar impact on models of both study areas. Coarse pixel resolutions, at 300 m and 500 m for STR and 5 km for the extensive study area, degraded the accuracy of the models. The scale of the circular moving window for frequency of land use cover did not change accuracy appreciably, except at the very largest spatial resolution (225 km^2).

The habitat model was used to estimate the area occupied by various habitat categories in the 13 districts in south-central Madhya Pradesh (Table 5-7). ‘Optimal’ habitat was 5.2% of the study area, ranging from 0.5 to 8 percent of each district. As an absolute measure it can be said that approximately 11500 km^2 of habitat is likely to support leopard populations. The districts with the most optimal habitat are Betul, Hoshangabad and Chhindwara. These districts are geographically adjacent to each other and constitute a compact block of about 2000 km^2 of optimal habitat. The Satpura Tiger Reserve lies in Hoshangabad district and is already protected, but Betul and Chhindwara districts can be prioritized when allocating resources for leopard conservation efforts in Madhya Pradesh. In conclusion the ENFA model seems to work better at larger spatial areas for a generalist species like the leopard. It is a useful tool to explore the characteristics of the leopard’s niche as well as to produce habitat suitability maps that can aid in conservation management.

Table 5-1. Districts, sampling effort and leopard presence in the extensive study area in south-central Madhya Pradesh.

District	Sampled Area (km^2)	Number of transects	Transects with Leopard presence
Balaghat	419.9	50	0
Betul	10041.5	622	23
Bhopal	57.1	1	0
Chhindwara	11815.8	553	57
Dewas	1296.7	30	0
East Nimar	2104.4	100	8
Harda	3329.0	163	2
Hoshangabad	6734.1	351	111
Jabalpur	258.5	27	2
Narmsimhapur	4420.3	107	17
Raisen	3293.9	92	16
Sehore	3266.8	112	23
Seoni	5891.4	361	41

Table 5-2. List of ecogeographical variables (EGV) with explanation and source for south-central Madhya Pradesh.

Ecogeographical Variables	Explanation	Transformation	Source
Elevation	DEM in meters at 100 m spatial resolution, averaged to 1 km spatial resolution.	None	SRTM data
Ruggedness (Elevation standard deviation)	Calculated with a moving window of 3x3 cells from DEM.	None	Calculated
Slope	Calculated from DEM	None	Calculated
NDVI	Calculated from bands 3 and 4 of Landsat ETM + imagery.	None	Calculated
Forest	Percentage frequency of cells with forests, urban/bareground and agriculture in a circular window area 25 km^2.	None	Supervised classification of Landsat ETM+ imagery to obtain landcover; Frequency calculated.
Urban/bareground	Same as above	None	Same as above
Agriculture	Same as above	None	Same as above
Livestock	Distance-weighted interpolation of encounter rate (number seen/km) from line transects.	Square root	Calculated.
Nilgai encounter rate (ER)	Same as above	Box-Cox	Same as above
Sambar ER	Interpolated encounter rate (number seen/km) from line transects.	Box-Cox	Same as above
Wild pig ER	Interpolated encounter rate (number seen/km) from line transects.	Box-Cox	Same as above
Distance to Water	Distance to the nearest water source in meters.	None	Calculated.

Table 5-3. List of ecogeographical variables (EGV) with explanation and source for the Satpura Tiger Reserve.

Ecogeographical Variables	Explanation	Transformation	Source
Cervid Encounter Rate (ER)	Interpolated encounter rate (number seen/km) from line transects and vehicle transects	Box-Cox	This study
Langur ER	Same as above	Box-Cox	This study
Wild pig ER	Same as above	Box-Cox	This study
Small Prey ER	Interpolated ER of jungle fowl, spur fowl, peafowl and black-naped hare	None	This study
Bare ground	Percentage frequency of cells with in a circular window of area 1 km^2	Box-Cox	Supervised classification of Landsat ETM+ imagery to obtain landcover; frequency calculated.
Dry forest	Same as above	Box-Cox	Same as above
Teak dominated forest	Same as above	None	Same as above
Moist forest	Same as above	Box-Cox	Same as above
Tassled-cap 'greenness'	The first band of tassled-cap transform using Landsat ETM + imagery.	None	Calculated.
Elevation	DEM in meters at 100m resolution	Box-Cox	SRTM data
Slope	Calculated from DEM	Box-Cox	Calculated.
Distance from village	Distance to the nearest village	Box-Cox	Calculated
Distance to water	Distance from the nearest water source in meters	Box-Cox	Calculated.

Table 5-4. Measures of evaluation for habitat models at different pixel resolutions (with cross-validated standard deviations).

Study Site	Model Resolution	Circular moving window size	AVI	CVI	Continuous Boyce Index
STR	100 m	1 km^2	0.51 (0.11)	0.30 (0.11)	0.75 (0.18)
STR	100 m	54 km^2	0.48 (0.14)	0.33 (0.13)	0.69 (0.35)
STR	200 m	56 km^2	0.50 (0.19)	0.40 (0.19)	0.74 (0.25)
STR	300 m	52 km^2	0.49 (0.22)	0.34 (0.21)	0.36 (0.39)
STR	500 m	56 km^2	0.49 (0.17)	0.34 (0.16)	0.63 (0.26)
SC Madhya Pradesh	1000 m, with buffer	20 km^2	0.48 (0.12)	0.33 (0.11)	0.91 (0.13)
SC Madhya Pradesh	1000 m	21 km^2	0.48 (0.15)	0.33 (0.14)	0.72 (0.32)
SC Madhya Pradesh	2000 m	84 km^2	0.50 (0.19)	0.35 (0.18)	0.78 (0.24)
SC Madhya Pradesh	3000 m	81 km^2	0.52 (0.11)	0.29 (0.10)	0.77 (0.17)
SC Madhya Pradesh	5000 m	225 km^2	0.48 (0.11)	0.20 (0.10)	0.55 (0.25)

Note: AVI measures proportional accuracy in classifying habitat and ranges from 0 to 1. Higher values of AVI denote a more accurate model. CVI measures the difference between the model and a random model, with values ranging from 0 to AVI. High values of CVI indicate a model that is very different from random. The Boyce index measures the correlation between habitat suitability values and the area adjusted frequency of presence points in the habitat map.

Table 5-5. Correlation between ENFA factors and EGV for south-central Madhya Pradesh. The percentages quantify the amount of specialization attributed to the factor.

EGV	Factor1 (12%)+	Factor2♦ (22%)	Factor3♦ (12%)	Factor4♦ (10%)	Factor5♦ (9%)	Factor6♦ (8%)	Factor7♦ (7%)
Elevation	+	0	0	****	****	***	**
Elevation standard deviation	++++	0	0	*	0	*	0
Slope	++	0	0	0	0	0	0
NDVI	++	*	*****	***	***	*	**
Forest	+++++	*	****	***	*****	*****	*******
Bare ground/urban	--	********	****	***	***	**	***
Agriculture	----	*****	******	****	*****	******	*****
Livestock ER	-	*	*	***	0	****	**
Nilgai ER	+++	0	0	*	0	0	0
Sambar ER	++++	*	0	*	0	*	*
Wild pig ER	++	*	**	*****	*	**	**
Distance to water	0	*	0	**	***	*	**

Note: +For the marginality factor, the + symbol indicates that leopards presence was associated with values higher than average, and vice versa for -. The number of signs indicates the strength of the relationship. ♦ For the specialization factor, * indicates that leopards were found in narrower range of values than available. The number of * indicates the narrowness of the range. A 0 indicates low specialization. Factor 1 accounts for all the marginality.

Table 5-6. Correlation between ENFA factors and EGV for Satpura Tiger Reserve. The percentages quantify the amount of specialization attributed to the factor.

EGV	Factor1 + (22%)	Factor2 ♦ (42%)	Factor3♦ (9%)	Factor4♦ (6%)
Elevation	---	******	0	0
Slope	--	0	0	*
Langur ER	+	*	0	0
Cervid ER	++	0	0	0
Pig ER	++	0	0	0
Small-prey ER	+++	0	0	*
Tassled cap 'greenness'	++++	**	******	********
Teak Forest	+++	****	****	***
Moist Forest	+++	*****	*****	****
Dry Forest	---	****	*	**
Bare ground	----	*	***	***
Distance to water	+++	0	**	*
Distance to village	-	0	**	**

Note: +For the marginality factor, the + symbol indicates that leopards presence was associated with values higher than average, and vice versa for -. The number of signs indicates the strength of the relationship. ♦ For the specialization factor, * indicates that leopards were found in narrower range of values than available. The number of * indicates the narrowness of the range. A 0 indicates low specialization.Factor 1 accounts for all the marginality.

Table 5-7. Area under various leopard-habitat categories in south-central Madhya Pradesh.

District	Unsuitable (km^2)	Marginal (km^2)	Suitable (km^2)	Optimal (km^2)
Balaghat	118.3	210.6	86.2	5.0
Betul	5031.5	2387.9	1172.1	857.5
Bhopal	50.1	7.0	0	0
Chhindwara	5621.2	3528.2	1931.6	744.1
Dewas	776.2	288.8	166.5	66.2
East Nimar	1141.3	453.3	343.0	168.5
Harda	2187.3	490.4	415.2	238.7
Hoshangabad	3325.6	1577.5	1371.0	465.3
Jabalpur	38.1	172.5	28.1	20.0
Narmsimhapur	3265.4	638.8	303.9	215.6
Raisen	2464.1	535.5	282.8	14.0
Sehore	1590.6	882.5	583.7	212.6
Seoni	2951.5	1745.0	892.6	306.9

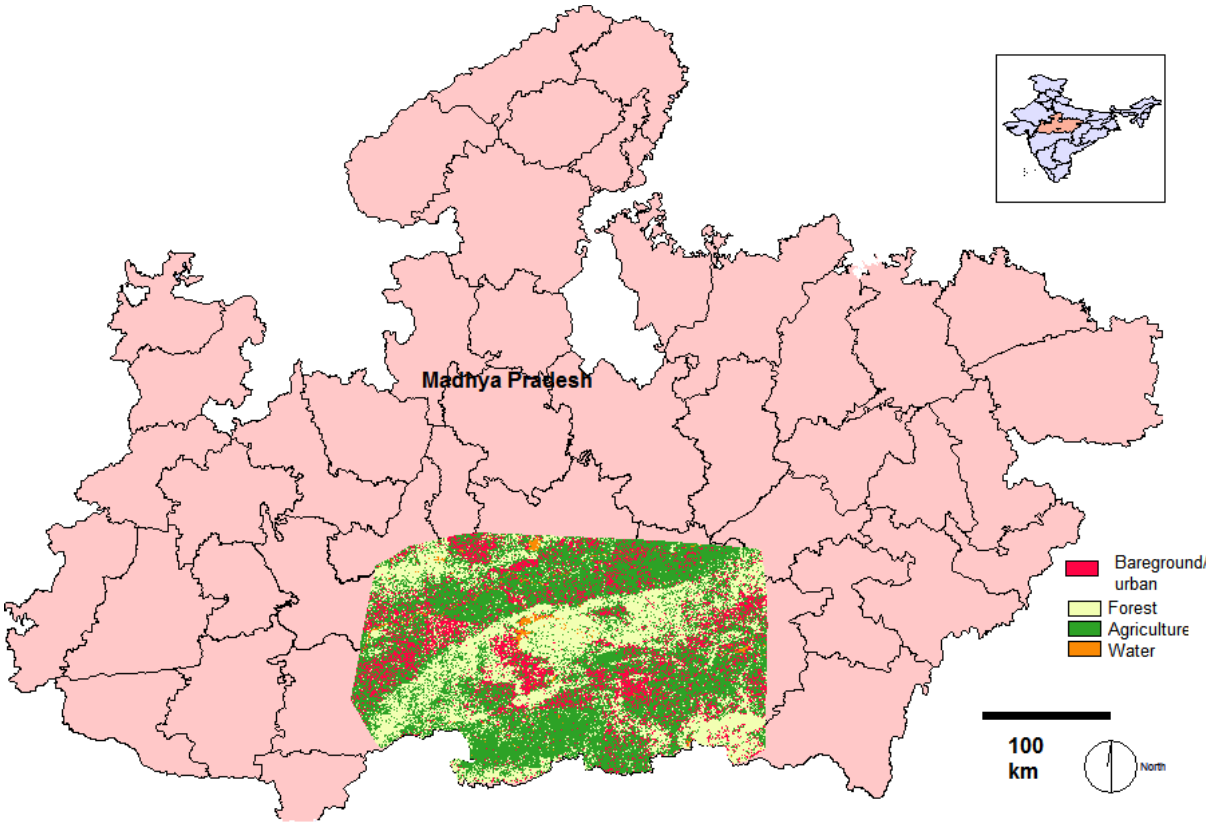

Figure 5-1. Cover map of the study area in south-central Madhya Pradesh.

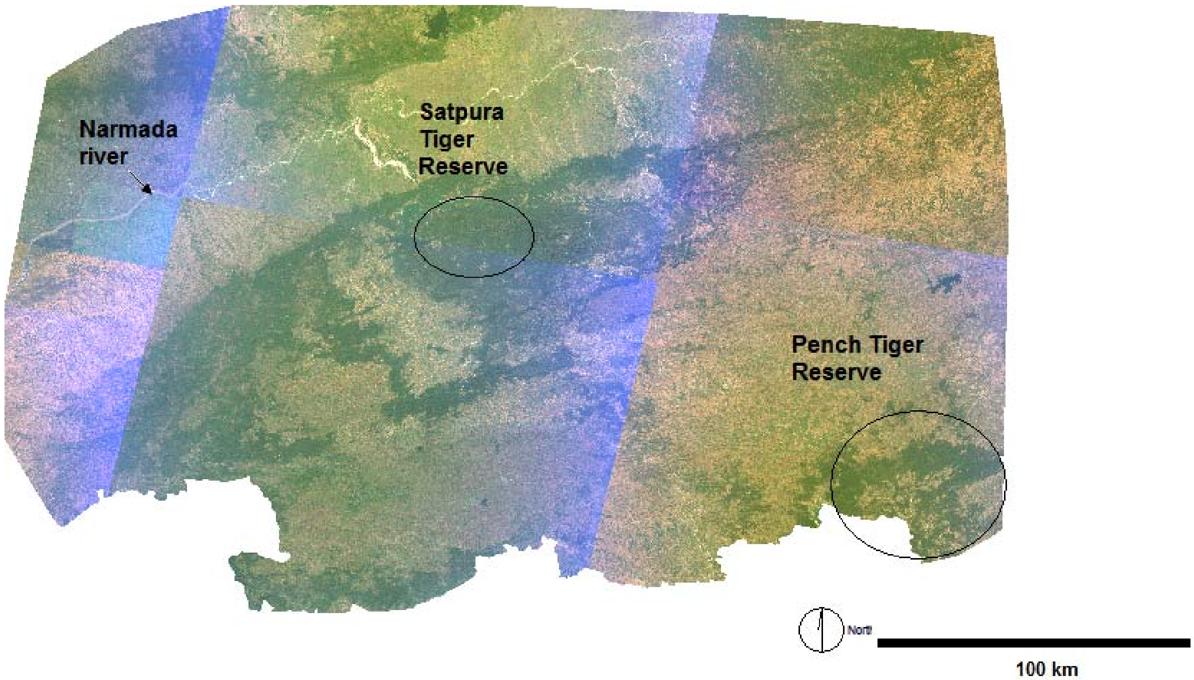

Figure 5-2. Mosaicked landsat satellite image of the study area in south-central Madhya Pradesh.

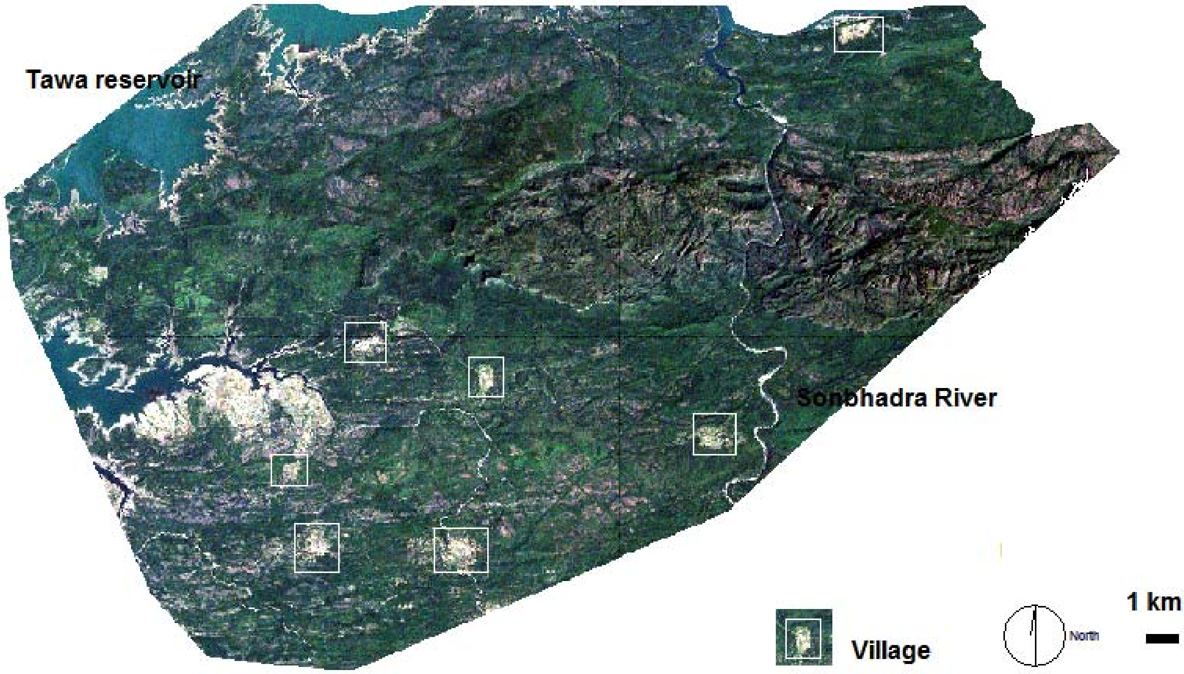

Figure 5-3. Landsat satellite image of the study area in Satpura Tiger Reserve.

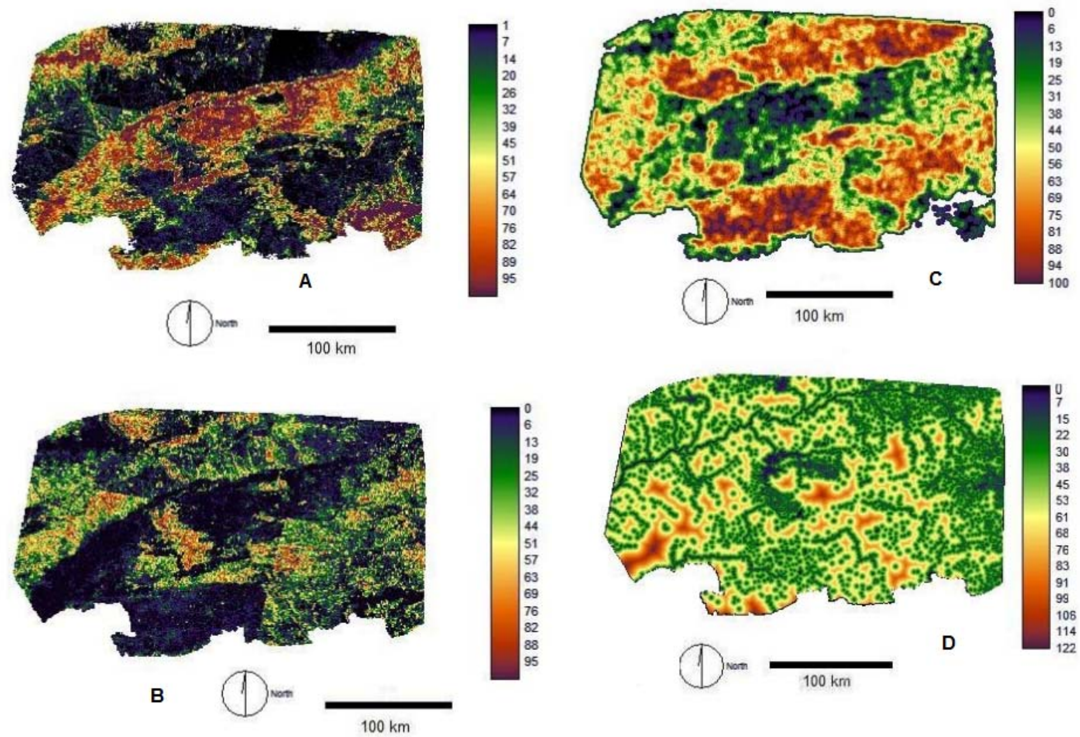

Figure 5-4. Maps of remotely derived variables for south-central Madhya Pradesh. A) Frequency of forests. B) Frequency of urban/bareground. C) Frequency of agriculture. D) Distance to water sources. . E: Elevation. F: Slope G: Ruggedness (Std deviation of elevation). H) NDVI. I) Nilgai abundance index . J) Sambar abundance index. K) Wild pig abundance index. L) Livestock abundance index.

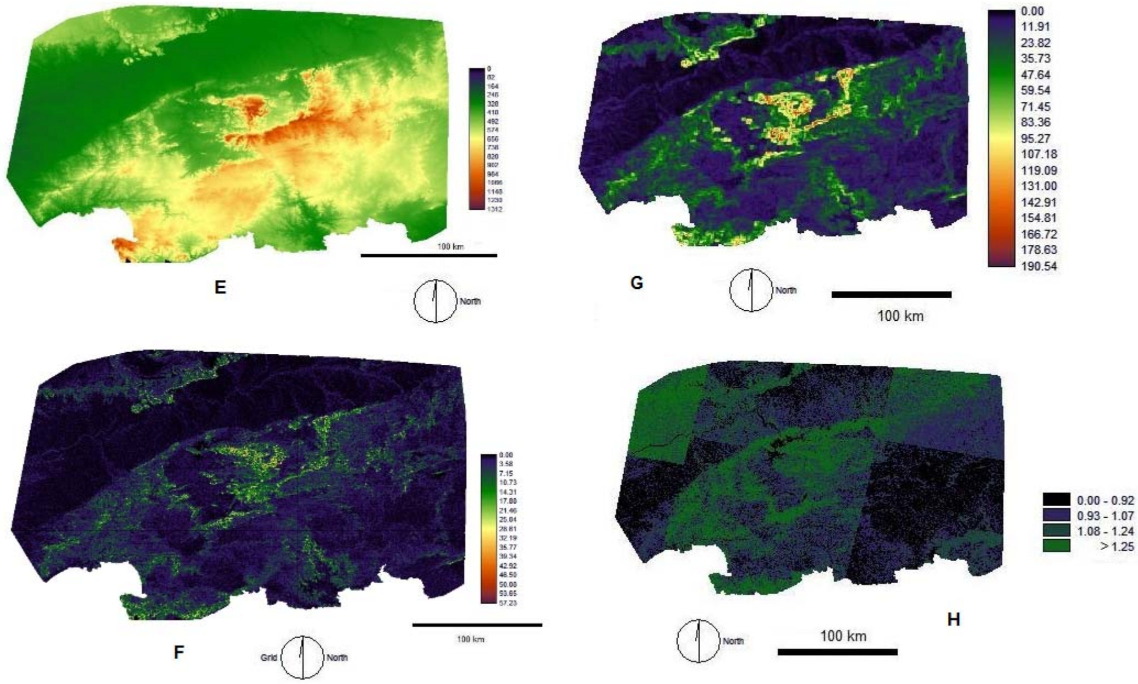

Figure 5-4. Continued.

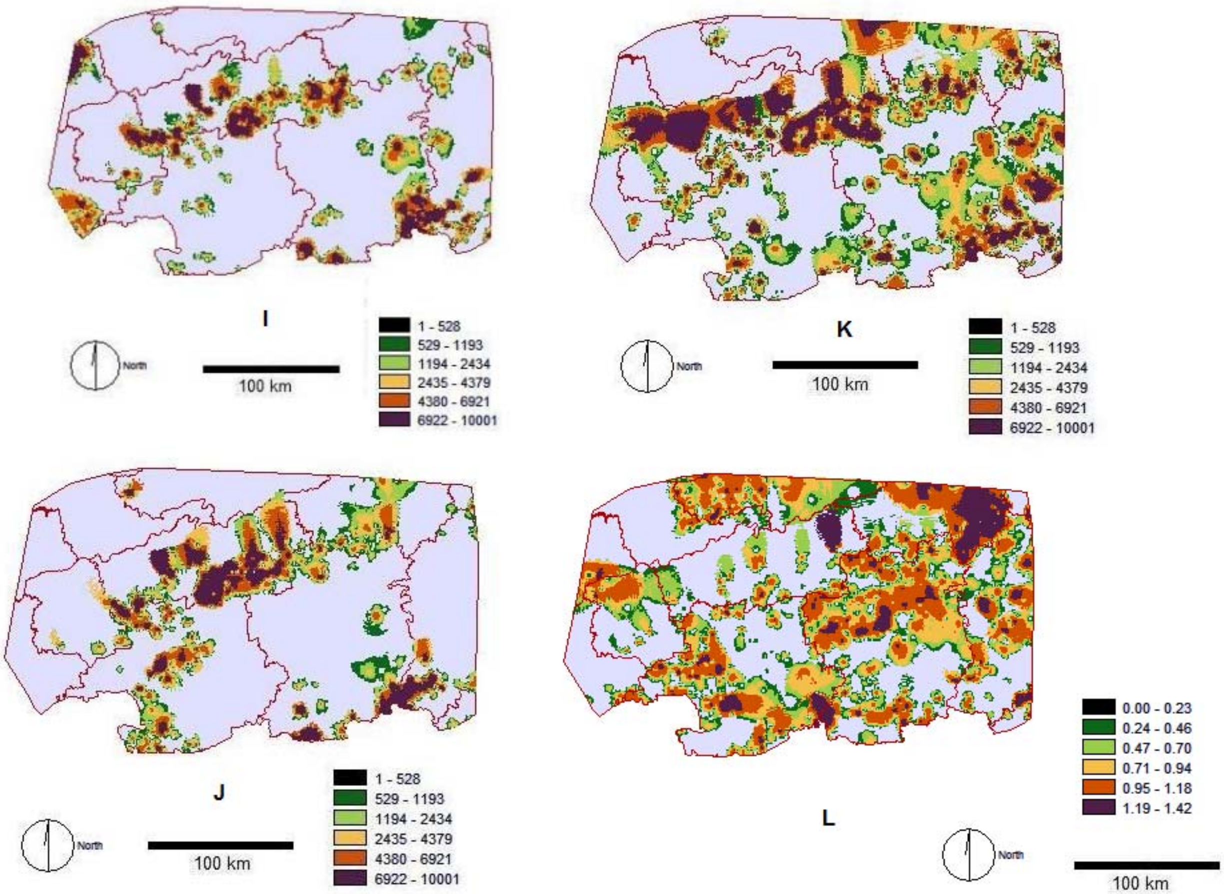

Figure 5-4.Continued.

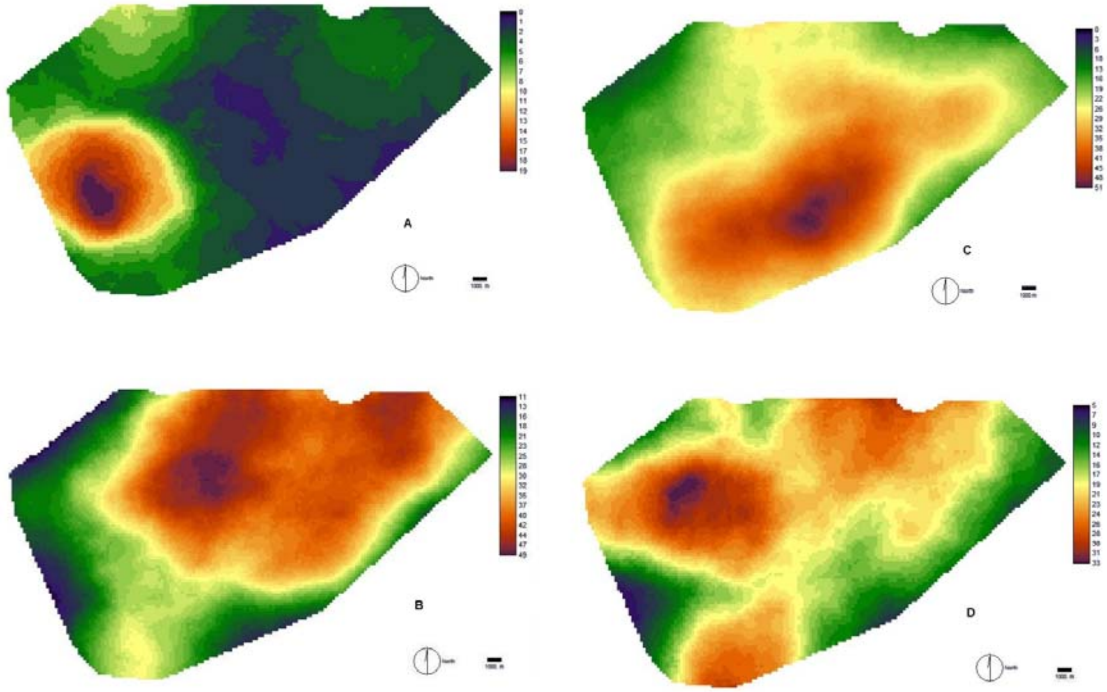

Figure 5-5. Maps of remotely derived variables for Satpura Tiger Reserve. A) Frequency of bareground. B) Frequency of moist forest. C) Frequency of dry forest. D) Frequency of teak forest. E) Cervid abundance index . F) Wild pig abundance index. G) Langur abundance index. H) Small prey abundance index. I) Elevation. J) Slope. K) Tassel cap ‘greenness’. L) Distance to village. M) Distance to water.

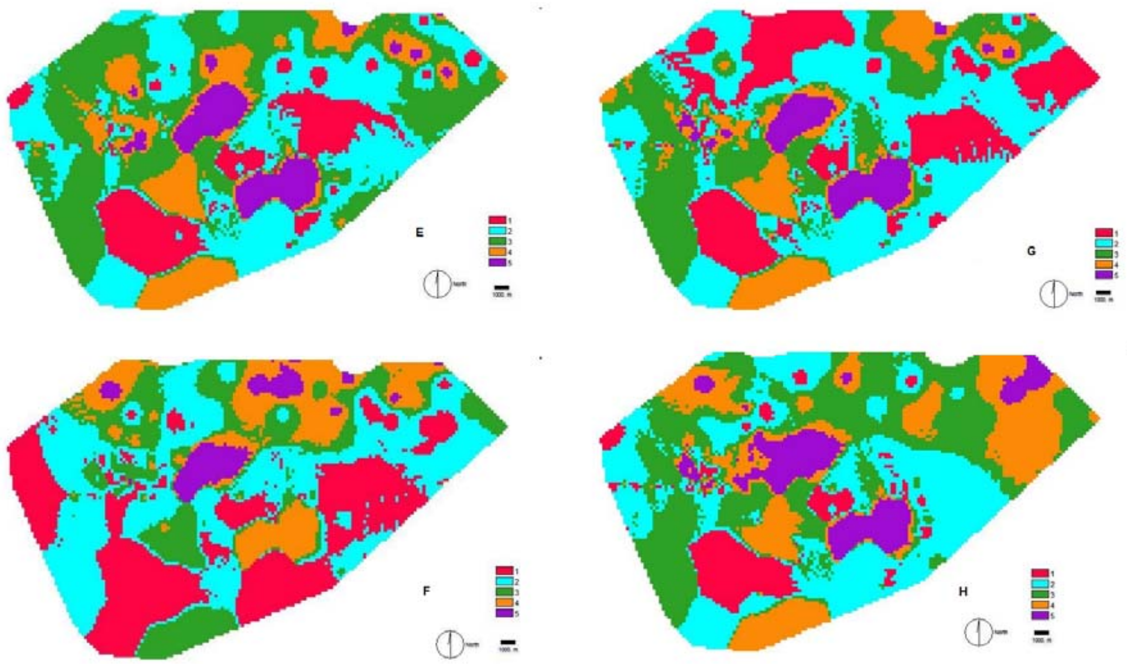

Figure 5-5. Continued.

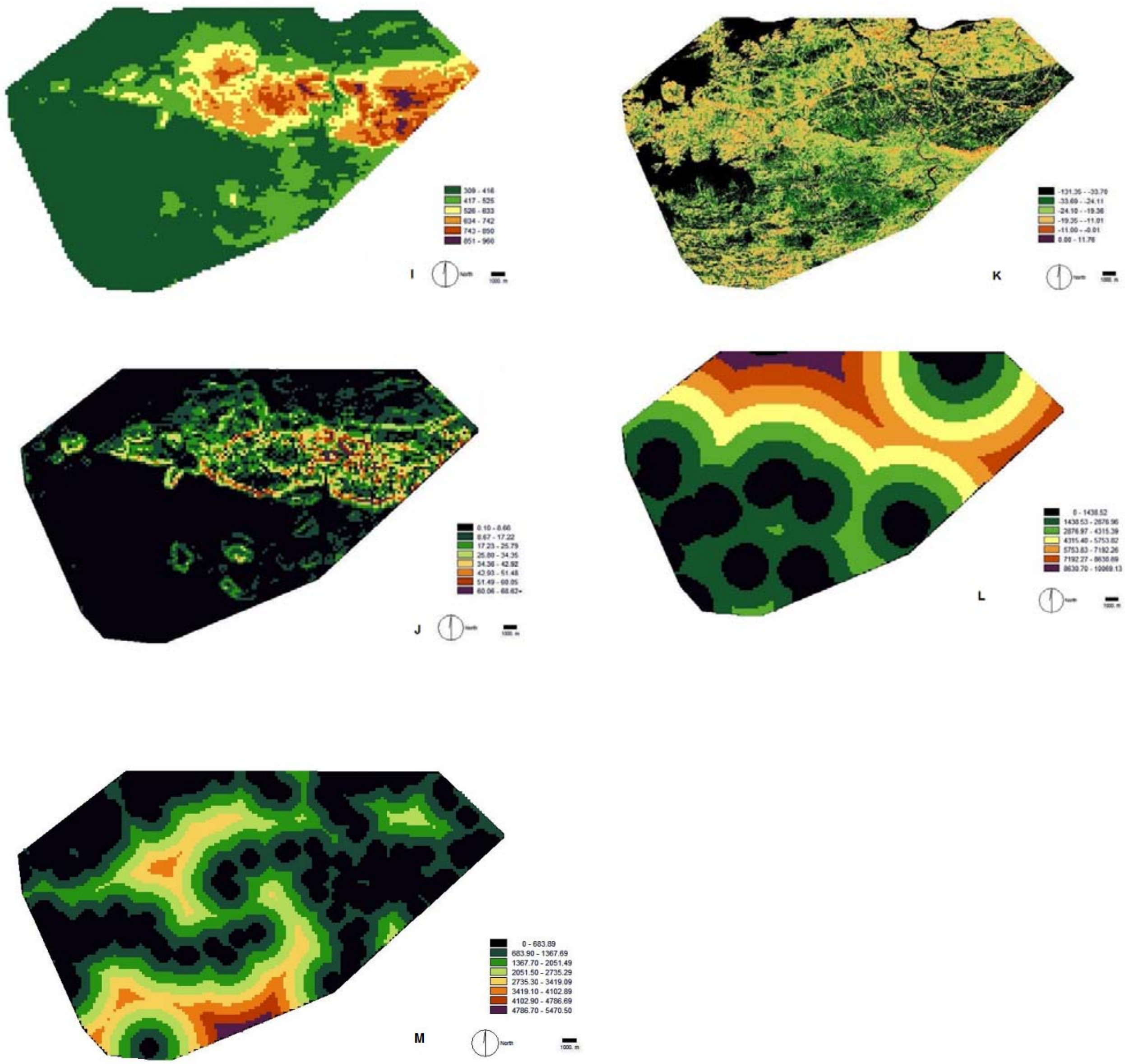

Figure 5-5. Continued.

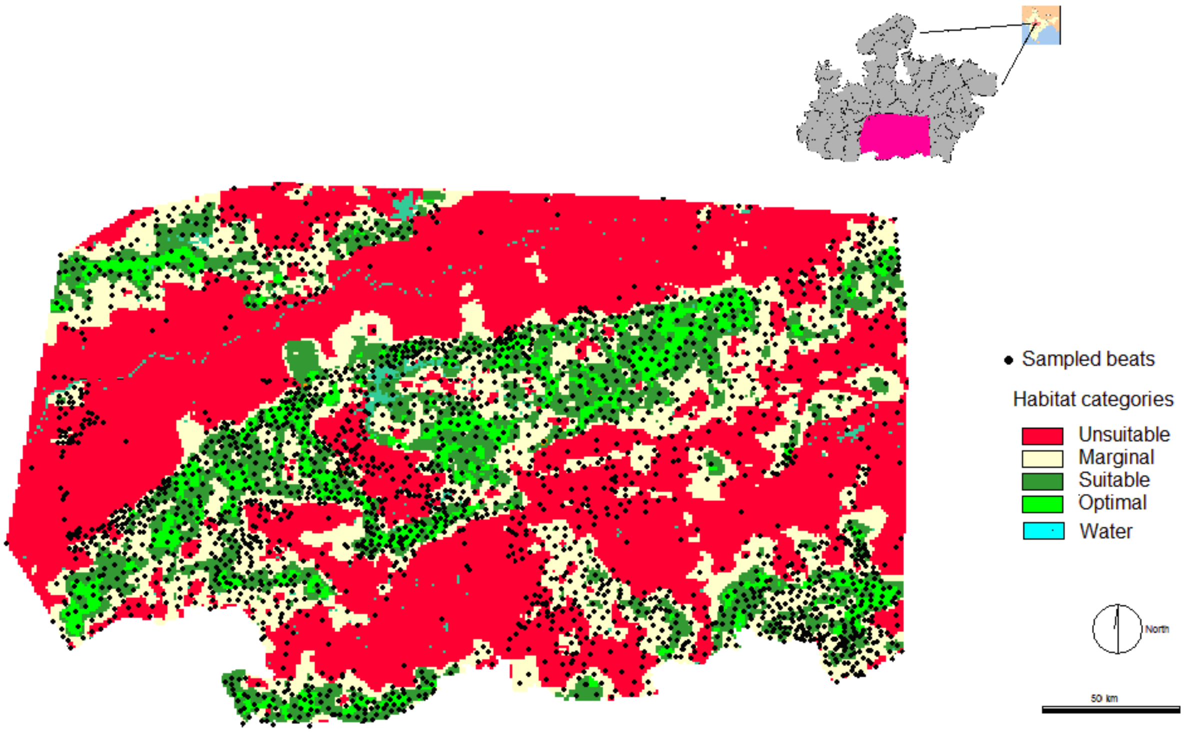

Figure 5-6. Leopard habitat suitability map for south-central Madhya Pradesh.

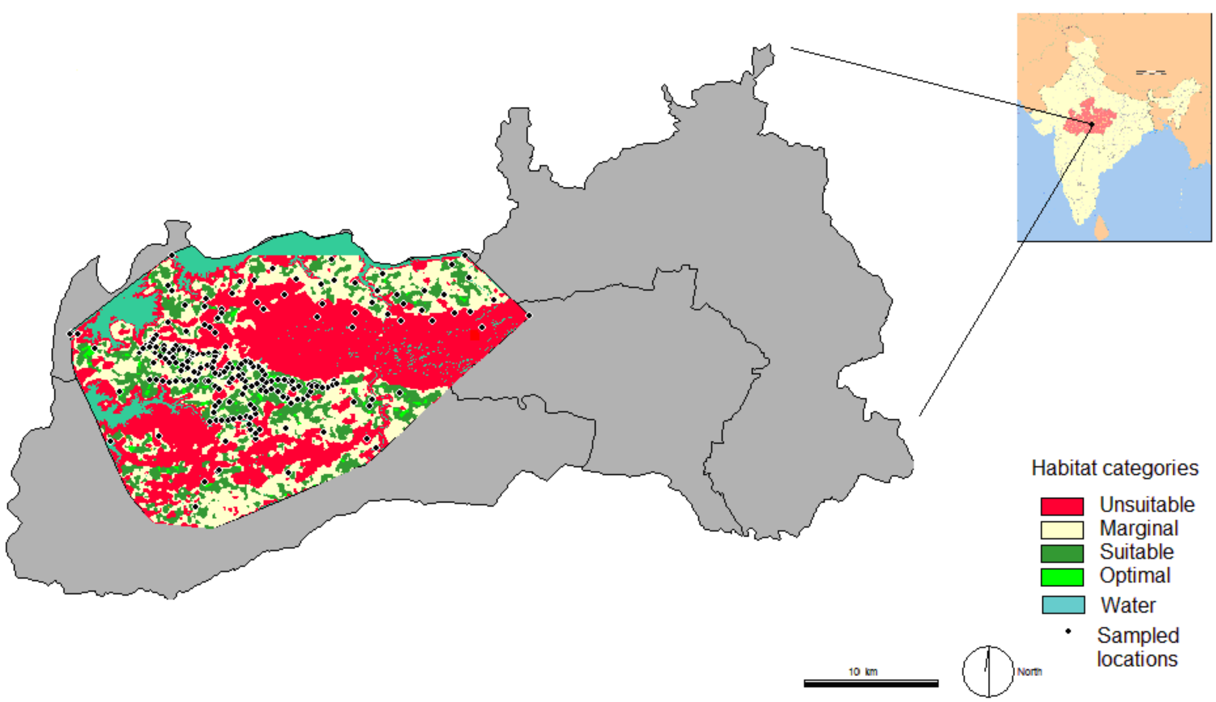

Figure 5-7. Leopard habitat suitability map for Satpura Tiger Reserve.

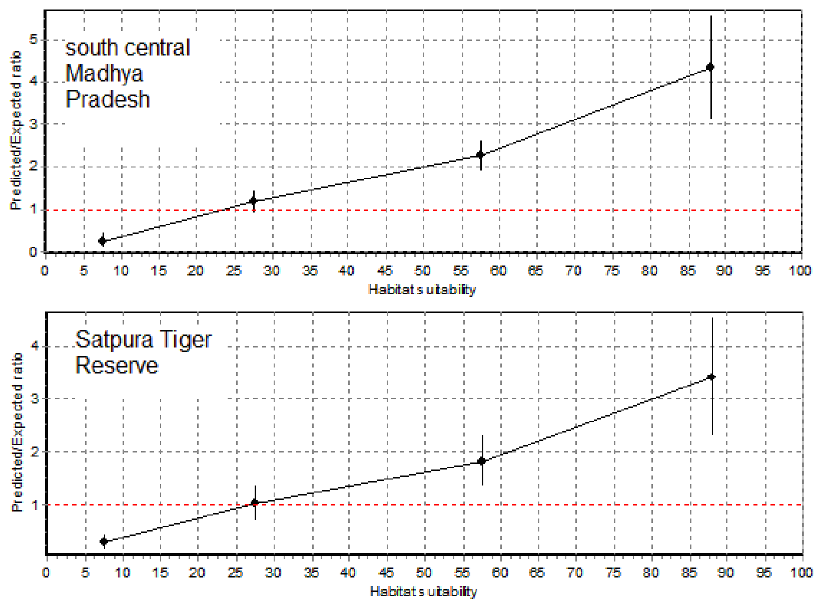

Figure 5-8. The predicted-to-expected frequency curves with habitat suitability values for both the models.

CHAPTER 6
CONCLUSION

Density of Potential Prey

Rigorous estimates of ungulate density were not available until now for the Satpura Tiger Reserve. The results of this study indicate that wildlife populations are lower than those in relatively well protected parks in India such as Nagarhole and Bandipur in southern India and Kanha and Pench tiger reserves in Madhya Pradesh. They are however in line with estimates from other central Indian protected areas like Tadoba, Melghat and Pench (Maharashtra). Though densities of most prey species are low in the study area, the ungulate community is still intact. Since the area is relatively large, a higher degree of protection and habitat management should increase prey and be able to support a relatively large population of carnivores. The coefficients of variation around the density estimates of most species generated by this study are low enough to be useful to monitor population changes. A note of caution should be sounded since the last year of sampling showed lower densities for all species. A monitoring program needs to be instituted to make sure that this population is not continuously declining. This monitoring program should involve distance sampling and can use vehicles to take advantage of the extensive trail network.

Preference of Prey

Leopards, dholes and tigers strongly prefer sambar in this study area. The density of sambar can be enhanced further using suitable habitat management techniques, but the main requirement is likely to be effective protection from poaching. Because the food habits of leopards, dholes and tigers overlap to a great extent, any increase in density of medium and large biomass will benefit all the predators.

Density of Leopards

There is no other published information on density of leopards in India, so comparison of these results with other areas is difficult. Indices computed for other parks are in the same range as ones calculated for this study. Index based approaches such as the number of photographs per night (RAI) have been recommended to be used for tigers when there are not enough data for mark recapture sampling (Carbone et al. 2001). In this study, the RAI did not index leopard density well and it cannot be recommended. Therefore the results of indices available for other study areas should be interpreted with caution. At the present time there appears to be no substitute to the mark-recapture framework used in this study. It is recommended that leopard densities be estimated across all protected areas and a reliable index be developed so that large areas in the country can be monitored for population changes. There is urgent need for more research to accurately estimate the effective trapping area. The spatially explicit maximum likelihood method offers hope for the future, but with the low population sizes it is difficult to obtain high precision, making it difficult to detect changes in population density. The logistics involved in sampling at a high enough intensity to get good precision and at a large enough spatial scale for a species of this size are very difficult. Given these limitations, there is urgent need for a calibrated index to be developed to monitor population changes of leopards.

Habitat Model

The leopard is an adaptable species, being able to live in a wide variety of environmental conditions. The habitat model showed that moist deciduous and teak dominant forests had a higher association with leopards. Prey densities, especially those of sambar, were also higher in these habitat types. The larger spatial scale model showed that leopards were negatively associated with land cover associated with human use. Though it has a reputation for tolerating human presence, leopard densities are negatively affected by disturbance and presence of agriculture. Given that it is a large-sized carnivore species that requires relatively large tracts of contiguous habitat, the model predicted a compact block of about 2000 km^2 of optimal habitat in the districts of Betul, Hoshangabad and Chhindwara. In addition, approximately 11500 km^2 of habitat is likely to support leopard populations in south-central Madhya Pradesh. It is recommended that protection for this habitat be adequately strengthened and resources prioritized accordingly when managing leopard conservation efforts in Madhya Pradesh.

APPENDIX A
INDICES OF UNGULATE AND CARNIVORE ABUNDANCE

Table A-1. Kilometric index values (number of individuals per km.) of selected species using dirt trails in the monsoon from 2002 to 2005 with bootstrapped 95% C.I.

Species	2002 N=9696.2 km	2003 N=9910.3 km	2004 N=91188.1 km	2005 N=9811.8 km
Chital	1.26 (1.01-1.54)	0.77 (0.64-0.92)	1.39 (1.12-1.71)	1.48 (1.16-1.87)
Sambar	0.43 (0.36-0.52)	0.31 (0.25-0.37)	0.19 (0.15-0.24)	0.14 (0.10-0.19)
Indian muntjac	0.08 (0.06-0.10)	0.04 (0.03-0.06)	0.04 (0.03-0.05)	0.04 (0.03-0.06)
Nilgai	0.13 (0.09-0.18)	0.08 (0.05-0.10)	0.06 (0.04-0.08)	0.06 (0.03-0.09)
Wild pig	0.43 (0.30-0.58)	0.36 (0.27-0.46)	0.24 (0.15-0.37)	0.17 (0.07-0.24)
Common langur	1.28 (1.05-1.54)	1.14 (0.98-1.3)	2.51 (2.22-2.79)	2.39 (0.21-0.28)
Indian peafowl	0.30 (0.24-0.35)	0.34 (0.29-0.38)	0.26 (0.22-0.31)	0.24 (0.19-0.29)

Table A-2. Encounter rates of tracks of selected carnivore species (frequency per 500 m section), with bootstrapped 95 % C.I. (November 2003 to June 2006).

Time period	Leopard	Dhole	Tiger	Sloth bear	Jungle cat	Palm civet
Nov'03-Feb'04	0.14 (0.08-0.19)	0.24 (0.18-0.31)	0.06 (0.03-0.11)	0.22 (0.17-0.28)	0.10 (0.06-0.14)	0.32 (0.26-0.39)
Mar'04-Jun'04	0.13 (0.10-0.16)	0.15 (0.12-0.18)	0.03 (0.02-.05)	0.43 (0.39-0.47)	0.09 (0.07-0.11)	0.35 (0.31-0.39)
Nov'04-Feb'05	0.11 (0.09-0.13)	0.07 (0.05-0.09)	0.08 (0.06-0.10)	0.10 (0.08-0.13)	0.02 (0.01-0.03)	0.22 (0.20-0.26)
Mar'05-Jun'05	0.03 (0.02-0.04)	0.03 (0.02-0.04)	0.02 (0.01-0.02)	0.36 (0.33-0.39)	0.06 (0.05-0.09)	0.27 (0.25-0.30)
Nov'05-Feb'06	0.11 (0.10-0.13)	0.14 (0.12-0.15)	0.02 (0.02-0.03)	0.11 (0.01-0.13)	0.12 (0.10-0.14)	0.45 (0.42-0.47)
Mar'06-Jun'06	0.12 (0.10-0.14)	0.08 (0.06-0.09)	0.02 (0.01-0.03)	0.26 (0.23-0.28)	0.09 (0.08-0.11)	0.33 (0.30-0.35)

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BIOGRAPHICAL SKETCH

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