

DISTRIBUTION AND DYNAMICS OF
TIGER AND PREY POPULATIONS
IN MAHARASHTRA, INDIA

FINAL TECHNICAL REPORT

December 2005

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H. Dhanwatey - Pench Tiger habitat, Dr. K. U. Karanth discussing sampling design with Park officials

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Field Project Sites

Tadoba-Andhari Tiger Reserve
Melghat Tiger Reserve
Pench Tiger Reserve

Distribution and Dynamics of Tiger and Prey Populations in Maharashtra, India

Final Technical Report
(October 2001 to August 2005)

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Executive Summary

Maharashtra is one of the important tiger range states in the country. The state has an impressive variety of wildlife habitats and has a potential tiger habitat of about 6,000 - 9,000 km². The state has implemented several positive measures to improve the status of wildlife and its habitat in Maharashtra. However, there are no reliable estimates of tiger populations for any of the key tiger habitats in Maharashtra or any measures of their relative abundance in order to adaptively react to their management needs. There is a need to monitor tiger and prey populations in a few select habitats with potentially viable breeding tiger populations in Maharashtra to ensure their long-term survival. This project established ecological benchmarks for monitoring three critical, productive tiger and prey populations in three of the high potential areas (Tadoba-Andhari, Melghat and Pench) of the state. The project also helped provide a valid base for the scientific management of these areas, as well as to evaluate to what extent tigers, prey and habitat are responding to the management and conservation interventions, which are being implemented by the states and non-governmental organizations under other projects. The original objectives of the project were:

1. To estimate population densities of the principal prey species in three selected sites, using the line transect method
2. To estimate population densities of tigers and leopards using camera trap capture-recapture surveys
3. To develop simple trend-indices of relative abundance for monitoring tiger and prey populations
4. To assess and map the current distribution status of tigers in Maharashtra
5. To train Maharashtra State Forest Department staff at different levels in monitoring activities
6. To identify motivated and qualified officers in the Forest Department and other personnel for advanced career development by offering support for registration and guidance for obtaining higher degrees in wildlife biology and management.

During the project period, intensive field survey modules were carried out at three high priority tiger habitats of the state. Major accomplishments include the first-ever abundance estimates of tiger and prey populations using state-of-the-art population monitoring methods in Tadoba-Andhari, Melghat and Pench Tiger Reserves; training of Maharashtra State Forest Department staff and local non-government volunteers in the application of sampling-based methods for monitoring large mammalian populations; and identification of highly motivated local community leaders for biological as well as conservation monitoring at three project sites. Field research activities specifically included camera trap surveys, line transect surveys, carnivore sign encounter surveys and carnivore diet studies at all the three project sites.

A total of 14 field workshops were organized, where 116 local volunteers and 82 departmental staff were trained in use of the line transect technique to estimate tiger and prey species densities. In addition, 5 training workshops were also conducted on the use of index-based surveys for monitoring tiger and prey populations. 50 field staff from the Forest Department and 80 volunteers from local NGOs participated in these sign encounter surveys. Four research assistants and one post-graduate student were trained in the field and analytical aspects of the research, as part of this project. A total of 4 slide-talks demonstrating the use of camera traps in tiger population surveys were conducted for staff of the Maharashtra State Forest Department. The Co-Principal Investigators and collaborating partners also gave several talks/presentations disseminating key findings of the project at various fora.

The results from this project have significant implications for the management and conservation of tiger habitats in Maharashtra. Although the results show lower densities of tigers in Maharashtra compared to some other high-density areas in the country, our surveys show that the extensive prime tiger habitats in Maharashtra have the potential to support higher densities of tigers, if prey densities can be increased to optimal levels through protection and habitat consolidation. It is hoped that our estimates of tiger and prey densities provide critical benchmarks to managers for setting up objectives, against which the success of future management and conservation interventions can be measured. Continuation of the long-term monitoring of the most productive tiger habitats in Maharashtra together with a state-wide assessment of the current distributional range of tigers using modern sampling-based methods will be the next step forward. We believe Maharashtra State Forest Department together with local community leaders for tiger conservation are well poised to forge synergic ties and pursue this goal.

Photo: K. U. Karanth



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- Rhinoceros and Tiger Conservation Fund, Division of International Conservation, US Fish and Wildlife Service
- US Geological Survey, Patuxent Wildlife Research Center

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Photo: Centre for Wildlife Studies



Personnel and Institutional Involvement

Project Personnel

K. Ullas Karanth, Wildlife Conservation Society, was the Principal Investigator and James D. Nichols, US Geological Survey - Patuxent Wildlife Research Center, was the advisor to the project. N. Samba Kumar, Centre for Wildlife Studies, was the Co-Principal Investigator.

Harshawardhan Dhanwatey and Poonam Dhanwatey were the Co-Principal Investigators and local collaborating partners at Tadoba-Andhari and Pench Tiger Reserves. Prachi Mehta and Jayant Kulkarni were the Co-Principal Investigators and local collaborating partners at Melghat Tiger Reserve.

The research assistants who worked on this project were: Arjun Gopaldaswamy, Raghavendra Mogaroy, Narendra Patil, Bharath Sundaram and R. Raghunath. V. Srinivas provided GIS support and Javaji Amarnath maintained equipment.

Institutions

Maharashtra State Forest Department was the collaborating partner and facilitated this study enthusiastically. The Chief Wildlife Warden, Maharashtra provided necessary permissions and support facilities at the field sites. The Field Directors and Deputy Wildlife Wardens of the three field sites provided full cooperation and support for implementing this project, besides nominating their field staff for training and capacity-building.

The Save the Tiger Fund (STF) of the National Fish and Wildlife Foundation and the Rhinoceros and Tiger Conservation Fund (RTCF) of the Division of International Conservation, US Fish and Wildlife Service provided funding support for the surveys in Maharashtra, under grant agreements NFWF #2001-0152-031, NFWF #2003-0087-006 and NFWF #2004-0103-007 and USFWS #98210-1-G946 and USFWS #98210-3-G544.

The Centre for Wildlife Studies, Bangalore, administered this project. Wildlife Conservation Society, New York (WCS-NY) provided the services of the Principal Investigator, in addition to providing some of the funding, logistic and technical support. The Patuxent Wildlife Research Center of the US Geological Survey provided the services of the Project Advisor and other scientists for data analysis.

Tiger Research And Conservation Trust (TRACT), Nagpur and Envirosearch, Pune provided local assistance and logistical support in addition to providing field support in organizing training workshops.

Introduction

In India, tigers are distributed over 1300,000 km² of area (Wikramanayake *et. al.* 1999). The Indian state of Maharashtra is an important part of the tiger's range in the country. The state has an impressive variety of wildlife habitats and has an estimated potential tiger habitat of about 6,000 - 9,000 km². The state has implemented several positive measures in the past to improve the status of wildlife and its habitat. However, the Forest Department is constrained by the absence of reliable population estimates of either tigers or their prey in some of the key tiger habitats, derived using modern sampling-based approaches. Deriving such estimates has been deemed to be a priority by the Government of India (Anon 1997, 2001). Further, there is also a need for deriving simpler measures of relative abundance of tigers and prey for annual monitoring. Overall, there is an immediate need to rigorously estimate tiger and prey populations in a few select habitats with potentially viable breeding tiger populations in Maharashtra to ensure their long-term survival.

Earlier studies (Karanth and Nichols 1998, 2000) have generated baseline ecological information on tiger and prey populations in several high-potential tiger habitats across India. These studies have also tested several cutting-edge

methodologies for effective monitoring of tiger and prey populations over large regions and at multiple scales (Karanth and Nichols 2002). The present project has implemented these ideas by actually carrying out field surveys to monitor tiger and prey populations at landscape scales in three key tiger habitats in the state of Maharashtra using the most advanced state-of-the-art tools available for population monitoring. Work is needed for developing methods for index surveys and spatial mapping of tigers and prey over larger landscapes. Furthermore, over the last five years, techniques such as distance sampling and capture-recapture sampling have undergone major technical advances. In collaboration with cutting-edge leaders in these fields, Dr. James Nichols (at USGS) and the Distance development team (at the University of St. Andrews), this project brought to bear the best scientific tools to the problem of reliably monitoring tiger and prey populations in the forested habitats of Maharashtra.

This project was initiated to establish benchmark estimates at three critical, productive tiger and prey populations (Tadoba-Andhari, Melghat and Pench Tiger Reserves) in Maharashtra, and to develop civil society and forest department capabilities for monitoring in the future.

Objectives

The overall goal of the project was to carry out advanced-level monitoring of tiger and prey populations in three high priority tiger conservation areas within the state using the state-of-the-art population monitoring tools, as well as to generate a state-wide distributional range map of tigers in Maharashtra. A major goal of the project was to train the staff of Maharashtra State Forest Department and volunteer naturalists in various monitoring techniques ranging from simplest relative density indices to relatively sophisticated estimation of density and population dynamics of tiger and prey populations. The original specific objectives of this project were:

1. To estimate population density of the principal prey species in three selected sites, using line transect method
2. To estimate population densities of tigers and leopards using camera trap capture-recapture surveys

3. To develop simple trend-indices of relative abundance for monitoring tiger and prey populations

4. To train Maharashtra State Forest Department staff at different levels in monitoring activities

5. To identify motivated and qualified officers in the Forest Department and other personnel for advanced career development by offering support for registration and guidance for obtaining higher degrees in wildlife biology and management.

6. To assess and map the current distribution status of tigers in Maharashtra: However, after consultations with senior officials of the Maharashtra State Forest Department, this component was not conducted as part of this project.

Photo: H. Dhanwatey



Ullas Karanth (right) and Samba Kumar setting up a camera trap

Project sites

The project sites comprised of three large blocks of tiger habitat in the state of Maharashtra. Administratively, these sites together cover nearly 1800 km² of prime tiger habitat in the state and offer high potential for long-term sustenance of breeding tiger populations in three different landscape patches within Maharashtra (see Figure-1). These sites cover the legally protected and designated reserves of Tadoba-Andhari in the south-east, Melghat in the north-west and Pench in the north-east parts of Maharashtra. These sites also form a part of the high priority Tiger Conservation Units identified under the WCS-WWF (USA) global priority setting exercise for long-term conservation of tigers and are described below.

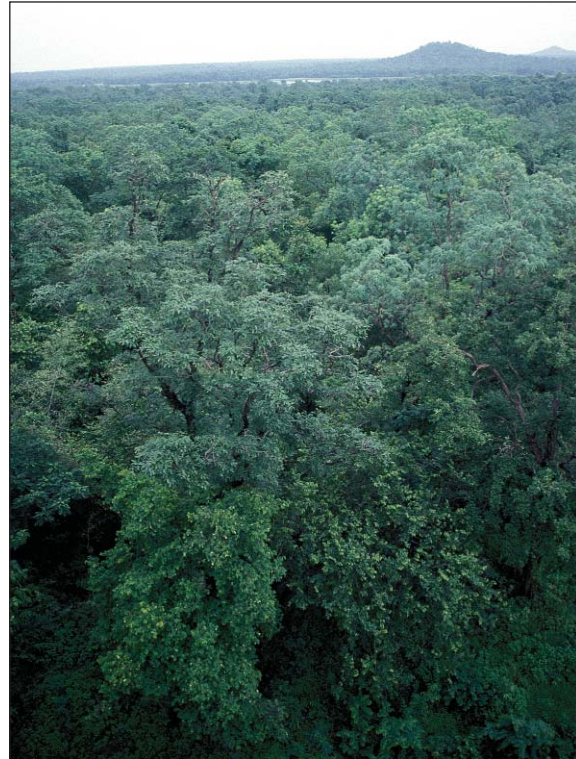
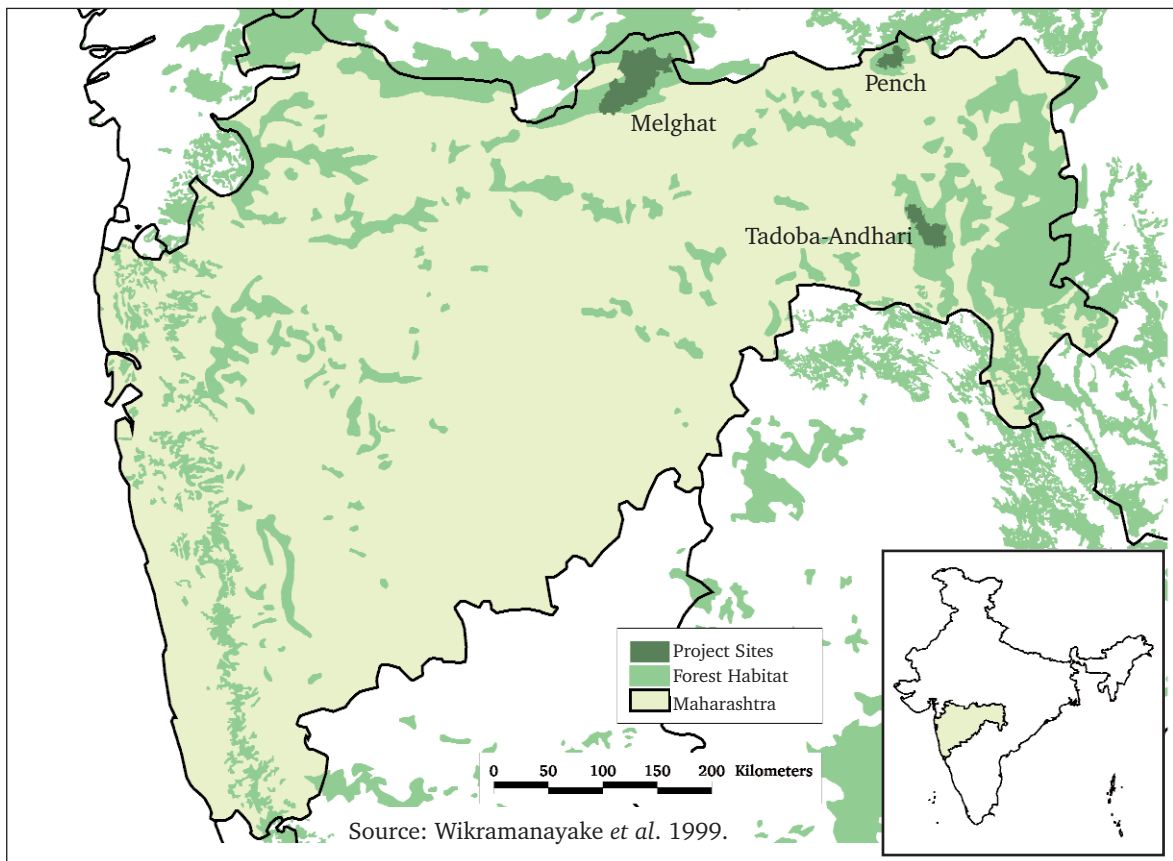


Photo: H. Dhanwathey

Tadoba-Andhari Tiger Reserve

Figure 1. Location of project sites in Maharashtra



I. Tadoba-Andhari Tiger Reserve

Tadoba-Andhari Tiger Reserve is the oldest National Park in Maharashtra State and was declared a tiger reserve in 1995. The tropical deciduous forests support an impressive mammalian fauna and comprise one of the prime tiger habitats of the state. The area is situated within Tiger Conservation Unit-44, one of the priority level III tiger conservation areas (Wikramanayake *et al.* 1999). The forests are connected with several adjoining protected and reserve forests together forming one of the largest blocks of contiguous forests of nearly 1,500 km² in central India. The State Forest Department has also initiated several management interventions including the relocation of six interior villages within the tiger reserve to consolidate this tiger habitat. The study site was located in the better-protected northern and central parts of the reserve.

Tadoba-Andhari Tiger Reserve is spread over 625 km² in Chandrapur district, in the Vidharbha region of eastern Maharashtra. It lies between 79° 13' E and 79° 33' E longitude, and 20° 05' N and 20° 26' N latitude. It receives an average of 1,175 mm of rainfall annually (Karanth *et al.* 2004b).

Photo: H. Dhanwatey



Tadoba-Andhari Tiger Reserve

The terrain is mostly undulating and hilly, interspersed with open grasslands and wooded areas. Elevation ranges from 212m to 351m above m.s.l. The dominant vegetation type is tropical dry deciduous forest, dominated by teak *Tectona grandis*, along with *Adina cordifolia*, *Anogeissus latifolia*, *Boswellia serrata*, *Diospyros melanoxylon*, *Madhuca indica*, *Pterocarpus marsupium*, *Terminalia tomentosa* and *T. bellerica* among others. Riparian vegetation includes species such as *Syzigium cumini*, *Terminalia arjuna* and *Mangifera indica*. The bamboo *Dendrocalamus strictus* forms an extensive under-storey. The large carnivores in the reserve are tiger *Panthera tigris*, leopard *P. pardus*, dhole *Canis aureus*, striped hyena *Hyaena hyaena* and sloth bear *Melursus ursinus*, with jungle cat *Felis chaus*, rusty-spotted cat *Prionailurus rubiginosus*, the small Indian civet *Viverricula indica*, the common palm civet *Paradoxurus hermaphroditus*, grey mongoose *Herpestes edwardsi*, ruddy mongoose *H. smithii*, jackal *Canis aureus* and ratel *Mellivora capensis* forming part of the small carnivore assemblage. The herbivore assemblage is typical of peninsular deciduous forests, comprised of sambar *Cervus unicolor*, chital *Axis axis*, muntjac *Muntiacus muntjak*, gaur *Bos gaurus*, chowsingha *Tetracerus quadricornis*, nilgai *Boselaphus tragocamelus*, and wild pig *Sus scrofa*. The larger arboreal mammals include common langur *Semnopithecus entellus* and large brown flying squirrel *Petaurista philippensis*. The reserve has 30 recorded species of reptiles, 5 species of amphibians and over 195 species of birds.

II. Melghat Tiger Reserve

Melghat Tiger Reserve is part of an extensive tiger habitat along the Satpura hill ranges that stretch across parts of Maharashtra and Madhya Pradesh States. It was declared a Tiger Reserve in 1974 and is the main catchment area for the river Tapti. The area is situated within Tiger Conservation Unit-28, one of the priority tiger conservation areas requiring immediate surveys to assess tiger population status (Wikramanayake *et al.* 1999). The forests are connected with several adjoining protected and reserve forests in Satpura hill ranges. The rugged topography and the contiguity of forests provide an excellent opportunity for the long-term conservation of tiger populations. The State Forest Department has recently completed the relocation of three interior villages within the tiger reserve and has initiated several management interventions to consolidate this tiger habitat. The study site was located in the better-protected south-central part of the reserve.

Melghat Tiger Reserve extends over 1677 km² in Amravati district. It is situated in the Gavilgarh hills, which is part of the Satpura range. It lies between 76° 57' E and 77° 30' E longitude, and 21° 15' N and 21° 45' N latitude. The average annual rainfall is 1100 mm (Karanth *et al.* 2004b). The terrain is rugged and hilly. Elevation ranges from 350m-1178m above m.s.l. The dominant vegetation type is tropical dry deciduous forest, dominated by teak *Tectona grandis*, with *Anogeissus latifolia*, *Butea monosperma*, *Diospyros melanoxylon*, *Embllica officinalis*, *Grewia tилаefolia*, *Lagerstroemia parviflora*,

Lannea coromandelica, *Mitragyna parviflora*, *Ougenia oojeinensis*, *Terminalia alata* and *Zizyphus xylopyra*, being some of the common species. Large carnivores in the reserve are tiger, leopard, dhole, hyena and sloth bear, with jungle cat, the small Indian civet, the common palm civet, grey mongoose, jackal, smooth-coated otter *Lutrogale perspicillata* and ratel being some of the small carnivores of the area. The herbivores are sambar, chital, muntjac, gaur, chowsingha, nilgai, and wild pig. The larger arboreal mammals include large brown flying squirrel, common langur and rhesus macaque *Macaca mulatta*. Over 215 species of birds (Mehta 2000), and 30 species of reptiles and amphibians have been recorded within the reserve.

Photo: H. Dhanwatey



Melghat Tiger Reserve

III. Pench Tiger Reserve

Pench Tiger Reserve is a typical representation of the floral and faunal wealth along the Satpura-Maikal hill range. The Government of Maharashtra declared the area as Pench National Park in 1975 and as a Tiger Reserve in 1999. This area is also contiguous with the tiger reserve under the same name in Madhya Pradesh on its eastern fringes and together forms a high potential tiger habitat in central India. The area is situated within the Tiger Conservation Unit-31 and has been identified as a level I priority area for tiger conservation (Wikramanayake *et al.* 1999). The State Forest Department has relocated illegal squatter fishermen from within the Park and has also initiated the relocation of villages within the tiger reserve to consolidate this tiger habitat. Several management initiatives such as total banning of fishing within the tiger reserve have helped reduce the anthropogenic pressures. The study site was located in the better-protected central part of the reserve.

Pench Tiger Reserve extends over 257 km² in Nagpur district of Maharashtra. It lies between 79° 04' E and 79° 24' E longitude,

and 21° 04' N and 21° 43' N latitude. The average annual rainfall is 1,400 mm (Karanth *et al.* 2004b). The terrain is undulating and hilly, dissected by the Pench river (which flows through the centre of the Park) and its tributaries. The highest point in the park is at 583m above m.s.l. The dominant vegetation type is tropical dry deciduous forest, dominated by teak *Tectona grandis*, with *Terminalia tomentosa*, *Lagerstroemia parviflora*, *Cleistanthus collinus*, *Lannea coromandelica*, *Anogeissus latifolia*, *Dalbergia paniculata*, *Pterocarpus marsupium*, *Adina cordifolia*, *Boswellia serrata* and *Diospyros melanoxylon* being some of the other common species. Large carnivores in the reserve are tiger, leopard, dhole, hyena and sloth bear, with jungle cat, the small Indian civet, the common palm civet, grey mongoose, jackal and ratel being some of the small carnivores of the area. The herbivores are sambar, chital, muntjac, chevrotain *Tragulus meminna*, gaur, chowsingha, nilgai, and wild pig. The larger arboreal mammals include common langur, rhesus macaque and Indian giant squirrel *Ratufa indica*. Over 164 species of birds have been recorded.

Photo: H. Dhanwatey



Pench Tiger Reserve

Methods and field techniques

Reconnaissance and mapping surveys

We first carried out extensive GPS (Global Positioning System) field surveys at each site in order to map and delineate the study area. Forest interior road/trail network, human settlements within the reserve, water tanks/reservoirs and other management-related features such as check-gates, anti-poaching camps and fire-watch towers/huts were mapped using GARMIN 12 XL GPS units. These overlays were used on a Geographical Information System (GIS) platform to finalize sampling designs for estimating tiger and prey abundance in the study areas.

Population estimates of tiger and large prey

An important component of managing tigers and their prey is to monitor their populations, in order to:

- i) Establish benchmark data that can serve as a basis for specific objectives for management and conservation efforts;
- ii) Evaluate success or failure of earlier management measures and conservation interventions, so as to react adaptively and solve problems (Walters 1986; Nichols *et al.* 1995); and
- iii) Improve our basic understanding of tiger and prey ecology through rigorous field studies, to develop a body of theoretical knowledge which, among other things, can generate predictive capacity to deal with new situations.

The monitoring of wildlife populations has recently seen several advances, both in theory (e.g. Williams *et al.* 2002) as well as practice. Karanth and Nichols (2002) have, based on their long-term studies of large carnivores and their prey, outlined methodological and field approaches to monitor tiger and prey populations in the tropical forests of south Asia, in terms of survey designs, field sampling protocols and rigorous analyses guidelines. They note that at different spatial scales, and with different objectives, monitoring can:

- a) Map the distribution of tigers and prey species on a regional and country-wide basis.
- b) Estimate the absolute densities of tigers (using capture-recapture sampling) and prey (using distance sampling) in high priority areas.
- c) Estimate population trends in order to understand whether populations are increasing or decreasing in selected reserves (using standardized indices of relative abundance such as encounter rates of tiger scats along roads).
- d) Estimate the rates of annual survival, recruitment and population change through long-term studies.

In line with objective b) above, we carried out field surveys to estimate absolute densities of tigers and their prey in the three high potential tiger habitats within the state

of Maharashtra. To estimate tiger densities, camera trap surveys were carried out, within a capture-recapture framework (Karanth and Nichols 1998; 2002). Prey densities were estimated using line transect surveys. All the field and analytical procedures prescribed by Karanth and Nichols (2002) were followed.

This project aimed at developing methodologies following objective c) above, to monitor tiger and prey population trends (over time, using standardized indices), to be applied at larger spatial scales than surveys to estimate absolute densities, with relatively low levels of resources. To monitor tiger population trends, carnivore sign (e.g. scats, scrapes) encounter rate along forest interior roads and trails were carried out, while for herbivores, dung/pellet count surveys in 50x2m plots were carried out. Survey design, field data collection and analytical protocols as prescribed by Karanth and Nichols (2002) were followed.

Photo: H. Dhanwatey



Tiger scrape marks on a tree

Carnivore diet profile

Carnivore scats collected during sign encounter surveys were analyzed using standard methods described by Karanth and Sunquist (1995, 2000) to understand the dietary patterns and food habits of tigers and their sympatric carnivores in each of the study sites. Scats were washed and the prey remains found in these scat specimens were used to identify the prey species by comparing with reference collections made during previous studies. Predator diets were reconstructed to make inferences on prey composition, and to estimate relative frequency of prey occurrence, prey biomass consumed and number of individual prey consumed by three large sympatric carnivores at the study sites, using the protocol described by Karanth and Sunquist (1995, 2000) and Sujai (2004). Prey selectivity patterns will be analyzed following Link and Karanth (1994).

Photo: H. Dhanwatey



Samba Kumar examining prey remains found in a tiger scat

Research activities and accomplishments

Tiger and prey population estimates

I. Tadoba - Andhari Tiger Reserve

We first completed a benchmark sample survey of tiger and prey abundance in Tadoba-Andhari Tiger Reserve in Maharashtra, Central India. After detailed reconnaissance surveys, we selected a study area of 367 km² for intensive sampling. 59 camera trap locations were sampled for a total of 706 trap nights during December 2001-February 2002. Subsequently, the field data were tabulated, camera trap films processed, photo-cataloguing of all camera trap pictures and individual identification of tigers 'captured' in the camera trap completed. We obtained 29 sets of tiger photo-captures which were used to build capture histories of each individual tiger for analysis under capture-recapture framework in Program CAPTURE. *Figure-2, p-22* depicts the survey design used for camera trapping in Tadoba-Andhari; *Table-1, p-23* provides the details of camera trap locations with geographical coordinates; *Table-2, p-24* provides the details of all photo-captures of tigers obtained during camera trap field surveys; and *Appendix-A, p-59* includes the photographs of individually identified tigers photo-captured during camera trap surveys in Tadoba-Andhari. Results of the camera trap surveys (Karanth *et al.* 2004b) are included in *Table-3, p-26*.

We continued camera trap surveys for the second successive year in Tadoba-Andhari using the same 60 trap locations that were established during December 2001. The field operations were carried out during December 2002-January 2003 and a total of 715 trap nights were spent to obtain the capture-recapture data. Tabulation of camera trap data, processing of film rolls, photo-cataloguing and identification of photo-captured tigers was also completed during July 2003. We obtained 44 sets of tiger photo-captures and analyses of these data are currently in progress.

In association with the Distance Sampling group at University of St. Andrews, we pioneered (in India) the new line transect sample survey designs using DISTANCE 4.0. The first prey density estimates, derived using a new survey design with square sampler geometry and automated survey design features, developed in consultation with Len Thomas and Samantha Strindberg, were first obtained in Tadoba-Andhari. The work included laying and marking of 36 square samplers in the study area within Tadoba-Andhari, with each transect covering a distance of 4 km. The schematic survey design is depicted in *Figure-3, p-27*

and the geographical coordinates of each transect sampler is included in *Table-4, p-28*. We conducted field surveys during March 2002. Data from a cumulative sampling effort of 1088 km were used to estimate prey densities at Tadoba-Andhari using Program DISTANCE 4.0 and the results are included in *Table-5, p-29*.

We conducted line transect surveys for the second consecutive year at Tadoba-Andhari

during March 2004. A total sampling effort of 816 km was walked to collect field data. The survey resulted in 485 sightings of prey animals, which included chital, sambar, nilgai, muntjac, chowsingha, gaur, wild pig and langur. *Table-6, p-29* provides the number of clusters sighted during transect walks. We are currently analyzing these data to derive estimates of absolute abundance of prey populations.

Figure 2. Tadoba-Andhari Tiger Reserve: Study area, with camera trap locations

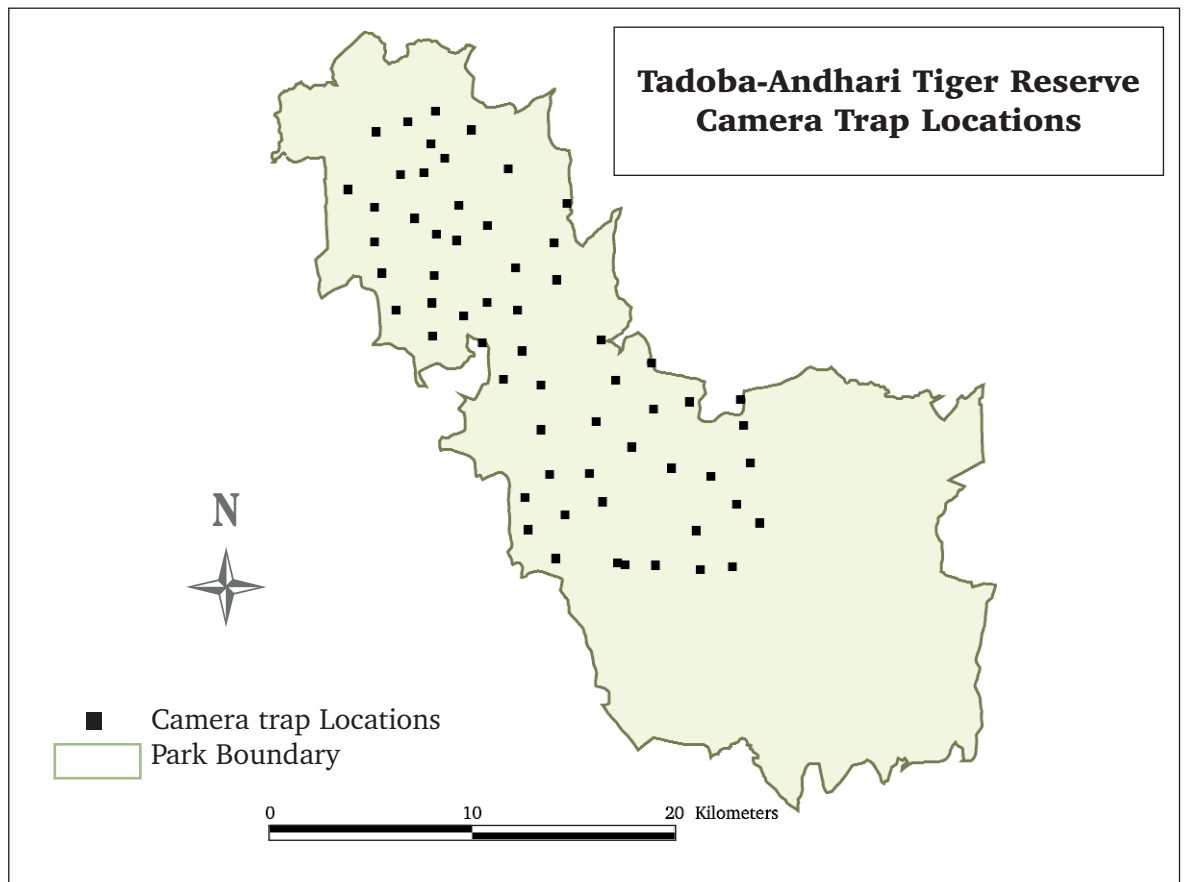


Table 1. Camera trap locations in Tadoba-Andhari Tiger Reserve

Location ID	Longitude	Latitude	Location ID	Longitude	Latitude	Location ID	Longitude	Latitude
ATR 2.3	79.29883	20.31265	TDMR 7.4	79.33176	20.27792	KPKR 7.7	79.40223	20.26259
MRR 1.4	79.29882	20.29797	TDMR 11.0	79.34878	20.25489	KPKR 9.6	79.41927	20.26547
KZR 4.5	79.28178	20.30995	WGDR 2.3	79.37118	20.23488	KRKR 0.8	79.44344	20.26601
KKAR 2.2	79.27558	20.32656	PPNR 0.8	79.35233	20.23467	KRKR 2.1	79.44459	20.25427
KKAR 4.0	79.27254	20.34045	ANDR 2.1	79.37705	20.22201	KRKR 4.4	79.44720	20.23766
TLKR 3.1	79.27292	20.35590	PPNR 2.9	79.35908	20.21649	TDMR 5.3	79.32220	20.29436
KPR 2.0	79.28566	20.37041	MBTR 0.0	79.35421	20.19726	KPKR 4.7	79.37494	20.25791
KBR 1.3	79.26066	20.36426	MBTR 3.2	79.38337	20.19463	JCR 4.9	79.36393	20.35550
UMR 3.2	79.27470	20.38964	MBTR 3.6	79.38686	20.19360	KDR 4.4	79.35811	20.32154
NMR 7.9	79.28972	20.39393	MBTR 5.2	79.40119	20.19308	JKR 7.3	79.34082	20.29024
AJR 1.3	79.30036	20.38370	RMTR 2.9	79.42077	20.20797	KPKR 0.8	79.34932	20.27474
AJR 3.3	79.30296	20.39831	RMTR 5.4	79.44021	20.21932	SPMR 3.6	79.37840	20.29424
BGR 3.5	79.31966	20.38934	RTBR 1.9	79.45089	20.21060	SPPR 2.8	79.38474	20.27596
BGR 1.4	79.30677	20.37700	MBTR 9.3	79.43744	20.19157	SPPR 5.0	79.40183	20.28345
NMR 5.2	79.29666	20.37092	MBTR 7.7	79.42233	20.19044	VBRR 1.0	79.30030	20.32484
JVR 1.9	79.31290	20.35594	TCR 0.0	79.34157	20.21033	VBRR 3.9	79.31371	20.30655
KLR 3.2	79.33665	20.37172	JMJR 0.5	79.34033	20.22469	JKR 2.8	79.33881	20.32745
JMR 3.2	79.32608	20.34647	KRKR 2.8	79.44804	20.24875	JCR 2.4	79.35739	20.33808
HTR 1.6	79.30190	20.34336	MBTR 2.0	79.37293	20.19829	SPRR 6.6	79.39151	20.24604
NMR 2.6	79.29175	20.35060	TLKR 3.0	79.27292	20.35590	JKR 5.1	79.33923	20.30851
JMR 1.3	79.31127	20.34029	SPRR 2.2	79.42841	20.23216	SPRR 4.5	79.41003	20.23619
KKR 2.7	79.32501	20.31228						

Road Acronyms

Road Acronyms	Road Names	Road Acronyms	Road Names
AJR	Aljhanja Road	KRKR	Karwa-Rantalodi-Kolsa Road
ANDR	Andhari Nala Road	KZR	Katezari Road
ATR	Ambethira Road	MBTR	Moharli-Botejhari Road
BGR	Bamangaon Road	MRR	Mangli Reeth Road
HTR	Hill Top Road	NMR	Navegaon Main Road
JCR	Jamni-Chauradev Road	PPNR	Pandarpani Road
JKR	Jamni-Khatoda Road	RMTR	Rantalodi-Moharli Road
JMJR	Jamunjhira Road	RTBR	Rantalodi-Botejhari Road
JMR	Jamni Main Road	SPMR	Singru-Palasmaon-Madnapur Road
JVR	Jamni Village Road	SPPR	Singru-Palasmaon-Piparda Road
KBR	Kala amba-Bhanushkindi Road	SPRR	Singru-Palasmaon-Rantalodi Road
KDR	Khatoda-Deori Road	TCR	Telia Circular Road
KKAR	Kosekanar Road	TDMR	Tadoba-Moharli Main Road
KKR	Katezari-Kala amba Road	TLKR	Tadoba Lake Kala amba Road
KLR	Kolara Road	UMR	Udharmatka Road
KPKR	Khatoda-Palasmaon-Karwa Road	VBRR	Vasantha Bhandara Road
KPR	Kala amba-Pandarpauni Road	WGDR	Waghdo Road

Table 2. Details of photo-captures of tigers in Tadoba-Andhari Tiger Reserve

Photo-Capture details of tigers: Tadoba-Andhari Tiger Reserve 2001-2003						
TIGER ID	LOCATION ID	PHOTO-CAPTURE DATE	PHOTO-CAPTURE TIME	EXPOSURE DETAILS		SEX
				LEFT FLANK ROLL AND FRAME NUMBER	RIGHT FLANK ROLL AND FRAME NUMBER	
TDT-101	JMR 3.2	25-Dec-01	21:22	TD-38/01-2	TD-37/01-1	FEMALE
TDT-101	NMR 5.2	27-Dec-01	19:36	NA	TD-15/01-2	FEMALE
TDT-101	JVR 1.9	01-Jan-02	04:15	TD-40/01-10	NA	FEMALE
TDT-101	AJR 3.3	02-Jan-02	23:18	TD-14/01-2	TD-13/01-1	FEMALE
TDT-101	UMR 3.2	03-Jan-02	00:29	TD-03/01-3	TD-04/01-2	FEMALE
TDT-101	NMR 5.2	03-Jan-02	21:36	TD-15/01-20	NA	FEMALE
TDT-101	JVR 1.9	20-Dec-02	21:31	NA	TD2/27/02-3	FEMALE
TDT-101	JVR 1.9	20-Dec-02	21:31	NA	TD2/28/02-3	FEMALE
TDT-101	AJR 1.3	21-Dec-02	22:39	TD2/38/02-6	TD2/37/02-6	FEMALE
TDT-101	NMR 2.6	26-Dec-02	06:18	TD2/21/02-29	NA	FEMALE
TDT-102	HTR 1.6	25-Dec-01	22:38	TD-20/01-2	TD-19/01-2	MALE
TDT-102	JMR 3.2	26-Dec-01	19:20	TD-38/01-3	TD-37/01-4	MALE
TDT-102	AJR 1.3	29-Dec-01	05:23	TD-02/01-1	TD-01/01-2	MALE
TDT-102	KZR 4.5	28-Dec-02	03:40	TD2/05/02-11	TD2/06/02-10	MALE
TDT-102	ATR 2.3	29-Dec-02	21:07	TD2/02/02-9	TD2/01/02-9	MALE
TDT-103	KKAR 2.2	26-Dec-01	18:03	TD-05/01-2	TD-06/01-2	FEMALE
TDT-103	KKAR 4.0	28-Dec-01	23:38	TD-27/01-3	TD-28/01-3	FEMALE
TDT-103	KZR 4.5	02-Jan-02	18:25	TD-08/01-13	TD-07/01-13	FEMALE
TDT-103	NMR 2.6	27-Dec-02	02:52	TD2/21/02-32	NA	FEMALE
TDT-103	ATR 2.3	30-Dec-02	20:19	TD2/02/02-10	TD2/01/02-10	FEMALE
TDT-104	BGR 3.5	27-Dec-01	05:30	TD-17/01-1	NA	FEMALE
TDT-105	ATR 2.3	28-Dec-01	04:59	TD-31/01-2	TD 32/01-3	FEMALE
TDT-105	MRR 1.4	03-Jan-02	21:39	NA	TD-30/01-4	FEMALE
TDT-105	JMR 1.3	11-Jan-02	19:26	TD-40/01-17	NA	FEMALE
TDT-105	JMR 1.3	16-Jan-02	19:34	NA	TD-40/01-28	FEMALE
TDT-105	HTR 1.6	28-Dec-02	02:58	TD2/23/02-3	TD2/24/02-3	FEMALE
TDT-105	JKR 2.8	07-Jan-03	01:53	TD2/31/02-9	TD2/32/02-9	FEMALE
TDT-106	JMR 3.2	29-Dec-01	04:53	NA	TD-38/01-8	MALE
TDT-106	KKAR 2.2	03-Jan-02	05:37	TD-06/01-3	TD-05/01-3	MALE
TDT-106	JKR 2.8	13-Jan-02	03:56	TD-10/01-24	TD-09/01-23	MALE
TDT-106	KKAR 4.0	23-Dec-02	18:21	TD2/10/02-2	TD2/9/02-2	MALE
TDT-106	KDR 4.4 - JKR 7.3	08-Jan-03	12:10	(AG) 4078-7	(AG) 4078-8	MALE
TDT-106	KKR 2.7 - JKR 5.1	11-Jan-03	09:21	(AG) 4078-20	(AG) 4078-18	MALE
TDT-107	KRKR 4.4	09-Jan-02	18:39	TD-51/01-3	NA	MALE
TDT-107	SPPR 2.8	15-Jan-02	18:52	TD-17/01-7	TD-41/01-9	MALE
TDT-107	SPRR 6.6	05-Jan-03	20:24	TD2/44/02-20	TD2/52/02-8	MALE
TDT-107	KPKR 4.7	05-Jan-03	21:15	TD2/10/02-19	TD2/09/02-23	MALE
TDT-107	SPPR 2.8	05-Jan-03	22:27	TD2/47/02-5	TD2/26/02-19	MALE
TDT-107	SPRR 2.2	07-Jan-03	01:05	TD2/36/02-28	TD2/53/02-1	MALE
TDT-107	SPPR 5.0	08-Jan-03	19:16	TD2/03/02-7	TD2/04/02-7	MALE

Table 2. contd...

Photo-Capture details of tigers: Tadoba-Andhari Tiger Reserve 2001-2003						
TIGER ID	LOCATION ID	PHOTO-CAPTURE DATE	PHOTO-CAPTURE TIME	EXPOSURE DETAILS		SEX
				LEFT FLANK ROLL & FRAME NUMBER	RIGHT FLANK ROLL & FRAME NUMBER	
TDT-108	JKR 7.3	12-Jan-02	6:14	TD-35/01-10	TD-36/01-10	FEMALE
TDT-108	KPKR 0.8	16-Jan-02	22:49	TD-52/01-10	TD-53/01-25	FEMALE
TDT-108	TDMR 7.4	19-Jan-03	00:17	TD2/64/02-21	TD2/63/02-24	FEMALE
TDT-109	MBTR 3.2	24-Jan-02	01:11	TD-70/01-1	TD-68/01-1	FEMALE
TDT-110	MBTR 3.2	24-Jan-02	21:59	TD-68/01-2	TD-70/01-2	FEMALE
TDT-110	MBTR 3.6	24-Jan-02	22:09	TD-41/01-10	TD-17/01-23	FEMALE
TDT-110	MBTR 5.2	29-Jan-02	18:53	TD-81/01-4	TD-80/01-3	FEMALE
TDT-111	AJR 3.3	21-Dec-02	01:14	TD2/36/02-2	TD2/35/02-1	MALE
TDT-111	AJR 1.3	21-Dec-02	02:59	TD2/38/02-5	TD2/37/02-5	MALE
TDT-112	JVR 1.9	22-Dec-02	18:44	TD2/27/02-6	TD2/28/02-6	UNKNOWN
TDT-113	JVR 1.9	22-Dec-02	18:44	TD2/27/02-6	TD2/28/02-6	UNKNOWN
TDT-114	JVR 1.9	22-Dec-02	18:44	TD2/27/02-6	TD2/28/02-6	UNKNOWN
TDT-115	TLKR 3.0	30-Dec-02	23:17	TD2/12/02-3	TD2/11/02-3	MALE
TDT-116	SPRR 4.5	01-Jan-03	18:44	TD2/24/02-5	TD2/23/02-5	FEMALE
TDT-116	SPRR 2.2	11-Jan-03	20:55	TD2/53/02-9	TD2/54/02-4	FEMALE
TDT-117	KPKR 4.7	05-Jan-03	03:16	TD2/09/02-21	TD2/10/02-17	FEMALE
TDT-117	SPRR 6.6	05-Jan-03	04:37	TD2/52/02-5	TD2/44/02-17	FEMALE
TDT-117	KPKR 4.7	09-Jan-03	23:10	TD2/10/02-24	TD2/09/02-33	FEMALE
TDT-118	SPRR 6.6	05-Jan-03	04:38	TD2/52/02-6	TD2/44/02-18	FEMALE
TDT-118	SPRR 6.6	05-Jan-03	04:39	TD2/52/02-7	TD2/44/02-19	FEMALE
TDT-118	SPRR 6.6	09-Jan-03	04:39	TD2/44/02-21	TD2/52/02-9	FEMALE
TDT-118	MBTR 2.0	15-Jan-03	18:07	TD2/51/02-5	TD2/43/02-12	FEMALE
TDT-118	MBTR 0.0	15-Jan-03	18:51	TD2/27/02-32	TD2/46/02-28	FEMALE
TDT-118	TCR 0.0	17-Jan-03	05:00	TD2/50/02-12	TD2/49/02-12	FEMALE
TDT-118	TCR 0.0	20-Jan-03	00:30	TD2/49/02-15	TD2/50/02-15	FEMALE
TDT-118	JMJR 0.5	24-Jan-03	21:08	TD2/18/02-26	TD2/17/02-24	FEMALE
TDT-119	SPRR 2.2	06-Jan-03	23:17	NA	TD2/53/02-F	FEMALE
TDT-119	KPKR 9.6	09-Jan-03	01:11	TD2/05/02-28	TD2/06/02-25	FEMALE
TDT-119	SPPR 5.0	10-Jan-03	22:25	TD2/04/02-8	TD2/03/02-8	FEMALE
TDT-120	SPMR 3.6	08-Jan-03	21:14	TD2/01/02-14	TD2/02/02-13	MALE
TDT-121	MBTR 5.2	17-Jan-03	19:19	TD2/01/02-18	TD2/03/02-12	MALE
TDT-121	MBTR 3.6	17-Jan-03	19:55	TD2/04/02-15	TD2/02/02-20	MALE



A tigress at Tadoba-Andhari Tiger Reserve

Table 3. Results of the camera trap surveys in Tadoba-Andhari Tiger Reserve

December 2001-February 2002	
Total number of camera trap locations	59
Sampling effort	706 trap nights
Number of sampling occasions	12
Camera trap polygon area	205 km ²
Estimated sampled area including buffer	367 km ²
Number of individually identified tigers	10
Capture-recapture model used to estimate population size	M_h
Estimated animal density for tigers in the sampled area	3.3 tigers/100 km ²

Figure 3. Tadoba-Andhari Tiger Reserve: Study area, with line transect samplers

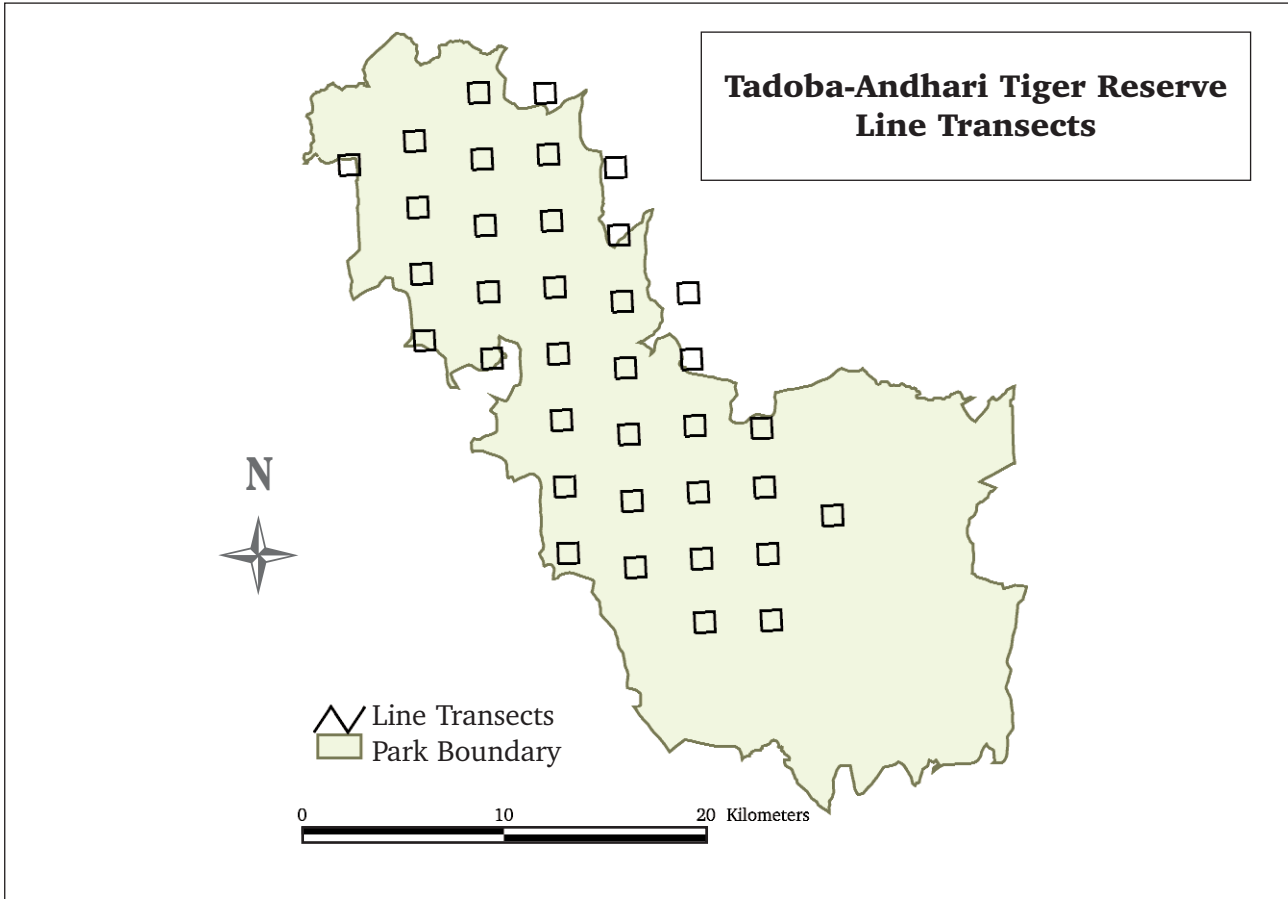


Photo: H. Dhanwatey



Survey volunteers collecting a carnivore scat

Table 4. Line transect sampler locations (longitude and latitude of bottom left (BL), bottom right (BR), top right (TR) and top left (TL) corners) and realized lengths (RL) in Tadoba-Andhari Tiger Reserve

Tr. No.	BL		BR		TR		TL		Length (km)
	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	
1	79.4662	20.2097	79.4758	20.2099	79.4756	20.2184	79.4660	21.2187	4.0
2	79.4359	20.1637	79.4455	20.1639	79.4453	20.1729	79.4357	20.1727	4.0
3	79.4351	20.1934	79.4447	20.1935	79.4446	20.2025	79.4350	20.2024	4.0
4	79.4344	20.2231	79.4440	20.2232	79.4438	20.2322	79.4342	20.2320	3.7
5	79.4337	20.2494	79.4433	20.2496	79.4432	20.2585	79.4336	20.2584	4.0
6	79.4008	20.3106	79.4103	20.3108	79.4102	20.3198	79.4006	20.3196	4.0
7	79.4015	20.2810	79.4111	20.2812	79.4109	20.2901	79.4013	20.2900	4.1
8	79.4022	20.2513	79.4118	20.2515	79.4117	20.2605	79.4021	20.2603	4.0
9	79.4030	20.2217	79.4126	20.2218	79.4124	20.2308	79.4028	20.2307	4.1
10	79.4037	20.1920	79.4133	20.1922	79.4131	20.2011	79.4036	20.2010	4.0
11	79.4044	20.1637	79.4140	20.1638	79.4138	20.1728	79.4043	20.1727	4.0
12	79.3724	20.1889	79.3819	20.1891	79.3818	20.1981	79.3722	20.1979	4.0
13	79.3716	20.2186	79.3812	20.2187	79.3810	20.2277	79.3715	20.2276	4.0
14	79.3709	20.2482	79.3805	20.2484	79.3803	20.2574	79.3707	20.2572	4.0
15	79.3701	20.2779	79.3797	20.2781	79.3795	20.2870	79.3700	20.2869	4.0
16	79.3694	20.3076	79.3790	20.3077	79.3788	20.3167	79.3692	20.3165	4.0
17	79.3687	20.3372	79.3782	20.3374	79.3781	20.3464	79.3685	20.3462	4.0
18	79.3680	20.3674	79.3775	20.3675	79.3774	20.3765	79.3678	20.3764	3.2
19	79.3407	20.1963	79.3503	20.1962	79.3501	20.2052	79.3406	20.2050	3.3
20	79.3400	20.2257	79.3496	20.2259	79.3494	20.2348	79.3398	20.2347	4.0
21	79.3392	20.2554	79.3488	20.2555	79.3487	20.2645	79.3391	20.2644	4.0
22	79.3385	20.2850	79.3481	20.2852	79.3479	20.2942	79.3383	20.2940	4.0
23	79.3378	20.3147	79.3473	20.3148	79.3472	20.3238	79.3376	20.3237	4.0
24	79.3370	20.3443	79.3466	20.3445	79.3464	20.3535	79.3369	20.3533	4.0
25	79.3363	20.3740	79.3459	20.3741	79.3457	20.3831	79.3361	20.3830	4.0
26	79.3356	20.4013	79.3452	20.4014	79.3450	20.4104	79.3354	20.4103	1.7
27	79.3041	20.4023	79.3137	20.4024	79.3135	20.4114	79.3040	20.4113	4.0
28	79.3049	20.3726	79.3145	20.3728	79.3143	20.3818	79.3047	20.3816	4.0
29	79.3056	20.3430	79.3152	20.3431	79.3150	20.3521	79.3054	20.3520	4.0
30	79.3064	20.3133	79.3159	20.3135	79.3158	20.3225	79.3062	20.3223	4.0
31	79.3071	20.2837	79.3167	20.2838	79.3165	20.2928	79.3069	20.2927	2.5
32	79.2732	20.3815	79.2828	20.3816	79.2826	20.3906	79.2730	20.3905	4.0
33	79.2739	20.3518	79.2835	20.3520	79.2834	20.3610	79.2738	20.3608	4.0
34	79.2747	20.3222	79.2843	20.3223	79.2841	20.3313	79.2745	20.3312	4.0
35	79.2754	20.2925	79.2850	20.2927	79.2848	20.3017	79.2753	20.3015	3.1
36	79.2420	20.3715	79.2516	20.3717	79.2514	20.3807	79.2418	20.3805	2.5

Table 5. Results of the line transect surveys in Tadoba-Andhari Tiger Reserve

Total numbers and length of permanent transects	36 lines, 136.2 km	
Sampler geometry	Square sampler	
Year	March 2002	
Total effort (length walked)	1088 km	
Species	n	Animal density (per km ²)
Chital	110	3.2
Sambar	160	3.3
Muntjac	56	0.9
Chowsingha	39	0.5
Gaur	62	1.8
Nilgai	48	0.7
Wild Pig	63	2.6

Photo: H. Dhanwatey

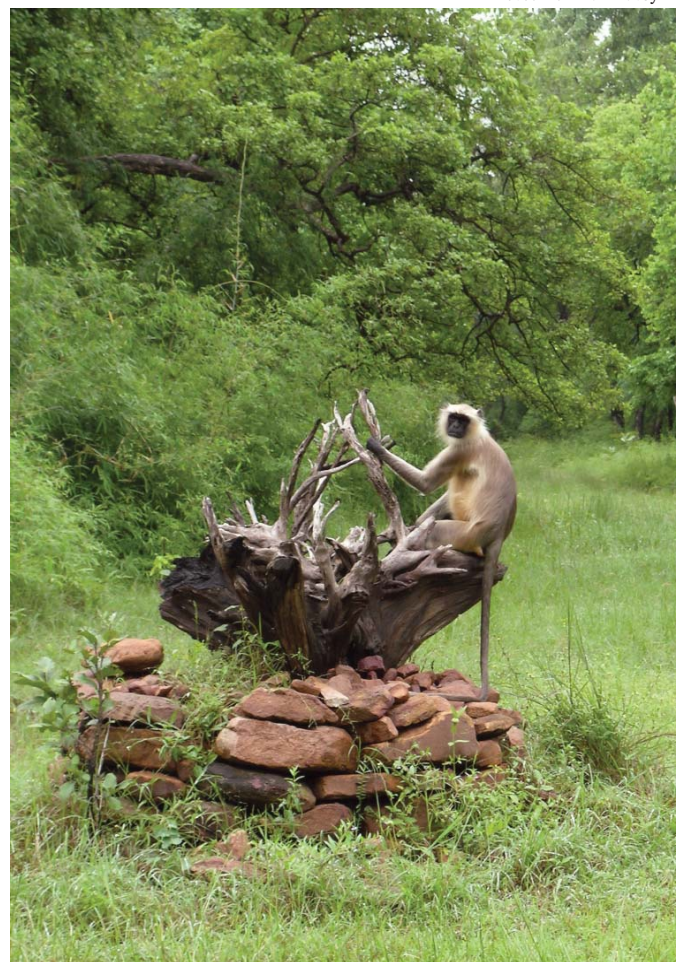


Gaur

Table 6. Number of detections during second year line transect surveys in Tadoba-Andhari Tiger Reserve

Tadoba-Andhari: 2004	
Species	Number of detections
Sambar	97
Chital	80
Muntjac	22
Gaur	45
Chowsingha	31
Chinkara	2
Nilgai	26
Wild Pig	37
Langur	126

Photo: H. Dhanwatey



Common Langur

I I . M e l g h a t T i g e r R e s e r v e

We completed a benchmark camera trap survey of tiger abundance at Melghat Tiger Reserve in Maharashtra during March-June 2002. 60 trap locations were selected after detailed field reconnaissance surveys and were sampled for a total of 896 trap nights to obtain capture-recapture estimates. The survey design used for camera trapping in Melghat is included in *Figure-4, p-31* and the details of camera trap locations with geographical coordinates are provided in *Table-7, p-32*. Field surveys were carried out in Melghat during March - June 2002. Subsequently, we tabulated the field data, processed camera trap films, photo-catalogued all camera trap pictures and individually identified tigers 'captured' in the camera trap. 27 sets of tiger photo-captures were obtained and were used to build capture histories of each individual tiger for analysis under capture-recapture framework, using Program CAPTURE. *Table-8, p-33* provides the details of all photo-captures of tigers obtained during camera trap field surveys and the photographs of individually identified tigers photo-captured during camera trap surveys in Melghat, are included in *Appendix-B, p-62*. The results of the camera trap surveys (Karanth *et al.* 2004b) are included in *Table-9, p-34*.

Using the new automated survey design feature in DISTANCE 4.0, we first estimated

prey densities at Melghat Tiger Reserve in Maharashtra in 2003. The sampling design (see *Figure-5, p-34*) consisted of 25 spatial replicates of square sampler geometry (see *Table-10, p-35* for the geographical coordinates of each transect sampler). The marking and laying of line transects in this rugged terrain took nearly five months and the field data was collected during April-May 2003. We spent total of 771 km of sampling effort to derive prey densities, which were estimated using Program DISTANCE 4.0 and the prey species that were sampled included chital, sambar, nilgai, muntjac, chowsingha, gaur, wild pig, langur and rhesus macaques. The results are included in *Table-11, p-35*.

Prior to the second and third year transect surveys, the field research team completed preparatory activities, including re-marking and re-laying of the 25 transect lines, and making those access roads/trails (to transect lines) which were completely washed off during the monsoon. Line transect surveys for the second and third consecutive year were conducted during May-June 2004 and February-March 2005. A total of 680 km was walked during these surveys and *Table-12, p-36* provides the number of clusters sighted during these transect-walks. The data from the 2004 and 2005 surveys are currently being analyzed.

Figure 4. Melghat Tiger Reserve: Study area, with camera trap locations

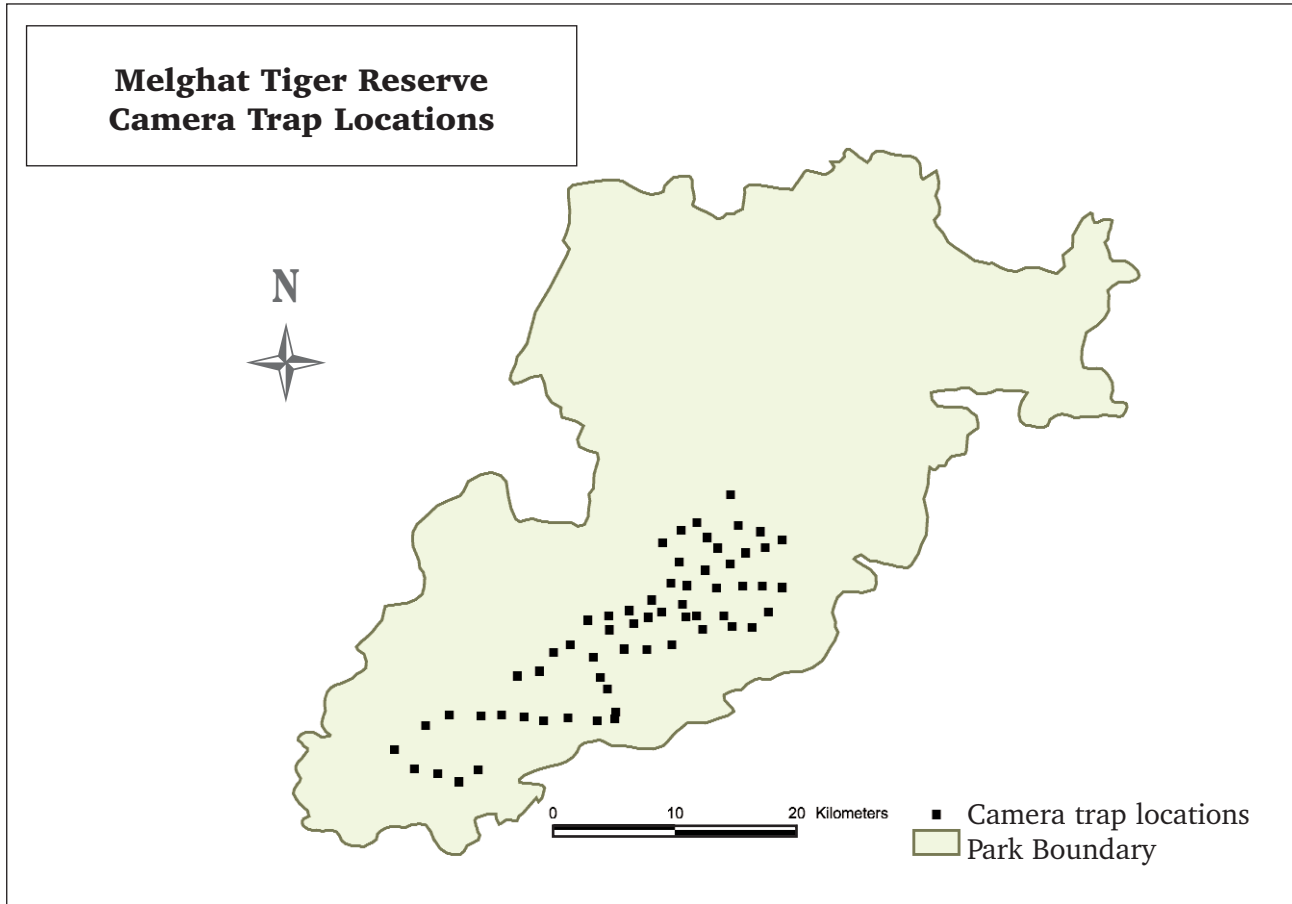
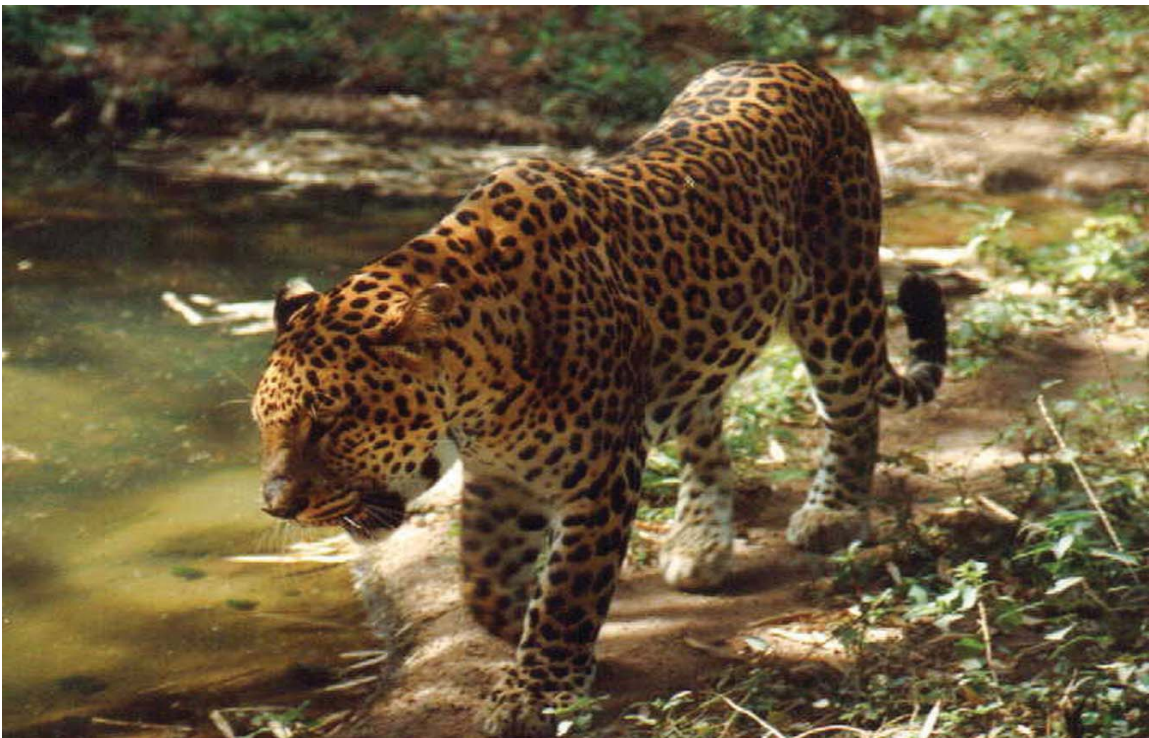


Photo: H. Dhanwatey



Leopard

Table 7. Camera trap locations in Melghat Tiger Reserve

Location ID	Longitude	Latitude	Location ID	Longitude	Latitude	Location ID	Longitude	Latitude
JPTR 1.0	77.22205	21.49514	KAR 8.2	77.13731	21.33430	KBR 11.6	76.97388	21.30704
JPKR 9.2	77.22776	21.47215	KADR 1.3	77.17802	21.42981	BPR 4.1	76.98875	21.29280
JAMR 11.1	77.24413	21.46762	KVR 4.1	77.18657	21.41391	BPR 6.4	77.00585	21.28930
JAM 13.0	77.24768	21.45588	MAR 1.8	77.19704	21.40558	PCR 0.1	77.02149	21.28314
BAKR 2.5	77.26026	21.46171	MAR 4.2	77.21713	21.40570	PCR 2.7	77.03576	21.29181
KPKR 3.7	77.23315	21.45216	KKLR 1.2	77.16115	21.40446	KBR 1.8	77.03797	21.33183
KPKR 8.1	77.22187	21.44370	KKLR 3.1	77.15064	21.39987	KKR 0.0	77.13657	21.32973
KPKR 10.6	77.20337	21.43940	KKLR 4.8	77.13247	21.39533	KKR 3.0	77.12365	21.32816
SKR 0.0	77.18983	21.42799	BAR 2.7	77.14353	21.38106	KKR 8.5	77.10195	21.33016
SKR 3.2	77.21161	21.42631	BAR 4.7	77.16022	21.38061	KKR 11.0	77.08396	21.32794
SKR 6.2	77.23116	21.42777	BAR 7.8	77.17877	21.38424	KKR 13.1	77.06957	21.33113
SKR 8.1	77.24555	21.42779	KAR 2.1	77.12072	21.37502	KKR 15.0	77.05313	21.33240
SKR 9.8	77.26022	21.42652	KSAJ 2.4	77.11674	21.40243	KAR 4.5	77.12587	21.35990
KAMR 2.6	77.24996	21.40851	SSR 4.1	77.13210	21.40569	RVR 9.4	77.23789	21.39698
KKUR 10.7	77.18423	21.44537	SSR 6.0	77.14734	21.40939	KBR 4.7	77.01437	21.33231
KKUR 6.7	77.17195	21.45930	SSR 8.0	77.16390	21.41719	KBR 6.9	76.99686	21.32469
DDR 1.9	77.18557	21.46858	KSRJ 11.4	77.17127	21.40838	KGR 4.1	77.09128	21.37840
JTAR 8.5	77.21251	21.45554	RVR 1.2	77.18919	21.40497	KGR 7.1	77.08099	21.36465
JTAR 5.0	77.20485	21.46349	RVR 4.3	77.20147	21.39563	KGR 9.5	77.06466	21.36106
JTAR 2.9	77.19719	21.47439	RVR 6.7	77.22333	21.39777	RVR 9.4	77.23789	21.39698
KGR 1.4	77.10370	21.38423						

Road Acronyms

Road Acronyms	Road Names	Road Acronyms	Road Names
BAKR	Bandarkahu Road	KGR	Koha-Gugamal Road
BAR	Bana Aam Road	KKLR	Kund-Koha Link Road
BPR	Bori-Pirkheda Road	KKR	Koha-Koktoo Road
DDR	Dhawda Da Road	KKUR	Keli-Kund Road
JAM	Jhunjhuru Aam	KPKR	Kilaphaata-Kund Road
JAMR	Jhunjhuru Aam Rai Road	KSAJ	Koha-Sipnakhanda-Adao Intersection
JPKR	Jaadaphaata-Kilaphaata Road	KSRJ	Koha-Seluphata-Rangrao Intersection
JPTR	Jaadaphaata Road	KVR	Kund-Vairat Road
JTAR	Jhandaballa-Teen Aam Road	MAR	Masan Aam Road
KADR	Kund-Adao Road	PCR	Pirkheda-Chiladhari Road
KAMR	Kolam Aam Road	RVR	Rangrao-Padao-Vairat Road
KAR	Koha-Akot Main Road	SKR	Sakri Nalla Road
KBR	Koktoo-Bori Road	SSR	Seluphaata-Sipnakhanda Road

Table 8. Details of photo-captures of tigers in Melghat Tiger Reserve

Photo-Capture details of tigers: Melghat Tiger Reserve 2002						
TIGER ID	LOCATION ID	PHOTO-CAPTURE DATE	PHOTO-CAPTURE TIME	EXPOSURE DETAILS		SEX
				LEFT FLANK ROLL AND FRAME NUMBER	RIGHT FLANK ROLL AND FRAME NUMBER	
MGT-101	SKR 6.2	22-Apr-02	19:10	MG-21/02-2	MG-22/01-6	MALE
MGT-101	KADR 1.3	25-May-02	23:37	MG-38/02-31	MG-71/02-16	MALE
MGT-102	SKR 0.0	24-Apr-02	22:47	MG-13/02-14	MG-14/02-23	MALE
MGT-102	SKR 3.2	25-Apr-02	23:25	MG-23/02-2	MG-24/02-2	MALE
MGT-102	SKR 3.2	27-Apr-02	21:38	NA	MG-23/02-6	MALE
MGT-103	JPTR 1.0	28-Apr-02	00:34	MG-43/02-18A	MG-42/02-10	MALE
MGT-104	DDR 1.9	29-Apr-02	03:24	MG-27/02-1	MG-28/02-2	FEMALE
MGT-104	BAR 4.7	28-May-02	02:56	MG-10/02-23	MG-09/02-24	FEMALE
MGT-104	BAR 7.8	28-May-02	01:08	MG-65/02-22	MG-64/02-22	FEMALE
MGT-105	SKR 6.2	29-Apr-02	19:25	MG-22/02-14	MG-21/02-10	FEMALE
MGT-105	SKR 8.1	01-May-02	19:08	MG-18/02-5	MG-17/02-5	FEMALE
MGT-106	SKR 8.1	03-May-02	00:41	MG-18/02-6	MG-17/02-6	FEMALE
MGT-106	SKR 9.8	03-May-02	00:03	MG-34/02-10	MG-33/02-10	FEMALE
MGT-106	SKR 9.8	03-May-02	02:38	MG-33/02-11	MG-34/02-11	FEMALE
MGT-107	KGR 7.1	08-May-02	05:12	MG-42/02-16	MG-43/02-24A	UNKNOWN
MGT-108	BPR 6.4	12-May-02	19:18	MG-62/02-2	MG-63/02-3	FEMALE
MGT-108	BPR 6.4	13-May-02	02:35	MG-63/02-4	MG-62/02-3	FEMALE
MGT-108	PCR 0.1	13-May-02	03:31	MG-17/02-35	MG-18/02-22	FEMALE
MGT-109	PCR 0.1	13-May-02	03:31	MG-17/02-36	MG-18/02-23	FEMALE
MGT-109	PCR 0.1	13-May-02	03:31	MG-17/02-R	MG-18/02-24	FEMALE
MGT-110	PCR 0.1	13-May-02	03:31	MG-17/02-R	MG-18/02-24	FEMALE
MGT-111	PCR 0.1	13-May-02	22:22	MG-18/02-25	MG-49/02-1	MALE
MGT-112	KBR 4.7	18-May-02	21:48	MG-28/02-32	NA	MALE
MGT-113	KKR 15.0	19-May-02	03:23	MG-15/02-14	MG-16/02-14	MALE
MGT-114	KKR 15.0	19-May-02	03:24	MG-15/02-15	MG-16/02-15	MALE
MGT-115	MAR 1.8	26-May-02	20:29	MG-01/02-15	MG-02/02-15	MALE
MGT-115	RVR 6.7	30-May-02	23:12	MG-27/02-33	MG-69/02-8	MALE

Table 9. Results of the camera trap surveys in Melghat Tiger Reserve

March-June 2002	
Total number of camera trap locations	60
Sampling effort	896 trap nights
Number of sampling occasions	15
Camera trap polygon area	203 km ²
Estimated sampled area including buffer	360 km ²
Number of individually identified tigers	15
Capture-recapture model used to estimate population size	M _h
Estimated animal density for tigers in the sampled area	6.7 tigers/100 km ²

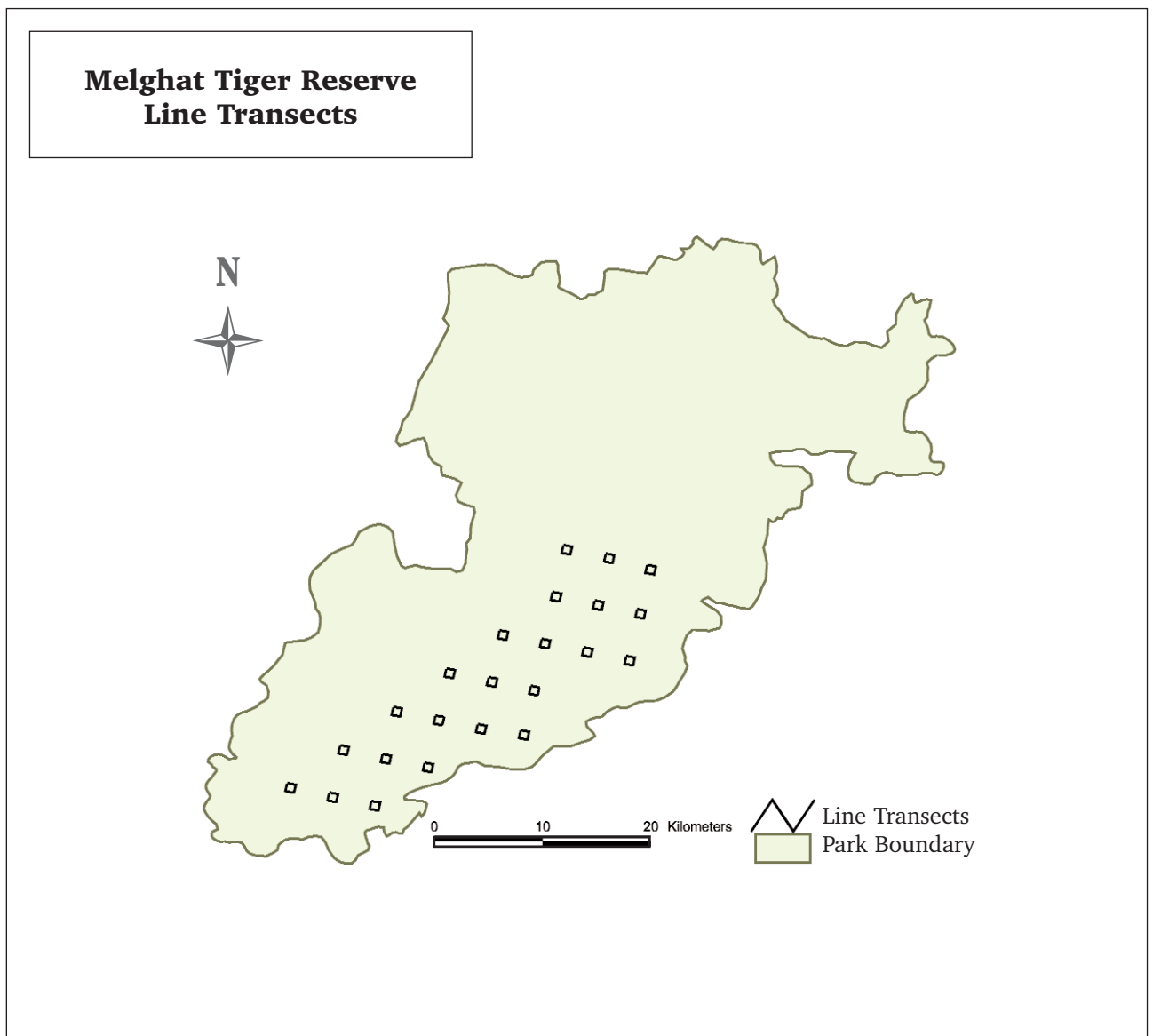
Figure 5. Melghat Tiger Reserve: Study area, with line transect samplers

Table 10. Line transect sampler locations (longitude and latitude of bottom left (BL), bottom right (BR), top right (TR) and top left (TL) corners) and realized lengths (RL) in Melghat Tiger Reserve

Tr. No.	BL		BR		TR		TL		RL
	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	
1	76.9808	21.3228	76.9900	21.3199	76.9932	21.3284	76.9840	21.3314	4.1
2	76.9689	21.2911	76.9781	21.2881	76.9813	21.2967	76.9721	21.2996	4.0
3	76.0266	21.3435	77.0358	21.3405	77.0390	21.3491	77.0298	21.3520	4.0
4	77.0147	21.3117	77.0239	21.3088	77.0271	21.3173	77.0179	21.3202	4.0
5	77.0029	21.2799	77.0120	21.2770	77.0152	21.2855	77.0060	21.2885	4.0
6	77.0724	21.3641	77.0816	21.3612	77.0848	21.3697	77.0756	21.3727	3.3
7	77.0605	21.3323	77.0697	21.3294	77.0729	21.3379	77.0637	21.3409	4.1
8	77.0486	21.3006	77.0578	21.2976	77.0610	21.3062	77.0518	21.3091	3.7
9	77.1295	21.4148	77.1386	21.4118	77.1418	21.4204	77.1326	21.4233	4.0
10	77.1182	21.3847	77.1274	21.3818	77.1306	21.3903	77.1214	21.3933	4.0
11	77.1063	21.3530	77.1155	21.3500	77.1187	21.3586	77.1095	21.3615	4.0
12	77.0944	21.3212	77.1036	21.3183	77.1068	21.3268	77.0976	21.3298	4.0
13	77.1878	21.4689	77.1970	21.4659	77.2001	21.4745	77.1909	21.4774	4.0
14	77.1759	21.4371	77.1851	21.4342	77.1882	21.4427	77.1790	21.4457	4.0
15	77.1640	21.4054	77.1732	21.4024	77.1764	21.4110	77.1672	21.4139	3.9
16	77.1521	21.3736	77.1613	21.3707	77.1645	21.3792	77.1553	21.3822	4.0
17	77.1402	21.3418	77.1494	21.3389	77.1526	21.3474	77.1434	21.3504	3.5
18	77.1292	21.3123	77.1384	21.3093	77.1415	21.3179	77.1323	21.3208	3.9
19	77.2336	21.4895	77.2428	21.4865	77.2459	21.4951	77.2367	21.4980	4.0
20	77.2217	21.4577	77.2309	21.4548	77.2340	21.4633	77.2248	21.4663	4.0
21	77.2098	21.4260	77.2190	21.4230	77.2221	21.4316	77.2130	21.4345	4.0
22	77.1979	21.3942	77.2071	21.3913	77.2103	21.3998	77.2011	21.4028	3.3
23	77.2556	21.4466	77.2648	21.4437	77.2679	21.4522	77.2588	21.4552	3.5
24	77.2437	21.4149	77.2529	21.4119	77.2561	21.4205	77.2469	21.4234	4.0
25	77.2318	21.3831	77.2410	21.3802	77.2442	21.3887	77.2350	21.3917	4.0

Table 11. Results of the line transect surveys in Melghat Tiger Reserve

Total numbers and length of permanent transects	25 lines, 97.2 km	
Sampler geometry	Square sampler	
Year	April-May 2003	
Total effort (length walked)	771.2 km	
Species	n	Animal density (per km ²)
Sambar	138	2.7
Muntjac	47	0.6
Chowsingha	46	0.5
Gaur	61	1.0



Wild Pig

Table 12: Numbers of detections during second and third year line transect surveys in Melghat Tiger Reserve

Species	2004	2005
Sambar	74	63
Chital	1	1
Muntjac	40	20
Gaur	63	32
Chowsingha	16	12
Nilgai	5	3
Wild Pig	17	6
Langur	338	286
Rhesus macaque	13	10



Photos: J. Kulkarni



Training session underway at Melghat Tiger Reserve

III. Pench Tiger Reserve

We completed a benchmark camera trap sample survey of tiger abundance in Pench Tiger Reserve in Maharashtra, Central India during November-December 2002. After detailed reconnaissance surveys in October 2002, a study area of about 280 km² was selected for intensive sampling (see *Figure-6, p-38* for the schematic survey design). 60 camera trap locations were sampled for a total of 715 trap nights. The details of camera trap locations with geographical coordinates are provided in *Table-13, p-39*. Tabulation of camera trap data, processing of film rolls, photo-cataloguing and identification of photo-captured tigers was completed during June 2003. 31 sets of tiger photo-captures were obtained to build capture histories of each individual tiger for analysis under capture-recapture framework. *Table-14, p-40* provides the details of all photo-captures of tigers obtained and *Appendix-C, p-64* includes the photographs of individually identified tigers photo-captured during camera trap field surveys in Pench. These data were also analyzed using Program CAPTURE and the results (Karanth *et al.* 2004b) are presented in *Table-15, p-41*.

In Pench, a survey design with 30 square samplers (*Figure-7, p-41*) was implemented to estimate prey densities. The geographical coordinates of each transect sampler is provided in *Table-16, p-42*. The preparatory work included laying and marking of 30 transect lines and field data collection was

carried out during December 2002 - March 2003. The line transect survey included eight temporal replicates, together accounting for a cumulative sampling effort of 894 km. The data were analyzed using Program DISTANCE, and the density estimates of prey species are reported in *Table-17, p-42*.

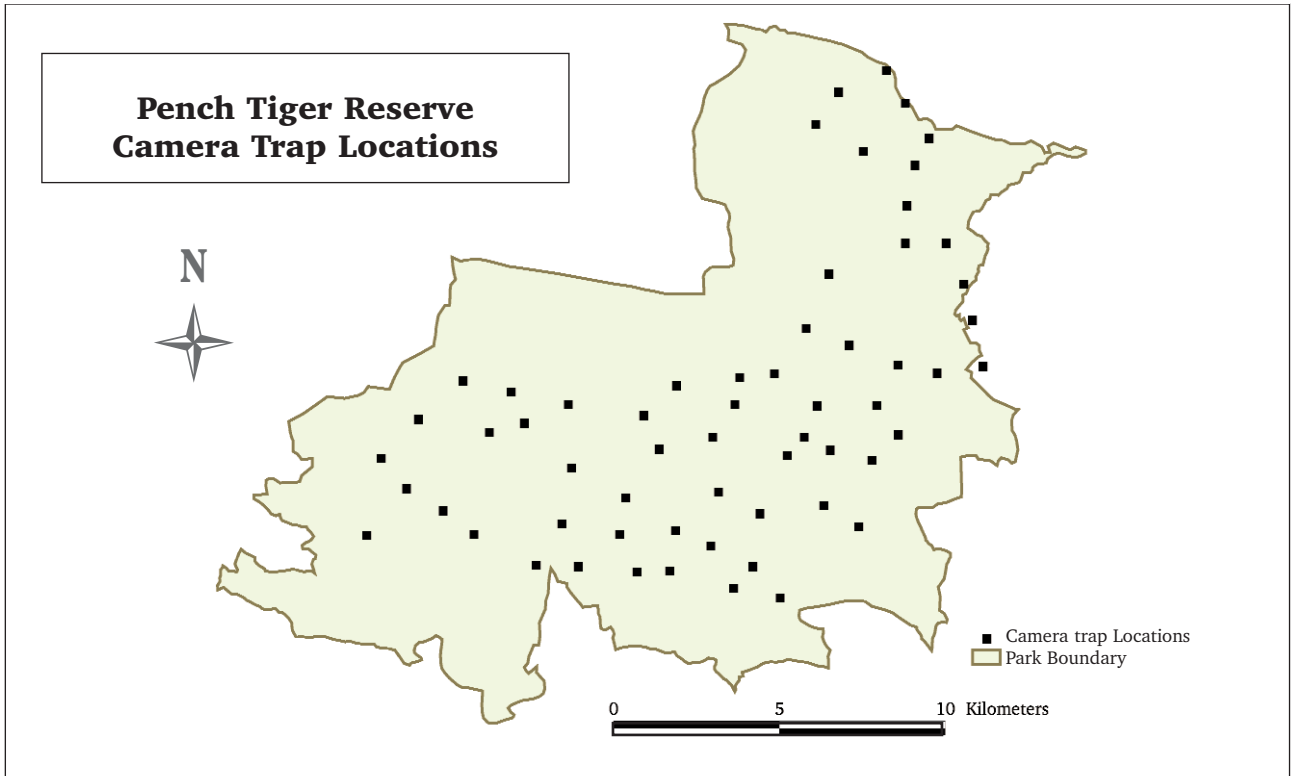
Although preparatory work (re-marking and re-laying of thirty transect lines) for carrying out line transect surveys for the second consecutive year was completed, line transect surveys could not be carried out due to logistical problems.

Photo: H. Dhanwatey



chital

Figure 6. Pench Tiger Reserve: Study area, with camera trap locations



Leopard, Dhole, Wild Pig and Four-horned Antelope photographed by the camera trap

Table 13. Camera trap locations in Pench Tiger Reserve

Location ID	Longitude	Latitude	Location ID	Longitude	Latitude
DPR 1.2	79.2785	21.6088	GLR 4.1	79.1665	21.6233
NPR 1.0	79.2724	21.6169	GLR 6.0	79.183	21.6195
SBR 3.4	79.279	21.6277	GLR 8.7	79.2048	21.6159
SBR 1.7	79.265	21.6335	GLR 10.5	79.2145	21.6238
SBR 4.8	79.2903	21.6252	DGR 1.6	79.209	21.6066
BBR 1.5	79.3037	21.6267	GGR 6.5	79.1701	21.6147
BBR 2.9	79.3009	21.6393	GGR 5.3	79.1598	21.6125
BBR 4.7	79.2987	21.6493	GGR 9.2	79.1834	21.6022
BBR 6.5	79.2939	21.6604	JLR 2.5	79.1802	21.5871
SDR 6.8	79.2829	21.6709	GGR 11.4	79.199	21.5937
GBR 1.4	79.2855	21.6818	GGR 13.2	79.1968	21.5837
SCR 2.4	79.2898	21.689	GGR 15.2	79.1846	21.5753
SDR 9.5	79.2706	21.686	GGR 18.8	79.1724	21.576
SPR 1.3	79.2571	21.6936	CHR 2.8	79.1546	21.5848
SPR 2.7	79.2639	21.7022	CHR 1.4	79.1458	21.5915
SPR 4.5	79.2779	21.7077	GNR 8.1	79.1353	21.5977
PBR 1.3	79.2832	21.6988	GNR 10.5	79.1235	21.5854
SDR 5.0	79.2821	21.6607	GNR 6.1	79.1283	21.6062
SDR 2.0	79.2596	21.653	GNR 4.0	79.1393	21.6165
SBR 0.2	79.2526	21.6383	PAR 0.9	79.2377	21.5883
RHR 0.8	79.2259	21.5945	RHR 5.0	79.2563	21.5902
GPR 3.5	79.2131	21.5845	SPR 1.4	79.2663	21.5842
GPR 4.7	79.2232	21.58	HBR 2.1	79.2461	21.6041
GPR 6.3	79.2353	21.574	BKR 3.5	79.233	21.6255
HBR 4.9	79.2247	21.6094	SKR 5.2	79.243	21.5654
HDR 4.6	79.2313	21.6183	SNR 3.3	79.2295	21.5683
HDR 1.8	79.2512	21.6089	GKR 3.9	79.2016	21.5734
HDR 0.8	79.2586	21.6051	GKR 2.3	79.2111	21.5736
HPR 0.3	79.2706	21.602	GLR 2.4	79.1526	21.6266
BKR 0.4	79.2551	21.6173	BKR 2.2	79.243	21.6262

Road Acronyms

Road Acronyms	Road Names	Road Acronyms	Road Names
BBR	Bakhari-Bhimsen Road	HPR	Hathigotta-Pheprikund Road
BKR	Bodhal Khapra Road	JLR	Jhilmili Road
CHR	Chippaad Road	NPR	Nelliparcha Road
DGR	Dhaatejhira-Ghuggusgadh Road	PAR	Powerjodi-Anicut Road
DPR	Dondapani Road	PBR	Pivarthadi Boundary Road
GBR	Garadiban Road	RHR	Ranidoh-Hathigotta Road
GGR	Ghatpindri-Gawlighat Road	SBR	Salama-Bakhari Road
GKR	Gawlighat-Kirangi Charra Road	SCR	Saddle dam-Chikhalkhari Road
GLR	Ghatpindri-Lamandoh Road	SDR	Saddle dam Road
GNR	Ghatpindri-Narhar Road	SKR	Sillari-Kirangi Charra Road
GPR	Gawlighat-Phuljhari Road	SNR	Saiban Road
HBR	Hathigotta-Bogda Road	SPR	Saddle dam-Pivarthadi Road
HDR	Hathigotta Devargota Road		

Table 14. Details of photo-captures of tigers in Pench Tiger Reserve

Photo-capture details of tigers: Pench Tiger Reserve 2002						
TIGER ID	LOCATION ID	PHOTO-CAPTURE DATE	PHOTO-CAPTURE TIME	EXPOSURE DETAILS		SEX
				LEFT FLANK ROLL AND FRAME NUMBER	RIGHT FLANK ROLL AND FRAME NUMBER	
PMT-101	BBR 4.7	09-Nov-02	21:53	PM-13/02-2	PM-14/02-1	FEMALE
PMT-101	DPR 1.2	11-Nov-02	21:56	PM-27/02-4	PM-28/02-4	FEMALE
PMT-101	SBR 4.8	12-Nov-02	01:22	PM-05/02-10	PM-06/02-10	FEMALE
PMT-101	BBR 4.7	14-Nov-02	03:12	PM-14/02-5	PM-13/02-7	FEMALE
PMT-101	SBR 3.4	17-Nov-02	03:57	PM-10/02-7	NA	FEMALE
PMT-101	SPR 1.4	23-Nov-02	22:53	PM-08/02-9	PM-07/02-9	FEMALE
PMT-102	SPR 2.7	10-Nov-02	19:13	PM-17/02-31	PM-18/02-3	FEMALE
PMT-102	BBR 4.7	11-Nov-02	18:42	PM-13/02-5	PM-14/02-4	FEMALE
PMT-102	BBR 4.7	14-Nov-02	03:48	PM-14/02-9	PM-13/02-11	FEMALE
PMT-102	PBR 1.3	18-Nov-02	00:17	PM-02/02-1	PM-01/02-2	FEMALE
PMT-102	SPR 1.3	19-Nov-02	20:17	PM-32/02-8	PM-31/02-8	FEMALE
PMT-102	BBR 4.7	20-Nov-02	06:28	PM-13/02-18	PM-14/02-16	FEMALE
PMT-103	GBR 1.4	12-Nov-02	19:36	PM-25/02-2	PM-26/02-2	FEMALE
PMT-104	BBR 4.7	14-Nov-02	03:12	PM-14/02-6	PM-13/02-8	FEMALE
PMT-105	BBR 4.7	14-Nov-02	03:16	PM-14/02-7	PM-13/02-9	MALE
PMT-106	BBR 4.7	14-Nov-02	03:16	PM-14/02-8	PM-13/02-10	FEMALE
PMT-106	BBR 4.7	14-Nov-02	04:13	PM-13/02-12	PM-14/02-10	FEMALE
PMT-106	HPR 0.3	29-Nov-02	21:20	PM-01/02-6	PM-02/02-5	FEMALE
PMT-107	BBR 1.5	14-Nov-02	19:00	PM-04/02-3	PM-03/02-4	MALE
PMT-107	HBR 4.9	28-Nov-02	22:15	PM-47/02-2	PM-24/02-32	MALE
PMT-108	GBR 1.4	17-Nov-02	18:16	PM-25/02-6	PM-26/02-6	FEMALE
PMT-109	GPR 4.7	26-Nov-02	01:18	PM-35/02-18	PM-36/02-18	FEMALE
PMT-109	GPR 6.3	27-Nov-02	23:45	PM-34/02-29	PM-33/02-29	FEMALE
PMT-110	GLR 2.4	05-Dec-02	05:15	PM-19/02-20	NA	MALE
PMT-110	GLR 2.4	05-Dec-02	05:16	NA	PM-19/02-21	MALE
PMT-110	GLR 4.1	05-Dec-02	06:03	PM-02/02-7	PM-01/02-8	MALE
PMT-110	GLR 8.7	05-Dec-02	18:36	PM-28/02-27	PM-27/02-27	MALE
PMT-111	DGR 1.6	07-Dec-02	21:41	PM-49/02-5	PM-48/02-5	FEMALE
PMT-112	GGR 18.8	12-Dec-02	18:06	PM-13/02-25	PM-14/02-23	MALE
PMT-113	GGR 13.2	13-Dec-02	02:03	PM-26/02-26	PM-25/02-26	UNKNOWN
PMT-114	GLR 8.7	14-Dec-02	04:48	PM-27/02-32	PM-28/02-32	FEMALE

Table 15. Results of the camera trap surveys in Pench Tiger Reserve

November-December 2002	
Total number of camera trap locations	60
Sampling effort	715 trap nights
Number of sampling occasions	12
Camera trap polygon area	112 km ²
Estimated sampled area including buffer	270 km ²
Number of individually identified tigers	14
Capture-recapture model used to estimate population size	M_h
Estimated animal density for tigers in the sampled area	7.3 tigers/100 km ²

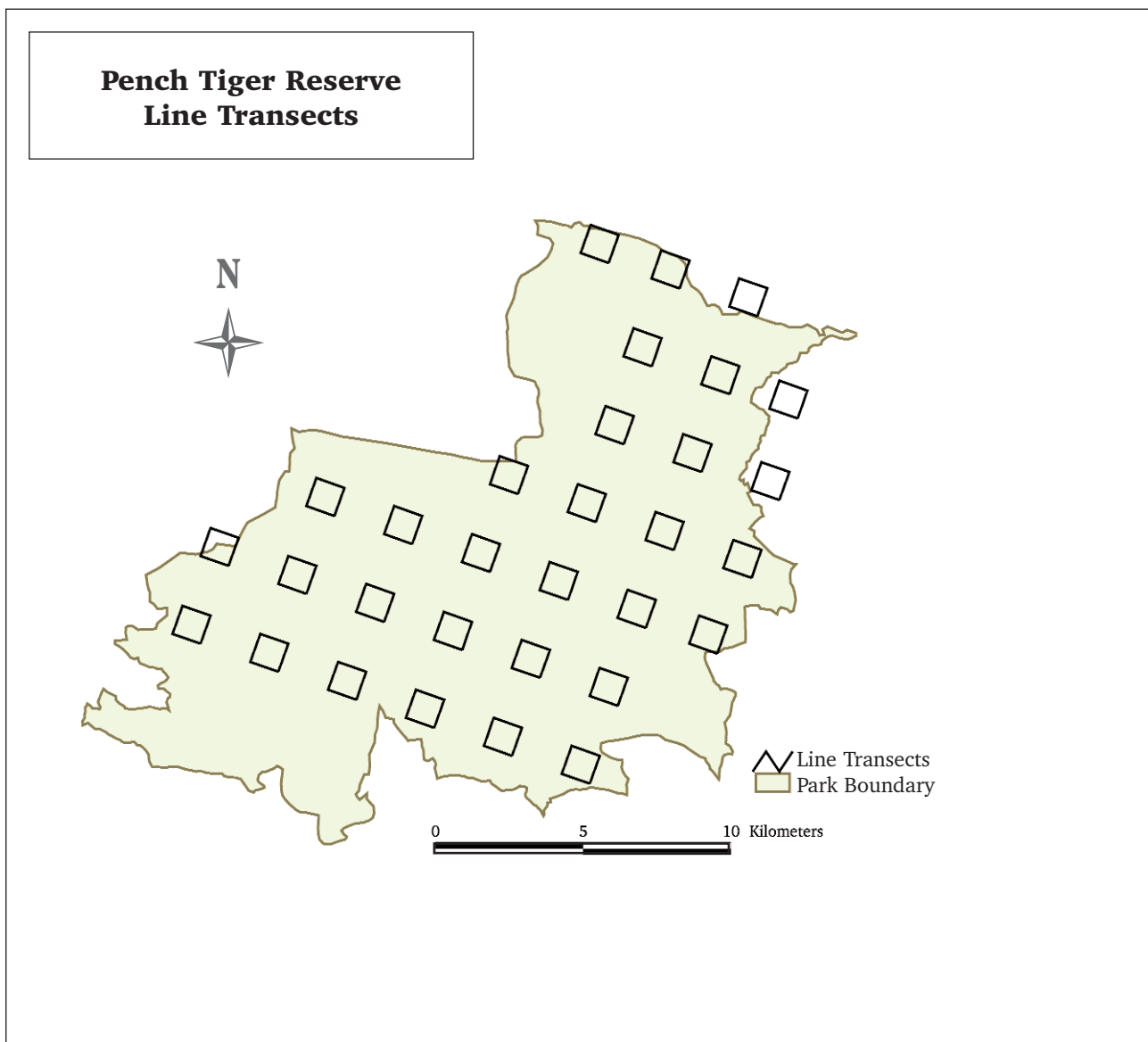
Figure 7. Pench Tiger Reserve: Study area, with line transect samplers

Table 16. Line transect sampler locations (longitude and latitude of bottom left (BL), bottom right (BR) top right (TR) and top left (TL) corners) and realized lengths (RL) in Pench Tiger Reserve

Tr. No.	BL		BR		TR		TL		RL Length (km)
	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	
1	79.2462	21.7114	79.2553	21.7082	79.2588	21.7166	79.2497	21.7198	4.0
2	79.2691	21.7031	79.2782	21.6998	79.2817	21.7083	79.2726	21.7115	4.0
3	79.2942	21.6939	79.3033	21.6907	79.3068	21.6991	79.2977	21.7024	4.0
4	79.2593	21.6796	79.2684	21.6764	79.2719	21.6848	79.2628	21.6880	2.7
5	79.2844	21.6704	79.2935	21.6672	79.2970	21.6756	79.2879	21.6789	4.0
6	79.3064	21.6624	79.3155	21.6592	79.3189	21.6676	79.3099	21.6709	4.0
7	79.2495	21.6561	79.2586	21.6529	79.2621	21.6613	79.2530	21.6646	3.0
8	79.2746	21.6470	79.2837	21.6437	79.2872	21.6522	79.0278	21.6554	4.0
9	79.2997	21.6378	79.3088	21.6346	79.3123	21.6430	79.3032	21.6463	4.0
10	79.2146	21.6418	79.2237	21.6386	79.2272	21.6470	79.2181	21.6503	4.0
11	79.2397	21.6327	79.2488	21.6294	79.2523	21.6379	79.2432	21.6411	4.0
12	79.2649	21.6235	79.2739	21.6203	79.2774	21.6287	79.2683	21.6319	4.0
13	79.2900	21.6143	79.2990	21.6111	79.3025	21.6195	79.2934	21.6228	4.0
14	79.1546	21.6367	79.1637	21.6334	79.1672	21.6419	79.1581	21.6451	1.7
15	79.1797	21.6275	79.1888	21.6243	79.1923	21.6327	79.1832	21.6359	4.0
16	79.2048	21.6183	79.2139	21.6151	79.2174	21.6235	79.2083	21.6268	4.0
17	79.2300	21.6092	79.2390	21.6059	79.2425	21.6144	79.2334	21.6176	4.0
18	79.2551	21.6000	79.2641	21.5968	79.2676	21.6052	79.2585	21.6085	4.0
19	79.2781	21.5916	79.2872	21.5884	79.2907	21.5968	79.2816	21.6000	4.0
20	79.1197	21.6223	79.1288	21.6191	79.1323	21.6275	79.1232	21.6308	4.0
21	79.1448	21.6132	79.1539	21.6099	79.1574	21.6184	79.1483	21.6216	4.0
22	79.1699	21.6040	79.1790	21.6008	79.1825	21.6092	79.1734	21.6125	4.0
23	79.1951	21.5949	79.2041	21.5916	79.2076	21.6001	79.1985	21.6033	4.0
24	79.2202	21.5857	79.2292	21.5825	79.2327	21.5909	79.2236	21.5941	4.0
25	79.2453	21.5765	79.2543	21.5733	79.2578	21.5817	79.2488	21.5850	2.1
26	79.1099	21.5989	79.1190	21.5956	79.1225	21.6041	79.1134	21.6073	4.0
27	79.1350	21.5897	79.1441	21.5865	79.1476	21.5949	79.1385	21.5981	4.0
28	79.1602	21.5805	79.1692	21.5773	79.1727	21.5857	79.1636	21.5890	4.0
29	79.1853	21.5714	79.1943	21.5681	79.1978	21.5766	79.1887	21.5798	2.5
30	79.2104	21.5622	79.2194	21.5590	79.2229	21.5674	79.2139	21.5727	4.0
31	79.2355	21.5531	79.2446	21.5498	79.2480	21.5583	79.2390	21.5615	4.0

Table 17. Results of the line transect surveys in Pench Tiger Reserve

Total numbers and length of permanent transects	30 lines, 116 km	
Sampler geometry	Square sampler	
Year	December 2002-March 2003	
Total effort (length walked)	894 km	
Species	n	Animal density (per km ²)
Chital	171	5.8
Sambar	248	5.9
Chowsingha	76	1.1
Gaur	34	0.8
Nilgai	36	0.5
Wild Pig	50	2.0

Development of indices for monitoring tigers and prey

Carnivore sign encounter surveys were first conducted in Tadoba-Andhari during February 2003, and later again in March 2004. A total of 24 sampling routes were identified to obtain scats of tigers, leopards and dholes, which together accounted for a cumulative sampling effort of 286 km in 2003, and 269.6 km in 2004. The schematic diagram of sampling routes is included in *Figure-8, p-44* and the route details together with distances are provided in *Table-18, p-45*.

In Melghat, carnivore sign encounter surveys were carried out in February 2005. In all, 33 sampling routes covering the entire study area were identified for carrying out the carnivore scat encounter surveys. *Figure-9, p-46* shows the sampling routes followed in Melghat and *Table-19, p-47* provide the route details with distances covered under each sampling route. A total of 326 km was walked along these sampling routes.

In Pench, a total of 21 sampling routes were identified to obtain scats of tigers, leopards and dholes, which together accounted for a cumulative sampling effort of 233 km. Carnivore sign encounter surveys were conducted in January 2004. The schematic diagram of the sampling routes used in Pench is included in *Figure-10, p-48*. *Table-20, p-49* lists the sampling routes with distances covered under each route. Scats of tigers and their sympatric predators

were recorded during encounter surveys. The number of carnivore scats encountered during these surveys together with an index of their relative abundance is presented in *Table - 21, p-50*.

In Tadoba-Andhari, herbivore pellet/dung of seven principal prey species was counted in 136 plots, each measuring 50x2m. Each dung plot was placed perpendicular to the transect segment and located at the mid-point of each segment. The rugged and steep terrain in Melghat was not suitable for implementing dung/pellet surveys, while these surveys could not be carried out in Pench due to logistic constraints.



Photo: K. U. Karanth



Photo: Center for Wildlife Studies

Scats and pellets can be used to construct indices of relative abundance for monitoring tiger and its prey

**Figure 8. Tadoba-Andhari Tiger Reserve: Study area, with
Carnivore Sign Encounter routes**

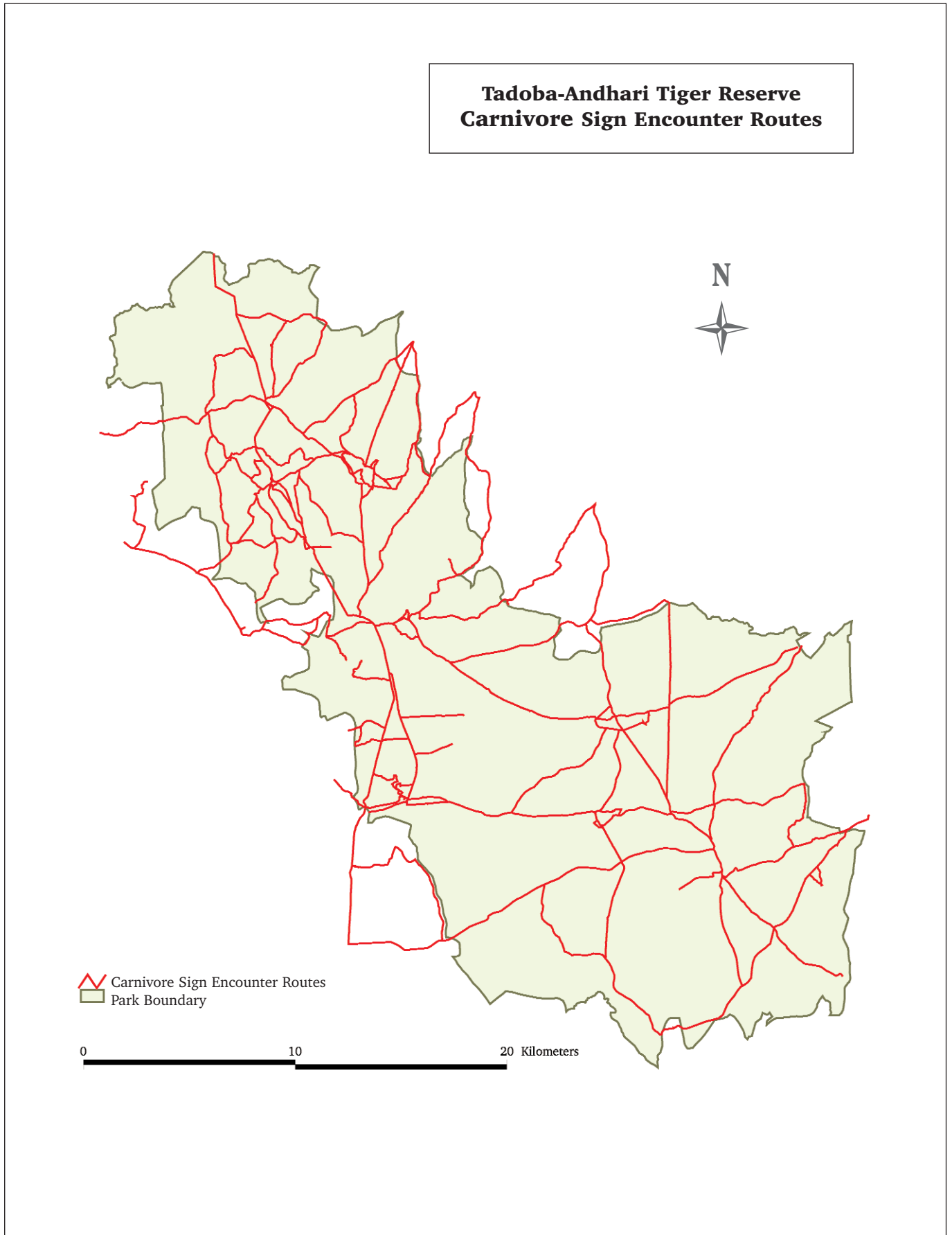


Table 18. Carnivore Sign Encounter Route details in Tadoba-Andhari Tiger Reserve

Route No.	Location	Route length (km)
SER-01	Tadoba-Vasant Bhandara-Jamunbodi Rd-Kosekanar Rd-Kumbi Tank Fireline-main road-Tadoba gate	15.0
SER-02(A)	Tadoba-Ambethira Rd-Katezari gate	7.0
SER-02(B)	Katezari gate-Jamunzora-Compartment 83 & 89 line-Compt 83 & 90-Tadoba lake-Tadoba	12.0
SER-03	Tadoba-Katezari Rd-Kalaamba Rd-Kalaamba machan	10.5
SER-04	Tadoba-Navegaon Rd-Bhanuskhindi Rd-Kalaamba machan-Bhanuskhindi gate	10.7
SER-05	Bhanuskhindi-Dhavana waterhole-Koramataka waterhole-Patel waterhole-Udharmatka-Navegaon gate	9.7
SER-06	Bhanuskhindi hut-Dhorghat-Compt 66 & 62 trail-Navegaon gate	6.6
SER-07	Pandharpani-Alianza fireline-Navegaon gate	10.7
SER-08	Pandharpani meadow-Bamangao Rd-Kolara gate	11.0
SER-09	Tadoba mandir-Hilltop-Compt 93 & 94-Pandharpouni-Navegaon Rd-Sasa Rd-Tadoba lake Rd-Tadoba	10.1
SER-10	Tadoba-Jamni Rd-Jamni chowk-Wagai chowk-Kolara Rd-Kolara gate	11.0
SER-11	Jamni chowk-Pipe nala-Silangpati Rd-Kolara Rd-Kolara gate-Jamni Kolara Rd-Jamni-Pipe nala-Jamni chowk	12.0
SER-12(A)	Jamni chowk-Jamni Rd-Chouradeo-Deori Khatoda Rd-Khatoda Deori Jamni Rd Jn.	14.1
SER-12(B)	Khatoda gate-Khatoda Jamni Rd-Jamni lake-Jamni chowk	10.6
SER-14	Tadoba-Vasant Bhandara Rd-Ambathira link Rd-Gawaraghat link Rd-Chisghat-main Rd-Khutvanda Khatoda Rd-MainRd-Khatoda	9.6
SER-15	Khatoda-main Rd-Khutvanda Rd-Compt 125 & 136 fireline Jn-Compt 125 & 136 fireline trail-Aswal Hira Ambegadh trail-Ambegadh hill-Ambegadh waterhole-Dhavadghat trail Jn-Pandharpani trail-Moharli Tadoba road-Khatoda	13.1
SER-16	Khatoda gate-main Rd-Palasmaon Rd-Palasmaon guard quarters-Madanapur Rd-Ambora nala-Piparda road-Palasmaon main Rd.	12.0
SER-17	Palasmaon guard quarters-Ambhora nala Jn-Karwa Rd-Karwa	9.7
SER-18	Ambhora nala Jn-Rantalodi Rd-Rantalodi-Karwa Rd-Karwa	12.5
SER-19	Botezari-Rantalodi-Moharli Botezari Rantalodi Jn-Botezari	9.0
SER-20	Moharli gate-Telia gate-149/150 Compt boundary fireline-Botezari Rd-Andhari nadi-Kosaba line-Pandharpani	12.6
SER-21	Moharli gate-Telia Rd-Kosaba line-Astkoni vahir-Andhari nadi-Kosaba line-Pandharpani	12.4
SER-22	Moharli gate-main Rd-Telia canal-Telia dam-Telia circular Rd-main Rd-Jamunzira-PH1 Rd-PH1	8.8
SER-23	Moharli gate-main road-Puranivahir-PH1	6.0
SER-24	PH1-Sitarampeth trail-Compt 140 fireline-Compt 144 fireline-main Rd-Compt 144 Rd-Kosaba line	6.8
SER-25	Tadoba-Vasant Bhandara Rd-Ambethira-Mangeli kuti-park boundary-Katezari gate.	12.6

**Figure 9. Melghat Tiger Reserve: Study area, with
Carnivore Sign Encounter routes**

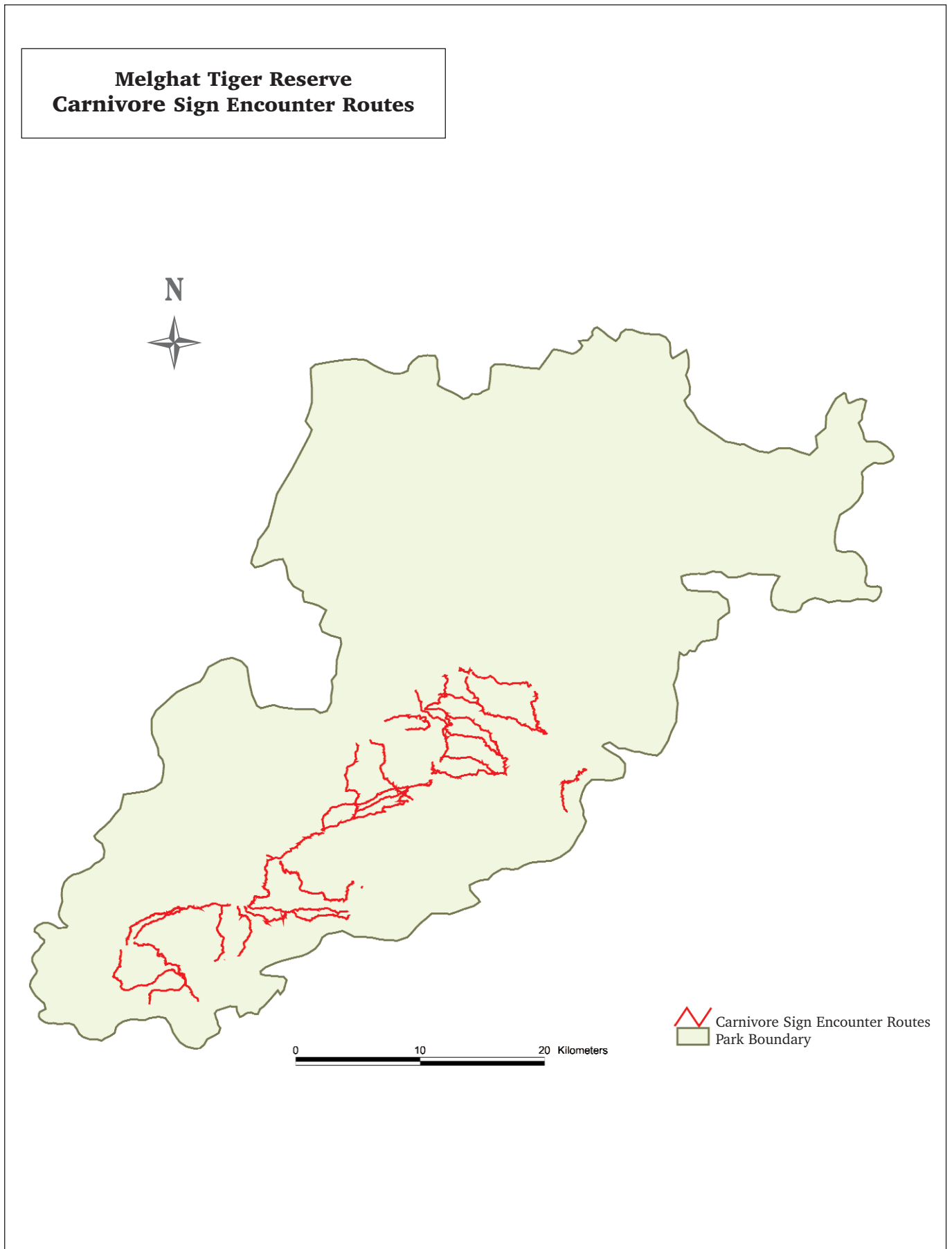


Table 19. Carnivore Sign Encounter Route details in Melghat Tiger Reserve

Route No.	Location	Route length (km)
SER-1	Jadaphati-Banderkahu	10.0
SER-2	Kolkaz-Sipnaballa-Jalban-Jadaphatiawlaballa-Banderkahu	14.5
SER-3	Sadhuballa-Sandaskhandi-Kilaphata-JodAam-Jhandu balla	10.4
SER-4	Jadaphata-Kilaphata-Bobar Nala-Haldu Balla-Kolam Aam	13.0
SER-5	Kolkaz-Sipnaballa-Gerukhandi-Halduballa-Teen Aam-Kund Quarters Gate	13.4
SER-6	Kelivillage-Simikapdi-Perrera Nala-Teen Aam-Bees Aam-Atna Dah-Sakri Road	12.0
SER-7	Kund Quarter-Detkahu-Tippa Ka Rasta-Sakri Road	6.6
SER-8	Kund Junction-Tarubanda Road-Tarubanda RH	12.0
SER-9	Tarubanda RH-Masan-Pavan Chakki-Dhawda Da-Chikal Patti-Kadri Baba-Tarubanda RH	7.0
SER-10	Masan Aam-Vairat	11.0
SER-11	Bana Aam Junction-Chapa pati-Manda Balla-Seluphata Road-Kund Road-Nilikahu-Kund Road	6.8
SER-12	Tarubanda RH-Hatkuva-Tarubanda RH-Voda Khandi-Lawa balla-Jamun Balla-Dhalte-Malate-Sipnakhandi	10.2
SER-13	Bana Aam Junction-SER 11 start-Manda Bala-Bhivigattal-Dunda Aam Khind-Bana Dhap-Pipri Da-Hori Topi Khandi-Parchmoau-Gungruburru Tarubnada RH	7.7
SER-14	Bana Aam Junction-Bana Aam Line-	8.1
SER-15	Koha Quarters-Sipnakhandi-Road	11.2
SER-16	Koha Road-Sipnakhandi Hut	10.0
SER-17	Belkund line no.17-Jogi Joli River-Wada Pati- Kongda Gate	7.5
SER-18	Belkund RH- Mandah Kundni-Patia Nalla-Kokar Jamun- Guagamal Boundary- Gugamal Raod	11.2
SER-19	Dhundri Aam-Koktoo RH	14.5
SER-20	Koktoo-Aamrai 1-Mor Matha-Teen Aam-Rajdeo Baba-Khatkali Road	14.0
SER-21	Koktoo-Dedrakhora-Champa Nala-Chiladari- Hanumanji Deo-Hatboru	8.0
SER-22	Koha Quarter-Gugamal Hut	8.4
SER-23	Kund Qaurters-Bittle Dhavda-Thuva paati-Police Khapa-Sakri Rd	7.4
SER-24	Koktoo- Aamrai no.2-Jiljil Pani-Babna Phata-Gugamal Anicut	8.0
SER-25	Koktoo- Gudgi Phata-Bana Poi-Mandva Phata-Bori Gate	7.5
SER-26	Koktu- Chatuballa-Chiladari	6.2
SER-27	Bori Nandi Deo-Salia Nala-Pirkheda Quarter-Panchgoli-Gaidnand-Dhargad Road	14.5
SER-28	Bori Gate-Dabri Nala-Chunabhatti-Hazaribad-Pirkheda-Datpadi-Gullar Ghat School	13.3
SER-29	Bori-Koktoo Road	11.0
SER-30	Koktoo- Gudgiphati-Bhatibhonga-Diya Patti-Salar Pati- Dolar	10.3
SER-31	Bori-Chiladari	10.0
SER-32	Kund Road-Masan Aam	4.7
SER-33	Ganjada-Semadoh Road	6.5

Figure 10. Pench Tiger Reserve: Study area, with Carnivore Sign Encounter Routes

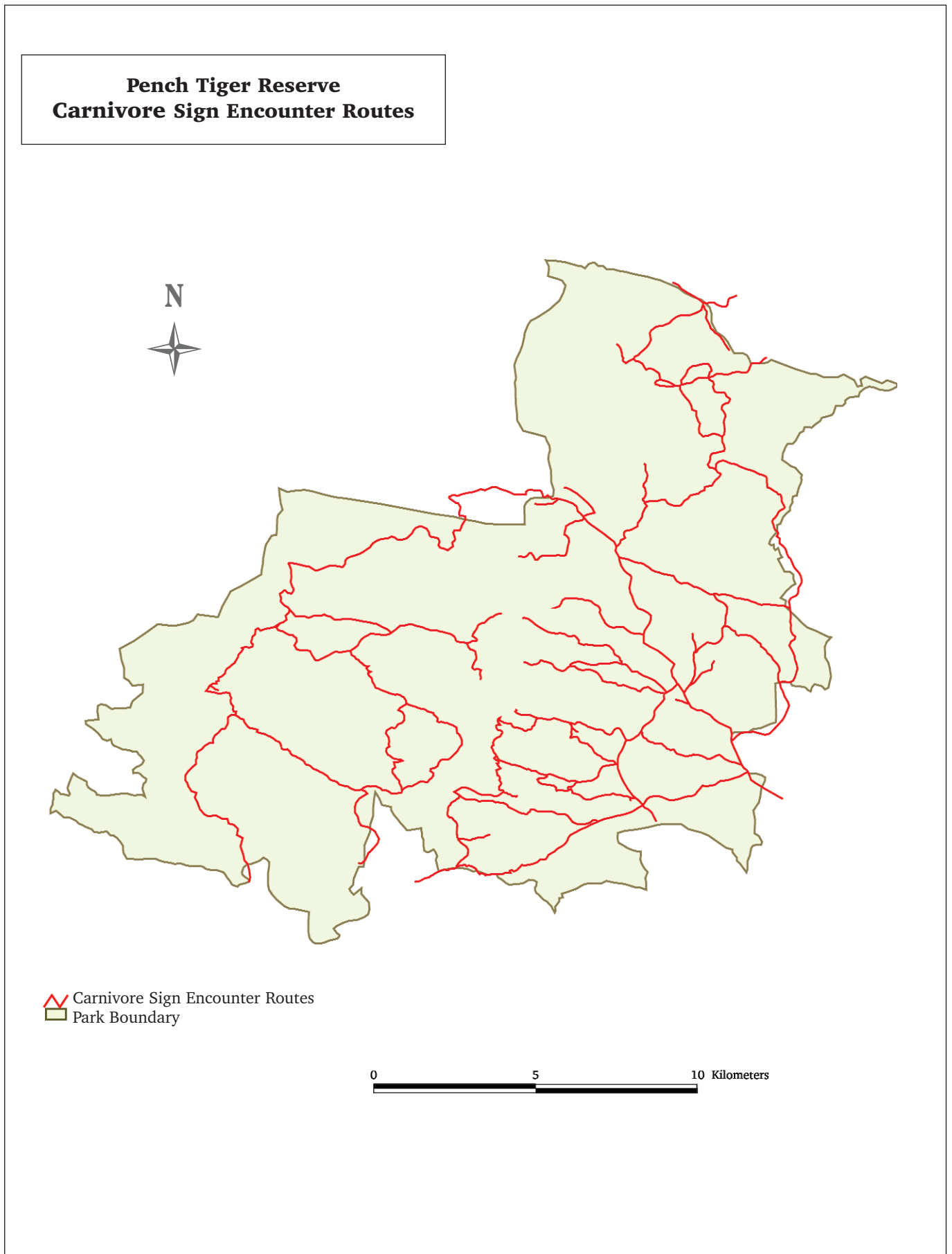


Table 20. Carnivore Sign Encounter Route details in Pench Tiger Reserve

Route No.	Location	Route length (km)
SER-1	Sillari-Ranidoh.	7.9
SER-2	Phuljhari-Hathigotta Rd-Gaulighat Rd-Saiban Rd Jn.	9.5
SER-3	Phuljhari-Ranidoh-Gaulighat Rd-Phuljhari.	7.8
SER-4	Saiban Rd-Gaulighat Rd-Kirangi Sarra Rd-Bedaphat Rd.	10.5
SER-5	Sillari-Kirangi Sarra.	11.0
SER-6	Bodalkhapda Rd Jn-Salama-Bakhari-Phepdikund Rd.	9.9
SER-7	Sillari-Khapa ring Rd-Khapa-Khapa Salama Rd-Phepdikund Rd-Khapa ring Rd.	11.0
SER-8	Bakhari-Fisherman trail-Saddle dam Rd-Salama-Totla Doh-Ambathori.	11.4
SER-9	Phuljhari-Hathigota-tunnel-Lamandoh Rd Jn.	10.0
SER-10	Hathigotta gate-Lamandoh-Ambakhori Rd-new Salama Rd.	11.0
SER-11	Sillari-Totladoh Rd-Bodalkhapda.	8.8
SER-12	Loha gate-Bhimsen-Saddle dam Rd-Bodaljhara.	12.0
SER-13	Bhimsen gate-Garadiban gate-Saddle dam Rd-Chikalkhari gate-Borbandar-Chitalkhari Garadiban Jn-Garadiban Rd-hut on Bhimsen Bakhari Rd.	11.3
SER-14	Saddle dam Rd trail-Chikalkari-Garadiban Rd-Devlapur range border-Chikalkari hut-Chikalkari Rd-Saddle dam camp.	11.0
SER-15	Saddle dam Rd-Nagdev Phadi-Pivarthadi Rd-State border-CPT-Nalla-Pagdandi-Pivarthadi Rd.	11.6
SER-16	Totladoh-Ghatpindri	11.3
SER-17	Ghatpindri-Pagdandi towards Lamandoh-Ghuggusgadh	8.7
SER-18	Ghatpindri-Sattalao pugdandi 1-Ghuggusgadh-Old coupe Rd-Nallitipat-Sattalao Rd-Ghatpindri Pagdandi 2.	10.0
SER-19	Ghatpindri-Sattalao Rd-Pagdandi-Suryawanikhind-Narhar Rd-Pagdandi-Nandpur Jn.	16.0
SER-20 (A)	Sattalao Rd Jn on Narhar Rd-Chipad Rd.	7.9
SER-20 (B)	Chipad Rd gate-Narhar Rd-Gothimatha-old coupe Rd-Ghorad Rd.	11.5
SER-21	Nallitipat-Gaulighat Rd-Dhobigota-Nandpur Jn-Gothimatha Rd.	13.1

Carnivore diet analysis

A total of 519 carnivore scats were collected during field surveys in Maharashtra (see Table-21). Scats collected during the Tadoba-Andhari and Pench surveys have been analyzed to examine the prey composition and food habits of tigers and their co-predators. Detailed studies on the prey selectivity patterns including the identification of the prey remains from scats collected in Melghat are underway.

Preliminary results (Sujai 2004) show that in Tadoba-Andhari, ten prey species occurred in tiger scats whereas leopard scats contained 8 prey species and dhole scats contained 4 prey species. Livestock presence was observed in two of the tiger scats. The food habit study indicates that large prey such as sambar and gaur contributed more than two-thirds of the prey biomass in tiger's diet in Tadoba-Andhari. Medium-sized prey like chital and wild pig accounted for 22% of its diet whereas remaining prey species together contributed only 9% in its diet.

Sambar, chital and wild pig appears to be the most important prey for all the three top predators in Tadoba-Andhari. Figure-11, p-51 depicts percentage occurrence of different prey species in predator scats found in Tadoba-Andhari.

At Pench, six prey species occurred in tiger scats whereas seven and four prey species occurred in leopard and dhole scats respectively (Sujai 2004). Sambar occurred in 50% of tiger scats followed by wild pig (23%) and chital (11%). Sambar and gaur together contributed to nearly 80% of the prey biomass consumed by tiger, whereas chital and wild pig contributed to nearly 50% of the leopard as well as dhole's diet. The contribution of the smaller prey (muntjac, chowsingha, langur, rhesus macaque and hare) was very low in the diets of all the three sympatric predators. Percentage occurrence of different prey species in predator scats found in Pench is depicted in Figure-12, p-51.

Table 21. Number of scats encountered and estimated scat encounter rates in Tadoba-Andhari, Melghat and Pench Tiger Reserves

	Tadoba-Andhari 2003		Melghat 2005		Pench 2004	
Effort (km)	286.4		326.0		233.2	
Species	No.	Encounter rate (scats/ 10km)	No.	Encounter rate (scats/ 10km)	No.	Encounter rate (scats/ 10km)
Tiger	57	1.99	55	2.36	56	2.40
Leopard	61	2.13	171	7.35	35	1.50
Dhole	6	0.21	64	2.75	14	0.60

Figure 11. Percentage occurrence of different prey species in predator scats found in Tadoba-Andhari Tiger Reserve

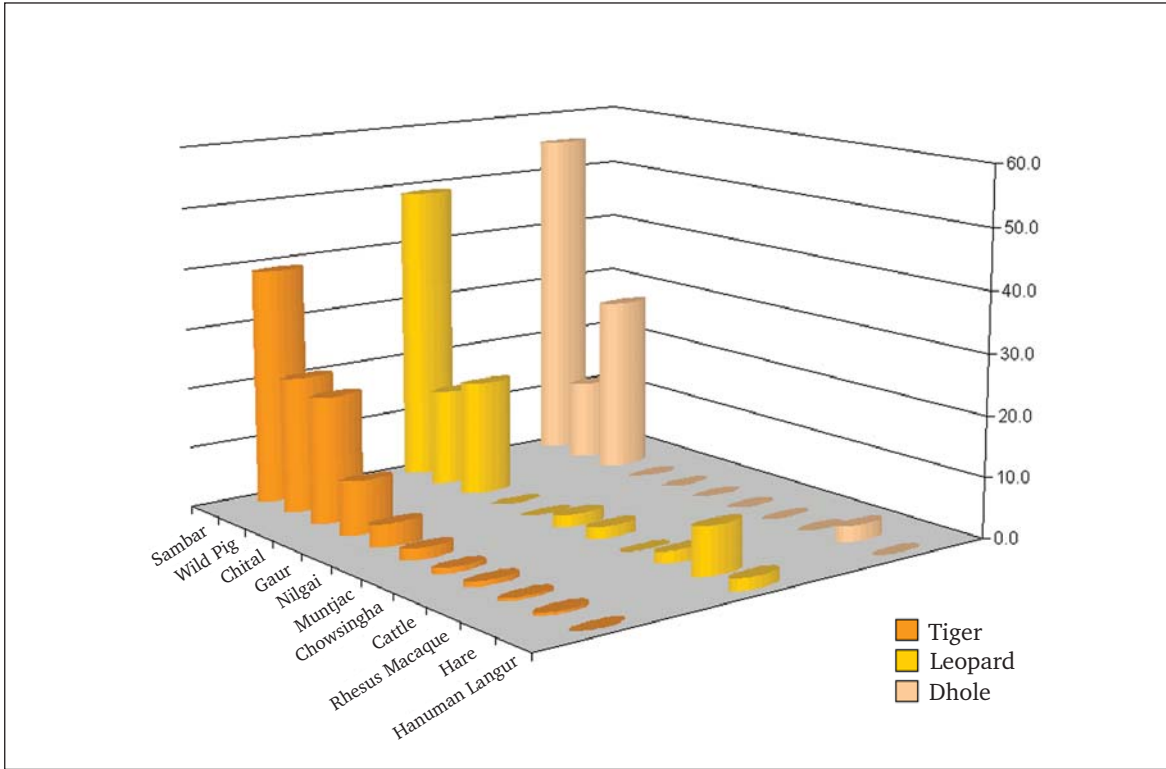
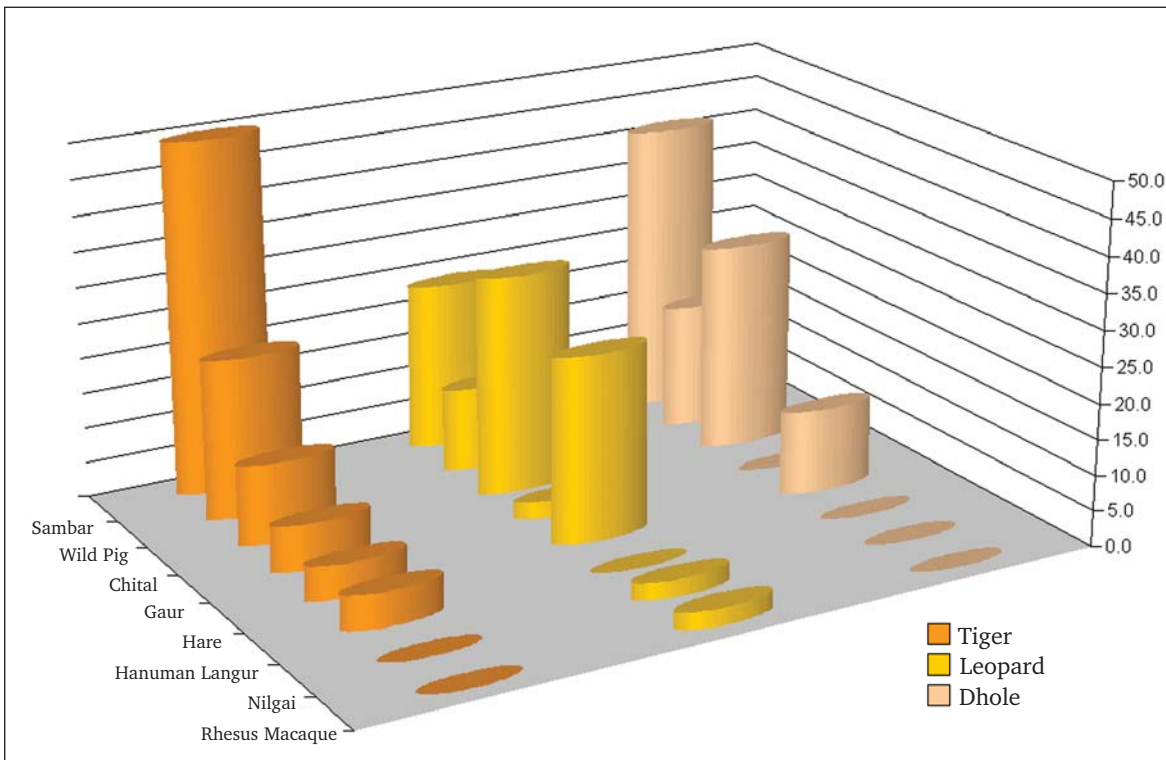


Figure 12. Percentage occurrence of different prey species in predator scats found in Pench Tiger Reserve



Training and capacity-building

A major thrust of the project was training and capacity-building, with emphasis given to building local capacity to an extent where local project collaborators, department staff and wildlife enthusiasts are able to continue monitoring tiger and prey population beyond the project period. The Co-Principal Investigator, N. Samba Kumar underwent advanced training at University of St. Andrews, Scotland and participated in the DISTANCE sampling workshops. In consultation with Dr. Len Thomas and Dr. Samantha Strindberg from the DISTANCE development group at the University of St. Andrews, Scotland, he developed the sampling designs for the long-term monitoring of prey populations in key sites of Maharashtra. Four of the research assistants (Arjun Gopalswamy, Raghavendra Mogaroy, Narendra Patil and Bharath Sundaram) who were trained under this project, gained proficiency and developed field skills to a high degree. Arjun Gopalswamy and Bharath Sundaram are undergoing further training to become professional wildlife biologists by pursuing their academic studies, while Raghavendra Mogaroy and Narendra Patil are pursuing careers in wildlife conservation and allied fields.

The project also imparted field training to V. Sujai, a graduate student from the Bharathidasan University, India. Sujai was trained in identifying prey remains from carnivore scats and to analyze the dietary

preferences of three large sympatric carnivores (tiger, leopard and dhole) at Tadoba-Andhari and Pench Tiger Reserves. Sujai's study also formed a part of his dissertation work.

The project identified and trained two highly motivated couples: Harshawardhan and Poonam Dhanwatey from Nagpur, who worked in Tadoba-Andhari and Pench Tiger Reserves; and Prachi Mehta and Jayant Kulkarni from Pune, who worked in Melghat Tiger Reserve. These keen wildlife enthusiasts worked as our long-term collaborating local partners in Maharashtra and coordinated the entire field operations at the study sites. Harshawardhan Dhanwatey and Poonam Dhanwatey are currently engaged in science-driven conservation activities in Tadoba-Andhari and Pench reserves, while Prachi Mehta and Jayant Kulkarni continue monitoring of tiger and prey populations in Melghat using the sampling protocol developed under this project.

Nine young and enthusiastic local field assistants (four from TRACT, an NGO based in Nagpur; three from Envirosearch, an NGO based in Pune; and three from Panna Tiger Project based in Panna, Madhya Pradesh) were also trained in the line transect and camera trap field operations. They currently assist the project collaborating partners in continuing field conservation and research activities.

The project also had an objective of identifying and supporting qualified officers in the Maharashtra State Forest Department for higher degrees in wildlife biology and management. Although this offer was not availed as part of this project, we are currently supporting a senior officer from the Rajasthan State Forest Department, keen to pursue an academic program by registering for his Ph.D under our guidance. This objective is being accomplished under another STF and RTCF supported project in Karnataka.

Fourteen field-training workshops (4 in Tadoba-Andhari, 8 in Melghat and 2 in Pench) were organized during the project period to train Maharashtra State Forest Department staff and local amateur naturalists in the application of sampling-based methods to estimate absolute densities of large prey and predators. A total of 82 field staff from the Forest Department and 116 volunteers from non-governmental organizations (NGOs) participated in these workshops. Each workshop was of one week's duration and these were conducted during March 2002 and March 2004 in Tadoba-Andhari; March 2003 in Pench; and May 2003, May-June 2004 and February-March 2005 in Melghat. Senior volunteer-instructors from Centre for Wildlife Studies assisted the project team in field training.

Five training workshops (3 in Tadoba-Andhari and one each in Melghat and Pench) were also conducted on the use of index-based surveys for monitoring tiger and prey populations. 50 field staff from the Forest Department and 80 volunteers from

local NGOs participated in these sign encounter surveys. These field workshops were typically of 3-5 days duration and focused primarily on imparting basic field skills in the identification of carnivore scats, herbivore pellets/dung and field sampling protocols. The workshops were conducted at Tadoba-Andhari in February 2003 and March 2004; at Pench in January 2004; and at Melghat in February 2005.

Four field demonstrations and slide talks were given to the field staff and officials of Maharashtra State Forest Department illustrating the use of camera trap technique in tiger population surveys. These talks and demonstrations were held at the Forest Department Headquarters in Nagpur (December 2001), at the field site in Tadoba-Andhari (December 2001), Semadoh Interpretation Centre at Melghat (May 2002) and at the field site in Pench (November 2002).

An international field-training workshop on sampling-based approaches for monitoring tigers and their prey was also organized in collaboration with WWF-International and WWF-India in January 2004 at Tadoba-Andhari. Fifteen field staff from seven WWF regional programs (India, Nepal, Bhutan, Malaysia, Indonesia, Indo-China, and Laos) participated in this workshop.



Photo: H. Dhanwatey

Training of forest personnel

Dissemination of results and Publication plan

This project has resulted in the first set of reliable density estimates derived using modern sampling-based methods of tigers and their prey for three of the most productive forested habitats in Maharashtra. These results have important conservation implications. Even though the estimates from Maharashtra show lower densities of tigers when compared to some of the other high-density areas in the country, our surveys show that prime tiger habitats in Maharashtra have the potential to support higher densities of tigers, if prey densities can be increased to optimal levels. Further, these tiger and prey density estimates provide an objective, ecological benchmark against which the success of future management and conservation interventions can be measured.

The first-ever ecological benchmark estimates of tiger and prey densities in the three project sites have been reported in the prestigious international journal *Proceedings of the National Academy of Sciences (PNAS)*, USA (Karanth *et al.* 2004b, included in *Appendix - D*, p66-70). The paper tested a macro-ecological model investigating the relationship between prey densities and densities of tigers at 11 sites across India including the three project sites in Maharashtra.

Insights and findings from this study have also been incorporated into the two other important scientific papers published

recently (Karanth, Nichols and Kumar 2004a; Karanth and Gopal 2005) included in *Appendix-D (p71-104)*.

The preliminary results of the project were also shared in a symposium on "Three decades of Project Tiger in Melghat", organized by the University of Amravati, Nature Conservation Society of Amravati in association with the Directorate of Project Tiger in October 2004. Here, two papers were presented by the Co-Principal Investigators of the project, Poonam Dhanwatey and Jayant Kulkarni. The proceedings of this symposium are currently in press. Presentations were also made by Poonam Dhanwatey in another symposium "Ten years of Tadoba-Andhari Tiger Reserve" organized by Maharashtra State Forest Department in Chandrapur in April 2005. Several presentations were also made in different fora by the Co-Principal Investigators.

The full process of data exploration and analysis from a long-term macro-ecological study such as this one takes a long time, and we are currently exploring ways of analyzing other scientific and conservation data generated from this study. Around 6-8 more peer-reviewed papers are envisaged to be published in important peer-reviewed journals over the next 2-3 years. These proposed papers will cover different components of the project including abundance estimates of other sympatric

carnivores (leopard and hyena), herbivore densities, carnivore diet profiles, carnivore encounter rate estimates, and results of the capacity-building exercises.

The preliminary results of this project are now being shared at the request of the Chief

Wildlife Warden through this report. We hope this report will convey some impression of the substantial scientific and conservation contributions made by this project to the understanding of tiger ecology in Maharashtra.

Photo: H. Dhanwatey



Forest Department staff attending a training programme

Bibliography

- Anon. 1997. *Guidelines for estimating tigers*. Letter No. 7-1/99-PT. Dated, 28th April 1997. Directorate of Project Tiger, New Delhi.
- Anon. 2001. *Guidelines for estimating tigers*. Letter No. 7-1/99-PT. Dated, 15th June 2001. Directorate of Project Tiger, New Delhi.
- Karanth K. U. and Gopal R. 2005. An ecology-based policy framework for human-tiger coexistence in India. Pages 373-387. In *People and wildlife: Conflict or coexistence?* Woodroffe, R., Thirgood, S. and Rabinowitz, A. (Eds), Cambridge University Press.
- Karanth, K. U. and Nichols, J. D. 1998. Estimating tiger densities in India from camera trap data using photographic captures and recaptures. *Ecology* **79** (8): 2852-2862.
- Karanth, K. U. and Nichols, J. D. 2000. *Ecological Status and Conservation of Tigers in India*. Final Technical Report to USFWS (Division of International Conservation) and WCS. Centre for Wildlife Studies, Bangalore, India (124 pages).
- Karanth, K.U. and Nichols, J.D. 2002. (Ed) *Monitoring Tigers and their Prey: A manual for researchers, managers and conservationists in tropical Asia*. Centre for Wildlife Studies, Bangalore, India (184 pages).
- Karanth, K. U. and Sunquist, M. E. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology* **64**: 439-450.
- Karanth, K. U. and Sunquist, M. E. 2000. Behavioural correlates of predation by tiger, leopard and dhole in Nagarahole, India. *Journal of Zoology*, London **250**: 255-265.
- Karanth, K.U., Nichols, J.D., and Kumar, N.S. 2004a. Photographic sampling of elusive mammals in tropical forests. Pages 229-247. In *Sampling rare or elusive species*. Thompson, W.L. (Ed). Island Press.
- Karanth, K. U., Nichols, J. D., Kumar, N. S., Link, W. A. and Hines, J. E. 2004b. Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of National Academy of Sciences, USA* **101** (14): 4854-4858.
- Link, W. A. and Karanth, K. U. 1994. Correcting for overdispersion in testing for prey selectivity. *Ecology* **75** (8): 2456-2459.
- Mehta, P. 2000. A study on the impact of forestry practices on bird communities of Satpura Hills. Ph.D thesis. Saurashtra University.
- Nichols, J. D., Johnson, F. A. and Williams, B. K. 1995. Managing North American waterfowl in the face of uncertainty. *Annual Review of Ecology and Systematics*. **26**: 177-199
- Sujai, V. 2004. Diet profile of three large sympatric carnivores in Central India. M.Sc. thesis, AVC College, Mayiladuthurai.
- Walters, C. J. 1986. *Adaptive management of renewable resources*. Macmillan Publication Company, NY (374 pages).
- Wikramanayake, E. D., Dinerstein, E., Robinson, J. G., Karanth, K.U., Rabinowitz, A., Olson, D., Matthew, T., Hedao, P., Conner, M., Hemley, G. and Bolze, D. 1999. Where can tigers live in the future? A framework for identifying high priority areas for the conservation of tigers in the wild. In *Riding the Tiger: Tiger conservation in human dominated landscapes* Seidensticker, J., Christie, S. and Jackson, P. (Eds), Cambridge University Press (Pages 255-272).
- Williams, B. K., Nichols, J. D. and Conroy, M. J. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, CA (817 pages).

APPENDICES

Appendix A

Individually identified tigers
photo-captured in
Tadoba-Andhari Tiger Reserve
during 2001-2003



TDT 101



TDT 102



TDT 103



TDT 104



TDT 105



TDT 106



TDT 107



TDT 108



TDT 109



TDT 110



TDT 111



TDT 112, 113, 114



TDT 115



TDT 116



TDT 117



TDT 118



TDT 119



TDT 120



TDT 121

Appendix B

**Individually identified tigers
photo-captured in Melghat Tiger Reserve
during March - June 2002**



MGT 101



MGT 102



MGT 103



MGT 104



MGT 105



MGT 106



MGT 107



MGT 108



MGT 109



MGT 110



MGT 111



MGT 112



MGT 113



MGT 114



MGT 115

Appendix C

Individually identified tigers
photo-captured in Pench Tiger Reserve
during November - December 2002



PMT 101



PMT 102



PMT 103



PMT 104



PMT 105



PMT 106



PMT 107



PMT 108



PMT 109



PMT 110



PMT 111



PMT 112



PMT 113



PMT 114

Appendix D

Publications

Tigers and their prey: Predicting carnivore densities from prey abundance

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The goal of ecology is to understand interactions that determine the distribution and abundance of organisms. In principle, ecologists should be able to identify a small number of limiting resources for a species of interest, estimate densities of these resources at different locations across the landscape, and then use these estimates to predict the density of the focal species at these locations. In practice, however, development of functional relationships between abundances of species and their resources has proven extremely difficult, and examples of such predictive ability are very rare. Ecological studies of prey requirements of tigers *Panthera tigris* led us to develop a simple mechanistic model for predicting tiger density as a function of prey density. We tested our model using data from a landscape-scale long-term (1995–2003) field study that estimated tiger and prey densities in 11 ecologically diverse sites across India. We used field techniques and analytical methods that specifically addressed sampling and detectability, two issues that frequently present problems in macroecological studies of animal populations. Estimated densities of ungulate prey ranged between 5.3 and 63.8 animals per km². Estimated tiger densities (3.2–16.8 tigers per 100 km²) were reasonably consistent with model predictions. The results provide evidence of a functional relationship between abundances of large carnivores and their prey under a wide range of ecological conditions. In addition to generating important insights into carnivore ecology and conservation, the study provides a potentially useful model for the rigorous conduct of macroecological science.

Ecological investigations basically involve efforts to understand interactions that determine the spatial distribution and abundance of organisms (1–3). Ecologists strive for a predictive science in which they can identify key attributes as potential limiting factors for a focal species, measure these attributes at different locations, and make predictions about the abundance of the focal species based on these measured attributes. An alternative popular approach to the study of spatial distribution and abundance is to search for patterns in existing data and then to treat perceived patterns as phenomenological models to be used for making predictions. Regardless of research approach, the study of the distribution and abundance of organisms at large spatial scales (i.e., macroecological patterns) has received substantial emphasis recently (3–8).

Analyses directed at macroecological questions require data collected at a scale far beyond the typical study areas of most field ecologists. As a result, such analyses are usually based on either large-scale count surveys of animal populations (6) or on metaanalyses of results from numerous individual studies (8). However, most large-scale count surveys of animal populations fail to yield strong inferences for two reasons: they are based on raw count data (indices) bearing an unknown relationship to true animal abundance, and spatial sampling units are not selected in a manner that permits inference about the entire area of interest (9–11). Individual studies used in metaanalyses also frequently suffer from these two problems, besides being constrained by their individual sets of objectives, field techniques, and analytic methods. As a result, the inferences about existence and non-existence of potential patterns derived from macroecological

analyses are often weak and unreliable. The detection and nondetection of patterns may have more to do with spatial variation in detectability of animals and selection of sample locations than with true ecological variations.

The study reported here represents an effort to avoid the above weaknesses associated with many macroecological investigations. This effort focuses on two key aspects (11) of such investigations: (i) modeling and prediction and (ii) sampling and estimation. With respect to modeling and prediction, instead of looking for macroecological patterns and then treating such patterns as phenomenological models to be tested, we emphasize a more mechanistic approach based on the ecological concept of “limiting factors,” factors that are determinants of equilibrium population size or, more generally, of the stationary probability distribution of population densities (12–14). Changes in limiting factors are expected to cause corresponding changes in equilibrium population densities (12–15), thus providing a logical basis for prediction. This approach is more direct and mechanistic than the use of phenomenological models.

With respect to sampling and estimation, we selected 11 study sites located within protected areas throughout India. Each site was sampled by teams of trained investigators, using methods developed specifically to estimate densities of the focal species (the tiger) and their primary resource (prey species). This field study required 8 years and substantial effort to complete but resulted in data that were adequate to test our model-based predictions at a landscape-level spatial scale.

Materials and Methods

Model Development. Generally, carnivores (order *Carnivora*) appear to be limited by food resources (8, 16), with species in the family *Felidae* being obligate meat eaters. Tigers are the largest of the felids and prey almost exclusively on large ungulates (17, 18). They are socially dominant over other sympatric carnivores (18, 19). Consequently, tiger densities in protected habitats are likely to be mediated chiefly by prey abundance rather than interspecific social dominance and competitive exclusion. Therefore, we proposed a mechanistic model that predicts tiger density as a function of prey density.

Based on earlier field studies of large carnivore guilds (17, 18, 20), we hypothesized that predators annually removed ≈15% of all available prey, with tigers cropping ≈10% and other sympatric predators such as leopards *Panthera pardus* and/or dholes *Cuon alpinus* exploiting the remaining 5%. The body masses of individual ungulates killed by tigers (20–1,000 kg) and the proportion of the kill actually consumed are both highly variable factors (18). Therefore, we represented prey availability in terms of ungulate numbers rather than biomass (21) in our model. We applied the average kill rate of 50 ungulates/tigers per year consistently observed in field studies of tigers (18, 21). Thus, we

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predicted tiger density, T_j at location j , based on prey density, U_j , according to the following expression:

$$T_j = \frac{0.10}{50} U_j \delta_j,$$

where δ_j is a mean one random variable.

The above model of the functional relationship between prey density and tiger density could potentially be tested by manipulating prey density at multiple locations to look for the predicted response in tiger density. However, because manipulative experimentation on populations of these rare endangered animals was neither possible nor desirable, we tested our model by estimating population densities of both tigers and prey in a field study that covered a total area of 3,024 km² in 11 ecologically diverse landscapes across India. Our study sites represented a wide range of ecological variations in terms of both abundance and composition of the prey assemblages.

Estimation of Prey Abundance. Ungulate prey species were visible during the day and could be directly counted by investigators. However, investigators could not detect all animals present in the surveyed areas during field counts because of dense cover and other factors. Thus the estimation of prey density required the estimation of detection probability (9–11). Therefore, prey densities were estimated by using line transect surveys in conjunction with distance sampling methods (22). Investigators walked along forest trails established to representatively sample the surveyed areas. Visual detections of ungulates were followed by counts of group (cluster) size and measurements of sighting distances and sighting angles (22, 23) to obtain perpendicular distances of sighted animals from the transect line. The animal counts and associated distance data were later used to model visual detection probabilities as a decreasing function of distance from the transect line. This modeling and the subsequent estimation of prey densities and their variances were accomplished by using the estimation algorithms implemented in computer software DISTANCE (24). Generally, models of detectability based on the half-normal key function with one or no adjustment terms adequately fitted data from most prey species–habitat combinations, with the hazard rate or uniform–cosine key function fitting data adequately in the remaining cases (22–24).

Estimation of Tiger Densities. Tigers were photographed by using surveys deploying automatic camera traps activated by animal movement (25, 26). Because tigers can be individually identified from their stripe patterns, it is possible to photographically “capture” and “recapture” them on one or more sampling occasions. Resulting data can be summarized as capture histories, vectors of 1s and 0s reflecting whether each individual tiger was captured (1) or not (0) on each sampling occasion. These data are then used in conjunction with capture–recapture models developed for closed animal populations (11, 27) to estimate tiger abundance (25, 26, 28). Specifically, we used program CAPTURE (29) to compute test statistics for the hypothesis of a closed population and model selection statistics based on a discriminant function developed from extensive simulations and to derive estimates of capture probability (p) and tiger abundance (N) at each site using various possible models and associated estimators. Because of our interest in comparing tiger density estimates across sites, we preferred a single model and estimator for use on data from all sites.

Tiger density was then estimated by dividing the estimated population size (N) by the estimated area sampled by the camera traps. This area was estimated by first computing the area (A) of the polygon connecting the outermost traps. Then, half the mean maximum distances moved by individual tigers between photo-

captures at each site was used to estimate the width of a buffer strip (\hat{w}) that was added to the polygon area to estimate $\hat{A}(\hat{w})$, the area effectively sampled by camera traps (25, 28, 30). Density was then estimated as: $\hat{D} = \hat{N}/\hat{A}(\hat{w})$.

Modeling the Relation Between Tiger and Prey Numbers. We supposed that the natural logarithms of prey density and tiger density have a bivariate normal distribution. This model induces a regression relation

$$E(\log(T_j) | \log(U_j)) = a + b \log(U_j),$$

with the regression coefficients determined by the parameters of the bivariate normal distribution, as follows:

$$b = \rho \frac{\sigma_T}{\sigma_U},$$

where σ_T and σ_U are the standard deviations corresponding to tiger and prey densities, respectively; ρ is the correlation coefficient; and

$$a = \mu_T - b \mu_U,$$

where μ_T and μ_U are the means corresponding to tiger and prey, respectively. It follows that, conditional on U_j ,

$$T_j = A U_j^b \delta_j,$$

where δ_j is a mean one random variable and

$$A = \exp\left(a + (1 - \rho^2)\sigma_T^2/2\right).$$

Thus the model corresponds to our *a priori* prediction of the relation between tiger and prey density, with $A = 0.002$ and $b = 1$. Because we express tiger density as animals per 100 km² and prey density as animals per km², we actually predict $A = 0.2$.

We fitted this model by means of a hierarchical Bayesian analysis (31–33) based on estimates \hat{T}_j and \hat{U}_j and their estimated standard errors \hat{S}_{T_j} and \hat{S}_{U_j} . We treated the density estimates as normally distributed and unbiased. In a preliminary analysis, we treated the estimated standard errors as though they were true values, known without error. Subsequently, we investigated the effect of uncertainty in the estimated standard errors by supposing that the sampling distributions of the ratios

$$\frac{\hat{S}_{T_j}^2}{\hat{S}_{T_j}^2} \quad \text{and} \quad \frac{\hat{S}_{U_j}^2}{\hat{S}_{U_j}^2}$$

could be approximated by the distribution of a χ^2 random variable divided by its degrees of freedom (df). Jackknife analyses of the raw data suggested the use of df = 20 as a reasonable representation of the uncertainty in these estimates, specifying that there is an 80% chance that the estimated standard error is within 20% of the true value and a 95% chance that it is within 30% of the true value.

We used flat normal priors for the means μ_T and μ_U and a uniform prior on $[-1, 1]$ for ρ . Posterior distributions of parameters of interest were sampled by Markov chain Monte Carlo, implemented by using the program WINBUGS (34). Code and output are available at www.mbr-pwrc.usgs.gov/pubanalysis.

These analyses were based on data from 9 of the 11 surveyed sites, because there were *a priori* reasons (25) for our expectation that the other two sites would not conform to the model relationship. At Pench-MP, intensive poaching just before our survey was suspected to have depressed tiger densities below levels that could have been supported by the prey base. At

Table 1. Combined density estimates for principal ungulate prey species of tigers [$\hat{U}(S\hat{E}[\hat{U}])$] derived from line transect sampling at 11 ecologically diverse study locations in India and the corresponding tiger densities (T) predicted by the model

Location	Annual rainfall, mm	Forest type	Sampling effort, km	$\hat{U}(S\hat{E}[\hat{U}])$, nos. per km ²	(T), nos. per 100 km ²
Melghat	1,100	Dry forest	771	5.3 (0.76)	1.04
Tadoba	1,175	Moist and dry forest	1,088	13.1 (1.41)	2.61
Pench-MR	1,400	Moist forest	894	16.2 (2.72)	3.24
Bhadra	2,200	Moist forest	728	16.8 (1.75)	3.36
Panna	1,100	Dry forest	532	30.9 (1.49)	6.18
Bandipur	1,200	Moist and dry forest	476	35.2 (7.55)	7.04
Nagarahole	1,500	Moist forest	732	56.1 (3.95)	11.22
Kanha	1,500	Moist forest	476	57.3 (4.07)	11.46
Kaziranga	3,000	Alluvial grassland	158	58.1 (6.51)	11.62
Ranthambore	800	Dry forest	448	60.6 (3.44)	12.12
Pench-MP	1,400	Moist forest	517	63.8 (3.14)	12.76

Kaziranga, large predators other than tigers were virtually absent, leading to the expectation that tigers take a larger proportion of prey at that location and likely achieve higher densities relative to prey density there than at the other study sites.

Results

Prey Abundance. The composition of the ungulate prey assemblage varied among our study sites. The principal ungulate prey of tigers were: wild pig, *Sus scrofa* (11 sites); sambar, *Cervus unicolor* (10 sites); axis deer, *Axis axis* (nine sites); gaur, *Bos gaurus* (seven sites); muntjac, *Muntiacus muntjak*; and four-horned antelope, *Tetracerus quadricornis* (six sites each); nilgai, *Boselaphus tragocamelus* (five sites); barasingha, *Cervus duvacoeli*; and chinkara, *Gazella bennetti* (two sites each); wild buffalo, *Bubalus bubalis*; and hog deer, *Axis porcinus* (one site each).

The sampling effort involved walking a total distance of 6,820 km at 11 sites, resulting in detections of a total of 8,061 clusters of prey species. The estimated average probabilities for visual detection of prey in the sampled strip varied greatly among species and sites, ranging between 0.2 and 0.8, clearly showing the need for an estimation method such as distance sampling that could model and estimate these variations.

The estimates of combined wild ungulate densities at different sites ranged between 5.3 and 63.8 animals per km² (Table 1). The study areas in Kanha, Nagarahole, Pench-MP, Ranthambore, and Kaziranga had prior histories of effective protection from adverse human impacts such as livestock grazing and hunting. Although these sites varied ecologically, they supported comparable ungulate densities, which were substantially higher (56.1–63.8 ungulates per km²) than at other sites. The prey densities at Panna (30.9 ungulates per km²) and Bandipur (35.2 ungulates per km²) appeared to be lower because of less effective protection mechanisms. Ungulate densities at comparably productive sites at Bhadra (16.8 ungulates per km²), Tadoba (13.1 ungulates per km²), Pench-MR (16.2 ungulates per km²), and Melghat (5.3 ungulates per km²) appeared to be well below their potential capacity, because of adverse anthropogenic impacts from several villages located within these reserves. Thus, a combination of both natural and anthropogenic factors produced a >10-fold difference in densities of wild ungulates across the 11 sites, providing a range of ecological conditions under which our model could be tested.

Tiger Population Size and Density. We invested a total effort of 8,677 camera trap-days at 11 sites, photo-capturing 167 individual tigers. We could clearly identify individual tigers from their photographs based on differences in the shape and arrangement of stripes on their flanks, limbs, and faces (Fig. 1). The number of individual tigers photo-captured (denoted as M_{t+1}) varied

from a minimum of five tigers in Pench-MP to a maximum of 26 in Kanha. The effectively sampled areas at each site were estimated based on distances between multiple captures of the same individuals, as described in *Materials and Methods*. The camera trapping data are reported in Table 2.

We constructed capture histories for individual tigers photographed at each site and analyzed these histories using the program CAPTURE (25–29). Closure test statistics provided little evidence that these tiger populations violated the assumption of closure during our surveys. Among the eight possible models of the underlying capture–recapture process likely to have gener-

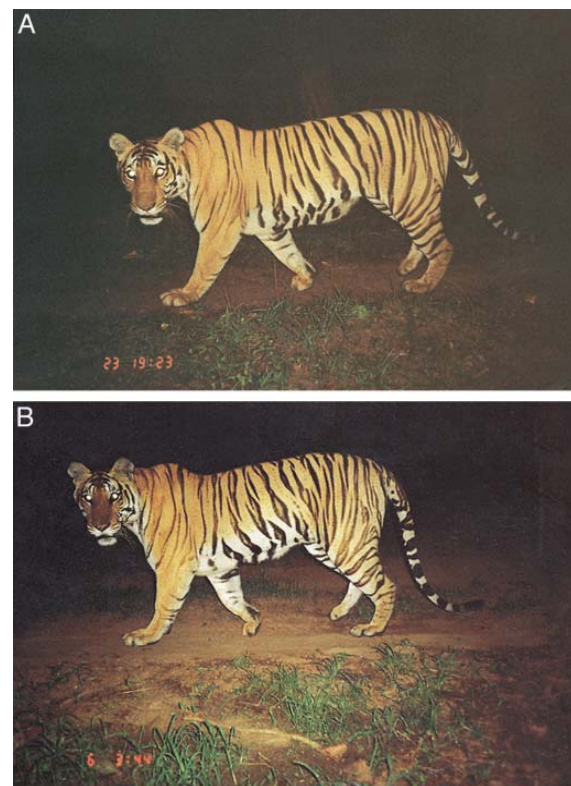


Fig. 1. Individual identification of tigers from differences in stripe patterns, exemplified by photographs of two different animals in A and B.

Table 2. Estimates of tiger densities derived from photographic capture–recapture sampling at 11 study locations in India

Location	C (trap-days)	$\hat{A}(\hat{w})$, km ²	M_{t+1}	$\hat{\rho}$	$\hat{N}(\hat{SE}[\hat{N}])$	$\hat{D}(\hat{SE}[\hat{D}])$, tigers per 100 km ²
Tadoba	706	367	10	0.174	12 (1.97)	3.27 (0.59)
Bhadra	587	263	7	0.220	9 (1.93)	3.42 (0.84)
Pench-MP	788	122	5	0.220	6 (1.41)	4.94 (1.37)
Melghat	896	360	15	0.058	24 (6.09)	6.67 (1.85)
Panna	914	418	11	0.039	29 (9.65)	6.94 (3.23)
Pench-MR	715	274	14	0.108	20 (4.41)	7.29 (2.54)
Ranthambore	840	244	16	0.115	28 (7.29)	11.46 (4.20)
Kanha	803	282	26	0.180	33 (4.69)	11.70 (1.93)
Nagarahole	938	243	25	0.120	29 (3.77)	11.92 (1.71)
Bandipur	946	284	16	0.055	34 (9.9)	11.97 (3.71)
Kaziranga	544	167	22	0.190	28 (4.51)	16.76 (2.96)

The count statistics and parameter estimates reported are as follows: sampling effort (C), estimated area sampled [$\hat{A}(\hat{w})$], number of photo-captured tigers (M_{t+1}), average estimated capture probability per sample ($\hat{\rho}$), estimated tiger population size $\hat{N}(\hat{SE}[\hat{N}])$, and density $\hat{D}(\hat{SE}[\hat{D}])$.

ated the capture histories we observed, model M_h seemed most appropriate for our data based on results of the various between-model tests and the overall discriminant function for model selection (27–29). The jackknife estimator under model M_h is known to be statistically robust relative to other available estimators (26, 27). Therefore, we used the jackknife estimator for model M_h (27), which permits each individual to have a different capture probability.

The capture–recapture analysis showed that average capture probability per sampling occasion estimated under model M_h varied widely among study sites ($\hat{\rho} = 0.039–0.220$, Table 2). The overall probabilities of photo-capturing tigers present at the study sites were computed as M_{t+1}/\hat{N} . These estimates were not only <1 at each site but also varied substantially among sites (0.38–0.86), once again highlighting the need for models that incorporate variable detection probabilities. Estimated tiger densities differed across the study sites, ranging from a low of 3.27 animals per 100 km² at Tadoba to a high of 16.76 tigers per 100 km² at Kaziranga (Table 2).

Relationship Between Prey Density and Tiger Density. The model we fitted implies that, conditional on U_j ,

$$T_j = AU_j^b \delta_j$$

where δ_j is a mean one random variable. Our *a priori* prediction was that $A = 0.2$ and $b = 1$. In a preliminary analysis in which standard errors were treated as known values, we obtained a Bayesian estimate (posterior mean) of $\hat{b} = 0.503$, with 95% credible interval (0.006, 0.982), providing some evidence against our prediction. Subsequent analyses accounting for sampling variation in the estimated standard errors led to a point estimate of $\hat{b} = 0.514$, with 95% credible interval (0.001, 1.009). Fig. 2A displays the mean prediction and 95% prediction intervals for tiger density and prey density based on this latter analysis. Point estimates (\hat{U}_j, \hat{T}_j) are plotted with 75% confidence ellipses and connected to posterior mean values of the pairs (U_j, T_j).

The evidence, although suggestive that $b < 1$, is not conclusive against our prediction. We thus fitted a reduced model with $b = 1$; this was accomplished by retaining the uniform prior on ρ and flat inverse γ prior on σ_T^2 and calculating $\sigma_U = \rho\sigma_T$. Under this reduced model, the posterior mean for A was 0.247, with 95% credible interval (0.181, 0.336), a result entirely consistent with our prediction. Fig. 2B reproduces Fig. 2A but with results for the reduced model.

As noted in *Materials and Methods*, the density estimates for two sites, Pench-MP and Kaziranga, were not included in the analyses displayed in Fig. 2 for reasons identified *a priori*. Indeed,

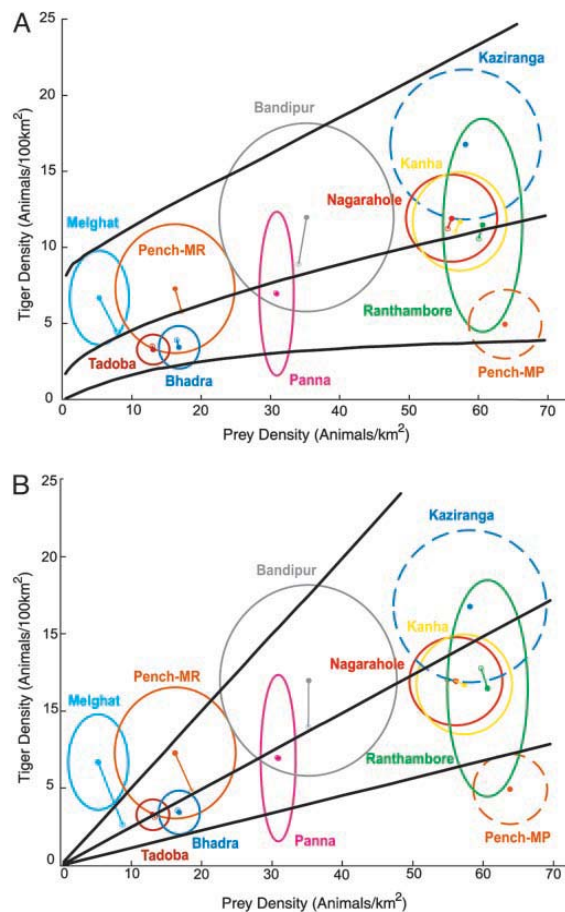


Fig. 2. Mean prediction and 95% prediction intervals for tiger density (animals per 100 km²), given prey density (animals per km²), based on the Bayesian analysis of the unrestricted model with no constraints on b (A) and the restricted model with $b = 1$ (B). The point estimates of densities (\hat{U}_j, \hat{T}_j) are plotted (solid dots) with 75% confidence ellipses, and connected to posterior mean values of the pairs (U_j, T_j ; open dots). Two data points omitted from analysis are indicated by confidence ellipses using dashed lines.

the density estimates for one of these sites, Pench-MP, fall outside the 95% prediction intervals of Fig. 2B. Estimates from one other site, Melghat, also fall outside the prediction interval of Fig. 2B. Although we made no *a priori* prediction of unusually high tiger density at Melghat, we speculate that this may be partially explained by the presence of large numbers of alternate prey in the form of livestock at this site.

Discussion

In general, the ability of our model to predict tiger densities from prey abundance was good. We consider our simple macroecological hypothesis to have been generally corroborated by these data, although there is some uncertainty associated with the exact form of the relationship (Fig. 2), as well as some additional variation in tiger densities beyond that explained by our model. As noted in the Introduction, we believe that two aspects of our study distinguish it from other types of macroecological analyses, and that these aspects merit brief discussion. First, we developed our predictions *a priori* based on simple mechanistic modeling (35) combined with empirical work on the focal species of interest. Despite the straightforward simplicity of identifying potential limiting factors and using these to predict abundance of a focal species, successful applications of this approach are rare in macroecological studies. Much of current macroecological work is not focused on potential limiting factors but instead attempts to take advantage of various landscape-level covariates available to the analyst.

The second characteristic distinguishing this work from many other macroecological studies involves the estimation of animal density. Such estimation is a nontrivial task on which statisticians and population biologists have expended substantial effort developing appropriate methods (9–11, 22, 24, 27, 29, 30, 36). As noted, many macroecological studies are based on indices, count statistics thought to be related to abundance or density through a proportionality constant that holds over space, time, and species (9–11, 36). Whenever the assumed relationship does not hold, that is, whenever the average fraction of animals counted is not a constant over time, space, and species, inferences about variation in abundance are confounded by potential variation in

sampling and detection probabilities. We estimated the animal population parameters of interest using methods that are specifically tailored to deal with variation in detection probabilities associated with our count statistics (9–11, 22, 27).

A recent discussion (3) of important unanswered questions in ecology emphasized the small spatial scale at which much serious ecological research is conducted. Although our large spatial scale approach required substantial field effort, it resulted in robust density estimates of multiple species of mammals at 11 locations throughout India. This study demonstrates the potential for carrying out ecological studies at landscape scales with a degree of rigor that usually characterizes only studies of small organisms conducted at small spatial scales. We hope that greater attention directed at developing models and associated predictions and at estimating relevant quantities with which to confront these predictions will permit more rapid advances in ecology.

From a conservation perspective, our study supports the hypothesis that prey density is a key determinant of large felid abundance (20, 25, 26). Although Bhadra, Tadoba, Melghat, and Pench-MR are ecologically similar to some of the high-tiger-density sites, during historical times, tiger densities at these sites appear to have readjusted downwards in response to human-induced depression of prey densities. Our results are consistent with the hypothesis that declines of wild tiger populations are primarily a consequence of prey depletion driven by adverse human impacts (21). Therefore, reducing these impacts through appropriate management interventions should be a central concern of conservationists.

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- Andrewartha, H. G. & Birch, L. C. (1972) in *The Distribution and Abundance of Animals* (Univ. Chicago Press, Chicago), p. 782.
- Krebs, C. J. (2002) in *Ecology: The Experimental Analysis of Distribution and Abundance* (Prentice-Hall, Upper Saddle River, NY), p. 608.
- May, R. (1999) *Philos. Trans. R. Soc. London B* **354**, 1951–1959.
- Brown, J. H. (1995) in *Macroecology* (Univ. Chicago Press, Chicago), p. 269.
- Rosenzweig, M. L. (1995) in *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, U.K.), p. 436.
- Keitt, T. H. & Stanley, H. E. (1998) *Nature* **393**, 257–260.
- Hubbell, S. P. (2001) in *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ. Press, Princeton), p. 375.
- Carbone, C. & Gittleman, J. L. (2002) *Science* **295**, 2273–2276.
- Yoccoz, N. G., Nichols, J. D. & Boulinier, T. (2001) *Trends Ecol. Evol.* **16**, 446–453.
- Pollock, K. H., Nichols, J. D., Simons, T. R., Farnsworth, G. L., Bailey, L. L. & Saur, J. R. (2002) *Environmetrics* **13**, 105–119.
- Williams, B. K., Nichols, J. D. & Conroy, M. J. (2002) in *Analysis and Management of Animal Populations* (Academic, San Diego), p. 817.
- Sinclair, A. R. E. (1989) in *Ecological Concepts*, ed. Cherratt, M. (Blackwell Scientific, Oxford), pp. 197–241.
- Murdoch, W. W. (1995) *Ecology* **75**, 71–87.
- Turchin, P. (1995) in *Population Dynamics: New Approaches and Synthesis*, eds. Cappuccino, N. & Price, P. W. (Academic, San Diego), pp. 19–40.
- Fretwell, S. D. (1972) in *Populations in a Seasonal Environment* (Princeton Univ. Press, Princeton), p. 217.
- Hairston, N. G., Smith, F. E. & Slobodkin, L. B. (1960) *Am. Nat.* **94**, 421–425.
- Karanth, K. U. & Sunquist, M. E. (1995) *J. Anim. Ecol.* **64**, 439–450.
- Karanth, K. U. & Sunquist, M. E. (2000) *J. Zool. London* **250**, 255–265.
- Seidensticker, J. (1976) *Biotropica* **8**, 225–234.
- Schaller, G. B. (1972) in *The Serengeti Lion: A Study of Predator-Prey Relations* (Univ. Chicago Press, Chicago), p. 480.
- Karanth, K. U. & Stith, B. M. (1999) in *Riding the Tiger: Tiger Conservation in Human Dominated Landscapes*, eds. Seidensticker, J., Christie, S. & Jackson, P. (Cambridge Univ. Press, Cambridge, U.K.), pp. 100–113.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. (2001) in *Introduction to Distance Sampling: Estimating Abundance of Biological Populations* (Oxford Univ. Press, Oxford), p. 432.
- Thomas, L. & Karanth, K. U. (2002) in *Monitoring Tigers and Their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia*, eds. Karanth, K. U. & Nichols, J. D. (Centre for Wildlife Studies, Bangalore, India), pp. 121–138.
- Thomas, L., Laake, J. L., Strindberg, S., Marques, F. F. C., Borchers, D. L., Buckland, S. T., Anderson, D. R., Burnham, K. P., Hedley, S. L. & Pollard, J. H. (2001) *DISTANCE User's Guide* (Research Unit for Wildlife Population Assessment, Univ. of St. Andrews, St. Andrews, U.K.), Ver. 4.0, p. 185.
- Karanth, K. U. & Nichols, J. D. (1998) *Ecology* **79**, 2852–2862.
- Nichols, J. D. & Karanth, K. U. (2002) in *Monitoring Tigers and Their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia*, eds. Karanth, K. U. & Nichols, J. D. (Centre for Wildlife Studies, Bangalore, India), pp. 121–138.
- Otis, D. L., Burnham, K. P., White, G. C. & Anderson, D. R. (1978) *Wildl. Monogr.* **62**, 1–135.
- Karanth, K. U., Kumar, N. S. & Nichols, J. D. (2002) in *Monitoring Tigers and Their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia*, eds. Karanth, K. U. & Nichols, J. D. (Centre for Wildlife Studies, Bangalore, India), pp. 139–152.
- Rexstad, E. & Burnham, K. P. (1991) in *User's Guide for Interactive Program CAPTURE* (Colorado State University, Fort Collins), p. 29.
- Wilson, K. R. & Anderson, D. R. (1985) *J. Mammal.* **66**, 13–21.
- Link, W. A., Cam, E., Nichols, J. D. & Cooch, E. G. (2002) *J. Wildl. Manage.* **66**, 277–291.
- Clark, J. S. (2003) *Ecology* **84**, 1370–1381.
- Wikle, C. K. (2003) *Ecology* **84**, 1382–1394.
- Spiegelhalter, D., Best, N. & Lunn, D. (2003) *WINBUGS User Manual* (MRC Biostatistics Unit, Cambridge, U.K.), Ver. 1.4, p. 60.
- Schoener, T. W. (1986) *Am. Zool.* **26**, 81–106.
- Seber, G. A. F. (1982) in *The Estimation of Animal Abundance and Related Parameters* (MacMillan, New York), p. 654.

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Photographic Sampling of Elusive Mammals in Tropical Forests

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Tropical forests harbor much of the planet's terrestrial biodiversity (Terborgh 1992; WCMC 1992), including many threatened mammal species. However, many tropical forest mammals naturally occur at low densities because of traits such as large body size, specialized diets, or spatially dispersed social structures (Eisenberg 1981). Among these, rodents and carnivores tend to be especially elusive because of their nocturnal and secretive behaviors. Many tropical mammals have now become even more rare and elusive due to excessive hunting (Robinson and Bennett 2000) and other anthropogenic pressures (Karanth 2002). Therefore, understanding the ecology of elusive tropical mammals and monitoring their populations are critical conservation needs. In addressing these challenges, biologists have only recently started to employ modern animal population sampling methods.

Animal sampling programs throughout the world typically focus on estimation of one or more "system state variables" (e.g., population size; Williams et al. 2002) at different points in space and/or time. Monitoring programs are frequently developed with the intention of drawing inferences about variation of such quantities over time, space, and associated environmental and management variables.

In this chapter we outline a conceptual framework for animal sampling that includes discussion of underlying rationale (why sample), selection of state variables (what to sample), and general estimation principles (how to sample). We then discuss some of the special challenges presented by elu-

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sive tropical mammals and stress the importance of these questions in such sampling situations. Here, we particularly focus on the new remote photographic sampling techniques (Karanth and Nichols 1998; O'Brien et al. 2003) that are increasingly being employed in studies of tropical mammals.

Sampling Animal Populations: General Principles

Many existing programs for sampling animal populations, particularly those targeting rare tropical mammals, are not as useful as they might be because investigators do not devote adequate thought (see Jenelle et al. 2002; Karanth et al. 2003) to fundamental questions associated with establishment of sound sampling programs (see reviews by Thompson et al. 1998; Yoccoz et al. 2001; Pollock et al. 2002). In this section, we present a brief outline of the sort of thinking that we believe should precede and underlie sound animal sampling programs by focusing on three basic questions.

Why Sample?

Efforts to sample animal populations are generally associated with one of two main classes of endeavor: science or conservation. When animal sampling is a component of a scientific research program, estimates of state variables (e.g., abundance) provide the means of confronting model-based predictions with measures of true system response (Hilborn and Mangel 1997; Nichols 2001; Williams et al. 2002). The differences between estimates and model-based predictions then form the basis for rejecting hypotheses in a hypothesis-testing framework or for updating model weights in a multiple-hypothesis framework.

Estimates of state variables for animal populations and communities serve three distinct roles in the conduct of wildlife conservation. First, estimates of system state (e.g., the number of animals) are needed to make state-dependent management decisions (e.g., Williams et al. 2002). Second, system state is frequently contained in the objective functions (explicit statements of management objectives, usually expressed in mathematical form) for managing animal populations and communities, and evaluation of the objective function is an important part of management, addressing the question "to what extent are management objectives being met?" Finally, effective management of wildlife requires either a single model thought to be predictive of system response to management actions or a

set of models with associated weights reflecting relative degrees of faith in the different models. The process of developing faith in a single model or weights for members of a model set involves the approaches described above as “science,” in which model-based predictions are evaluated with respect to estimated changes in state variables.

In summary, there are some very good reasons for sampling animal populations and communities to estimate relevant state variables. Our suggestion is simply that these reasons be made explicit before commencing a study and that the estimation of state variables be viewed not as an end in itself, but as a component of a larger process of either science or management.

What to Sample?

Certainly the selection of what state variable(s) to estimate will depend on the scientific or management objectives of the study. When dealing with single species, the most commonly used state variable is abundance or population size (sometimes expressed as density). Estimation of abundance frequently requires substantial effort, but it is a natural choice for state variable in studies of population dynamics and management of single-species populations. Study and management of single-species populations also focus on the vital rates responsible for state variable dynamics, such as survival, reproduction, immigration, and emigration.

For some purposes, a useful state variable in single-species population studies is occupancy, defined as the proportion of area, patches, or sample units that is occupied by the species (Mackenzie et al. 2002). Vital rates associated with this state variable are rates of local (patch) extinction and colonization.

When scientific or conservation attention shifts to the community level of organization, many possible state variables exist. The basic multivariate state variable of community ecology is the species abundance distribution, specifying the number of individuals in each species in the community. Many derived state variables are obtained by attributing different values or weights to individuals of different species (Yoccoz et al. 2001). A commonly used state variable is simply species richness, the number of species within the taxonomic group of interest that is present in the community at any point in time or space. Vital rates determining changes in richness are simply local probabilities of extinction and colonization (e.g., Boulinier et al. 1998a, 2001).

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The central point is that there is no single state variable that is preferred for the study of animal populations and communities. Instead, the selection of state variable should be closely tied to the objectives of the sampling programs, that is, the answer to the question, why sample?

How to Sample?

Reliable estimation of state variables and inferences about their variation over time and space require attention to two critical aspects of sampling animal populations—spatial variation and detectability (Lancia et al. 1994; Thompson et al. 1998; Yoccoz et al. 2001; Karanth and Nichols 2002). Spatial variation in animal abundance is relevant because investigators can seldom apply survey methods to every square meter of land in the area of interest. Instead, they must select a sample of locations to which survey methods are applied, and this selection must be done in such a way as to permit inferences about the locations that are not surveyed, and hence about the entire area of interest. Approaches to spatial sampling include simple random sampling, unequal probability sampling, stratified random sampling, systematic sampling, cluster sampling, double sampling, and various kinds of adaptive sampling (e.g., Cochran 1977; Thompson 1992).

Detectability refers to the fact that even in locations that are surveyed by investigators, it is very common for investigators to miss animals (i.e., animals go undetected). The investigator typically applies some survey method to each location that yields some sort of count statistic (number of animals seen, caught, harvested, photographed, etc.). Assume that the state variable of interest is abundance. Let N_{it} be the true number of animals associated with an area or sample unit of interest, i , at time t , and denote as C_{it} the associated count statistic. The count is best viewed as a random variable such that:

$$E(C_{it}) = N_{it} p_{it}, \quad (12.1)$$

where p_{it} is the detection probability (probability that a member of N_{it} appears in the count statistic, C_{it}). Estimation of N_{it} thus requires estimation of p_{it} :

$$\hat{N}_{it} = C_{it} / \hat{p}_{it}. \quad (12.2)$$

Typically, interest will not be in abundance itself but in relative abundance, the ratio of abundances at two locations ($\lambda_{ijt} = N_{it}/N_{jt}$), or in rate of population change, the ratio of abundances in the same location at two

times (e.g., $\lambda_{it} = N_{it+1}/N_{it}$). Sometimes count statistics are treated as indices, and it is hoped that the ratio of count statistics can be used to estimate these abundance ratios. For example, consider the estimator $\hat{\lambda}_{it} = C_{it+1}/C_{it}$. The expectation of this estimator can be approximated using equation (12.1) as:

$$E(\hat{\lambda}_{it}) \approx \frac{N_{it+1}p_{it+1}}{N_{it}p_{it}}. \quad (12.3)$$

As can be seen from equation (12.3), if the detection probabilities are very similar for the two sample times, then the estimator will not be badly biased, but when detection probabilities differ, then the estimator will be biased. If detection probability itself is viewed as a random variable, then we still require $E(p_{it}) = E(p_{it+1})$. Thus, we conclude that estimation of both absolute and relative abundance requires information about detection probability (also see Lancia et al. 1994; Karanth and Nichols 2002; Williams et al. 2002).

Sampling Tropical Forest Mammals: Ecological and Practical Issues

Because of their sensory acuity and evasive behavior, several tropical forest mammals (e.g., carnivores) usually cannot be surveyed by using methods based on visual detections like distance sampling (Buckland et al. 2001). Some other groups, such as ungulates or primates that are amenable to visual detection, may occur in dense cover or at low densities such that survey effort required (time invested or distances covered) to achieve adequate numbers of detections may be impractical. Often, because of prevailing social, environmental, and logistical constraints in tropical regions, investigators cannot employ potentially useful sampling approaches that involve animal-handling, such as radio-tagging (White and Garrott 1990) or traditional mark-recapture methods (Lancia et al. 1994; Thompson et al. 1998; Williams et al. 2002). Tropical biologists have tried to overcome these constraints by employing "camera-trapping" as an alternative, noninvasive sampling method for studying populations of rare and elusive animals.

Photographic Sampling of Animals

Cameras set in remote areas and activated by the animals themselves have been used to photograph mammals in tropical forests for many years

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(Champion 1927; McDougal 1977). However, the use of animal-activated cameras for wildlife research is somewhat more recent (e.g., Gysel and Davis 1956; Pearson 1959, 1960) and has become very popular in developed countries (Cutler and Swann 1999). Camera-traps have been increasingly used in the scientific study of elusive tropical mammals (Griffiths and van Schaik 1993; Karanth 1995; Karanth and Nichols 1998, 2002; O'Brien et al. 2003; Trolle and Kéry 2003) in recent years. Many such investigations are currently underway in Asia, Africa, and Latin America.

Photographs as Count Statistics

As noted earlier on the "how" of animal sampling, inferences about animal populations and communities are virtually always based on some sort of count statistic. In situations where individual animals can be identified from photographs, camera-trap studies can be designed and analyzed using methods used for conventional capture-recapture sampling (e.g., Karanth 1995; Karanth and Nichols 1998, 2002; Trolle and Kéry 2003). Such studies provide estimates of the state variable used most frequently in wildlife studies, abundance (or density).

When interest is focused on single species in cases where individuals cannot be identified from photographs, one option is to use camera-trap data to estimate occupancy as a state variable (e.g., see MacKenzie et al. 2002). The count statistic in this case would be the number of sample units (areas sampled by camera-traps) at which the species had been photographed and identified, and the quantity to be estimated would be the proportion of these units actually occupied by the species.

Finally, we note that interest may instead be directed at the community level of organization. In this case, species richness of some group of mammals may be the state variable of interest (Cam et al. 2002). The count statistic would be the total number of species identified from camera-trapping, and inference would require estimation about the proportion of species in the community that was actually detected.

Basics of Camera-Trapping

A camera-trap consists of an automated device that is activated when the targeted animal moves into range and triggers one or more previously positioned cameras to take pictures of that animal. Usually several traps are deployed based on various design considerations. The equipment used

can take a variety of forms ranging from cheap homemade pressure-pad devices to expensive, sophisticated commercial units (Cutler and Swann 1999; Karanth et al. 2002). The sampling process consists of deploying a number of camera-trap units in the surveyed area in a manner most conducive to obtaining photographs of the target species. Usually, the investigator periodically revisits and checks the traps to ensure their proper functioning and to replenish film or batteries.

PHOTOGRAPHIC IDENTIFICATION OF "CAPTURED" ANIMALS

For community-level surveys of mammal species richness or for single species surveys designed to estimate habitat occupancy or to derive an index of relative abundance, the photographs obtained must be of adequate quality to unambiguously identify the animal species. The choice of trap sites and the positioning of cameras are governed by this need. In community-level surveys of mammals, because of inter-specific differences in size, grouping patterns, and behavior, the positioning and spacing of camera-traps involves a compromise among competing needs for optimally photo-capturing different species. Consequently, some species in the surveyed area may have capture probabilities that approach zero, a situation analogous to the "hole in the sampled area" problem (Karanth and Nichols 1998) encountered in single species capture-recapture studies. The design of community-level camera-trap studies should thus focus on attaining nonzero detection probabilities for all of the species in the community, guild, or taxonomic group of interest.

In studies that try to estimate abundance or density of a single species, camera-traps must yield high quality pictures that permit identification of individual animals. Naturally occurring marks on animals, such as the shape, arrangement, and patterns of stripes (tigers *Panthera tigris*), spots (cheetahs *Acionyx jubatus*), or rosettes (jaguars *Panthera onca*, leopards *Panthera pardus*, and ocelots *Felis pardalis*); the shape and configuration of body parts such as head, tusks, and ears (elephants *Elephas maximus*, *Loxodonta africana*, skin folds (Javan rhinos *Rhinoceros sondaicus*), and even injuries and scars (manatees *Trichechus* spp.) can be used to identify individuals. In a few cases, it may be possible to first physically capture the animals and artificially mark individuals for photographic identification in subsequent samples.

Because natural markings on animals are asymmetric, unambiguous individual identifications may necessitate photographs of both flanks, requiring the deployment of two or more cameras with each trap. Unfor-

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tunately, investigators sometimes deploy single cameras to cut costs, thereby losing scarce data as well as diminishing the ability to apply powerful capture-recapture analytic methods to photographic count statistics.

EQUIPMENT AND DATA COLLECTION PROTOCOLS

Although homemade camera-traps can be constructed inexpensively, we do not recommend them for surveys of rare and elusive mammals because of their low reliability. Some of the commercial units are listed in publications (e.g., Karanth and Nichols 2002:187–188), and Web sites evaluate relative merits of different units (e.g., www.jesseshuntingpages.com/cams.html).

Most commercial camera-traps employ either “active” or “passive” tripping devices to fire the cameras. Active devices respond to an animal intercepting an electronic beam, whereas passive ones are triggered by the animal’s body heat (Karanth and Nichols 2002). The more sophisticated (and expensive) camera-trap equipment permits the investigators to target their study species using several means: firing multiple cameras with a single tripping device; varying the period of beam-breakage to avoid smaller creatures; varying the interval between consecutive pictures; electronically “waking up” cameras that “sleep” in battery-saving mode; setting specific “time zones” for picture-taking to avoid undesirable species, and electronically storing the date and time for each tripping event.

Most currently available camera-traps use flashlight photography and capture images on ordinary film. However, new equipment that offers digital image capture, infrared photography that avoids flash, and even video-capture of images is now on the market. Whatever the type of equipment employed, it is critically important to ensure that each picture obtained on a film roll (or disk or videotape) is given a unique identification number and that subsequent data collection and film processing protocols permit clear, unambiguous identification of the time, date, and location for any photographic capture event. We recommend using predesigned data forms (Karanth and Nichols 2002:183) to ensure that different field personnel obtain capture records in a consistent manner.

ENVIRONMENTAL AND SOCIAL FACTORS AFFECTING CAMERA-TRAP SURVEYS

In addition to ecology and behavior of study species, several environmental and social factors impose constraints on camera-trap surveys in the tropics. Commonly, rain and humidity restrict the work to certain seasons. Under humid conditions, camera-traps that rely on passive detection gen-

erally appear to perform more reliably than the more sensitive, active detection units (Kawanishi 2002).

In some cases, animal damage poses a threat to equipment. We found that elephants frequently damaged the equipment, and tigers did so occasionally. More often, human vandalism and theft are deterrents. Provision of a steel protective shell around the camera-trap (Karanth and Nichols 2002:184–186), locking devices, or cryptic hiding of the equipment are possible countermeasures against these problems.

Photographic sampling of rare mammals is usually conducted at landscape scales and over difficult terrain. Deployment of traps according to a predetermined survey design usually involves moving equipment over long distances, often on foot. This disadvantage is sometimes offset by the ready availability of inexpensive labor in the tropics. In many areas, camera-traps can be revisited only after several days. Locally hired labor may not have the skills necessary to record data or check the equipment, requiring the presence of the investigator even for routine revisits. The number of camera-traps deployed, the trap spacing used, the duration of the sampling periods, and consequently, the quality of the data obtained in camera-trap surveys, are thus influenced strongly by a variety of environmental and social factors.

Modeling and Estimation Using Photographic Data

This section describes how photographic count statistics on tropical forest mammals can be used to estimate state variables and rates of change in these variables. We will not present all of the relevant estimators or present their underlying rationale. Instead, we will point to literature with descriptions of these approaches and indicate how we believe these approaches might be used in camera-trap studies of tropical forest mammals.

Estimation of Abundance and Density

The appropriate methods for abundance estimation differ, depending on whether or not animals can be individually identified. For species and situations in which individuals cannot be identified, it may be possible to use the occupancy approach (Royle and Nichols 2003; also see next section) to draw inferences about abundance.

In some situations with no individual identification, it may be reasonable to use the count statistics as indices of relative abundance for compar-

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ing abundance at different times or locations. The reasonableness of such direct use of count statistics depends on the relationship between the counts and the true quantities of interest—abundances at the different times and places (Nichols and Karanth 2002). For example, if counts are related to abundance by a proportionality constant, such as detection probability in equation (12.1), then reasonable inference about relative abundance is possible only when that constant is very similar for the two times or locations being compared (see equation (12.3) and related discussion). Use of counts (trapping rates) as indices to abundance is thus based on restrictive, untested assumptions.

Given the above, when identification of individual animals is possible from photographs, capture-recapture models developed for closed populations provide a more robust approach to abundance estimation. Thus, there is little justification for conducting camera-trap surveys that generate only indices of abundance (e.g., some studies cited by Carbone et al. 2001). Instead it is preferable to compute estimates based on appropriate capture-recapture methods, because resources invested tend to be comparable in the two cases.

Under a capture-recapture sampling design, camera-traps are set throughout an area of interest, with attention devoted to eliminating holes—areas within the overall area of interest within which an animal might travel normally and never encounter a camera-trap (Karanth and Nichols 1998; Nichols and Karanth 2002; Karanth et al. 2004). If the investigators (or field assistants) have prior knowledge of habits and behavior of the target species, it is wise to use this knowledge in the deployment of camera-traps. For example, telemetry and sign studies clearly indicate the preference of tigers for traveling along trails and roads, so allocation of trap stations to trail or road systems is a reasonable means of sampling an area to get larger numbers of captures (Karanth et al. 2002). Placing camera-traps at mineral licks, water holes, animal latrines, bait stations, etc., may also increase capture probabilities and thereby improve the quality of the estimates.

If nothing is known about the habits of the target species, random allocation of traps, for example, using a grid system imposed on the study area, provides a reasonable means of sampling, although numbers of captures may be so low as to severely limit utility of results. The overall objective of the trap deployment should be that all individuals in the sampled area have nonzero probabilities (hopefully, similar across individuals) of encountering a camera-trap.

The most straightforward design involves setting camera-traps throughout the area of interest as discussed above and collecting photographs for a short period (say 5–45 consecutive days, depending on the species of interest). However, because camera-traps are expensive, enough units may not be available for this approach. Therefore, it sometimes may become necessary to move the traps around the area of interest with a different set of locations being sampled during each time interval (see designs suggested by Nichols and Karanth 2002).

Camera-trap designs for individually identifiable animals should yield capture histories of individuals. Each capture history (one per individual) is simply a record of whether or not the animal was caught at each sampling period. If we let “0” indicate no capture and “1” denote capture, then history 001010 indicates an animal caught only in periods 3 and 5 of a 6-period study. Capture histories for all individuals caught at least once provide the data needed to estimate abundance and hence, the number of animals exhibiting a capture history of all 0’s (present in the sampled area but never caught).

The statistical models that have been most useful for such work are based on “closed” populations that do not change by birth, death, immigration, or emigration over the course of the sampling (Nichols and Karanth 2002). The closure assumption imposes the restriction that sampling be carried out over a sufficiently short time frame during which closure violations are not expected to occur. The various members of this class of models differ with respect to the incorporated sources of variation in detection probability. Otis et al. (1978) and White et al. (1982) provided classic descriptions of these models. Some more recent estimators and models also were summarized in Williams et al. (2002). Computer programs CAPTURE (Rexstad and Burnham 1991) and MARK (White and Burnham 1999) can be used to analyze capture history data and provide statistics useful in model selection as well as estimates of abundance.

In many cases density (number of animals per unit area), rather than abundance, is the quantity of interest. In such cases, it is necessary to estimate the area actually sampled by the camera-traps. This area will typically be larger than the area over which traps are actually spread. Estimation of the area sampled requires ancillary data from radio telemetry or distances between capture locations of camera-trapped animals (e.g., Wilson and Anderson 1985; Nichols and Karanth 2002; Karanth et al. 2004).

In some cases, it will be possible to sample an area for some period each year (e.g., 4 weeks of camera-trapping each summer) for a number of

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years. Capture-recapture designs that include sampling at two different time scales are referred to as “robust designs” (Pollock 1982; Pollock et al. 1990; Williams et al. 2002). Within the robust design, sampling periods separated by relatively long time intervals (e.g., 1 year) are referred to as primary periods, whereas periods separated by relatively short intervals (e.g., 1 day or 1 week) are referred to as secondary periods. Capture history data can be aggregated across secondary periods and used to estimate survival rates between primary periods. Capture history data over secondary periods within primary periods can then be used to estimate abundance. Finally, resulting survival rate and abundance estimates can be used together to estimate recruitment. We have conducted such analyses for camera-trap data on tigers collected between 1991 and 2000 at Nagarahole Reserve, India (Karanth et al. in prep.).

We emphasize that the duration of the survey and sampling periods, the location, placement, and spacing of traps, etc., must be dictated by the ecology of the animal. Recommending standardized protocols for camera-trapping, regardless of species and ecological context (e.g., Fonseca et al. 2003), is likely to lead to violations of major capture-recapture assumptions (Otis et al. 1978; White et al. 1982; Nichols and Karanth 2002) related to population closure, nonzero capture probabilities for all animals, and even to a single animal population being sampled in the first place!

Estimation of Habitat Occupancy

When individual animals cannot be identified, patch occupancy estimation can be used to draw inferences about target species. Depending on the species and their habitats, occupancy survey designs might involve placing camera-traps systematically or randomly throughout an entire area of interest or over habitat patches or appropriate habitat in an area of interest. If habitat is patchy, patches themselves can be used as the sample units. If habitat is not found in discrete patches, sample units must be selected. In many cases, it will be sensible to simply select a grid cell size, place a grid over the area of interest, and randomly select cells to be sampled. In such situations, consideration should be given to the size of the sample unit (grid cell) relative to the individual range size of the target species. For example, if occupancy is to be used as a state variable in a monitoring program, it would not be reasonable to set sample unit size so small that a single animal could occupy many sample units. In the case of territorial species, use of appropriately sized grid cells (e.g., approximately the size of

the territory) might lead to occupancy estimates that could be interpreted as estimates of number of territorial animals.

In occupancy studies, identification of individuals is not assumed, and it is not necessary to deploy multiple cameras for unambiguous identification. Camera-traps should be deployed for a relatively short period of time (e.g., 2 weeks), as estimation of occupancy requires that the sampled locations be closed to changes in occupancy over the course of the sampling (i.e., animals do not move into the area and become established or depart the area permanently over the course of the sampling).

The data resulting from an occupancy study for a single season are detection histories (analogous to capture histories described above) for each sample unit. Detection histories are rows of 1's and 0's indicating days on which at least one individual of the species is or is not detected, respectively. For example, 0001000101, denotes a location at which the species was photographed on days 4, 8, and 10, by a camera left out for 10 days. Each sampled location has such a history. These detection histories differ from capture histories in that the number of locations at which no animals are detected (detection histories of all 0's) is known in occupancy studies. Detection probability is estimated from the patterns of detection and non-detection, at locations with at least one detection. The objective then becomes to estimate how many of these nondetection sites were actually occupied. The estimation thus explicitly accounts for the reality that non-detection does not equate to absence in so-called presence-absence (more properly "detection-nondetection") studies.

Detection history data are used to estimate the probability that a sample unit is occupied or, equivalently, the proportion of sample units occupied. This can be accomplished using a two-step approach that involves first estimating the number of sampled locations that are occupied and then dividing this estimate by the number of sampled locations (Nichols and Karanth 2002). A more efficient approach permits direct estimation of the occupancy parameter (MacKenzie et al. 2002; Royle and Nichols 2003; Chapter 8, this volume) in a single step. If the same locations are sampled with cameras each year, then the robust design approach can be used to estimate not only occupancy but also rate of change in occupancy over time and probabilities of local extinction and colonization of the sample units (Barbraud et al. 2003; MacKenzie et al. 2003). Programs PRESENCE (MacKenzie et al. 2002, 2003) and MARK (White and Burnham 1999) can be used to assist in model selection and to compute estimates of occupancy from detection history data.

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Although this statistical approach to occupancy estimation is relatively new, Kawanishi (2002) has already successfully used it with camera-trap data on tropical forest mammals. For example, she divided her study sites in Taman Negara, Malaysia, into 9 km² grid cells for the purpose of estimating occupancy for several mammal species. Using camera-trapping and surveys of secondary animal signs to assess occupancy, she computed a naive occupancy estimate of 0.36 (number of cells known to be occupied divided by the total number of cells) for sambar deer, *Cervus unicolor*, at her Merapoh study site. Using the approach of Nichols and Karanth (2002), however, she estimated that 0.64 ($\hat{SE} = 0.104$) of the grid cells were actually occupied by sambar. Although the differences between naive and estimated rates of occupancy computed by Kawanishi (2002) were not so large for all species, this example illustrates the potential importance of trying to properly account for detection probability in surveys of spatial distribution of tropical mammals.

Estimation of Species Richness

Instead of focusing on species-specific state variables such as occupancy and abundance, species richness within some group of mammals (e.g., ungulates, meso-carnivores) may be the target quantity for estimation in some studies. The sampling problem is that every species in the group may not be detected during survey efforts, and we would like a method that accounts for missed species. Spatial sampling and deployment of camera-traps will be similar to those used in occupancy studies. A key consideration in the design of community studies is that all of the species in the group of interest must have the potential to be detected. Single cameras are adequate, as animals must be identified to species only. Again, sampling should not extend over too long a period, because the mammal community is assumed to be closed over the period of sampling.

The data arising from a camera-trap study directed at species richness are detection histories for each species. Each detection history would indicate whether or not the species was detected at a sampling occasion. For example, assume that camera-traps were deployed for 10 consecutive nights. A history of 0011000101 would indicate a species that was detected on sample occasions 3, 4, 8, and 10, but not on other occasions. Each detected species has such a history. The different species are analogous to the different individuals in a standard capture-recapture setting. The patterns of detection and nondetection can thus be used to estimate species-

level detection probability, and hence total number of species (including those not detected), using the models developed for closed populations (e.g., Otis et al. 1978). Because of differences in detection probabilities of animals of different species, and because of different abundances that contribute to variation in detectability at the species level, we suspect that models permitting heterogeneity in detection probabilities will be especially useful (Burnham and Overton 1979; Boulinier et al. 1998b).

In addition to estimating species richness, if the same locations are sampled over time (e.g., every year), as in the robust design (Pollock 1982), resulting data can be used to estimate rate of change in species richness and temporal variation in richness, as well as local extinction probabilities and turnover (proportion of species that is new) (Boulinier et al. 1998a; Nichols et al. 1998). The Web-based program COMDYN was developed to estimate richness and associated community-dynamic parameters (Hines et al. 1999). Examples of use of this approach in community investigations include Boulinier et al. (2001), Cam et al. (2002), and Doherty et al. (2003). Most of the published uses involve avian point count data, but camera-trap data on rare tropical mammals are also certainly suitable for employing this capture-recapture-based approach to estimating species richness.

Discussion

We argue that photographic sampling provides a logistically reasonable approach to monitoring elusive mammals in tropical forests. In the first section of this chapter, we posed three questions relevant to any monitoring program—why monitor, what should be monitored, and how should one conduct monitoring? With respect to the why, we emphasized that monitoring is not a stand-alone activity to be considered in isolation but should instead be viewed as a component of a larger process, usually either science or management. The choice of state variable to monitor depends very heavily on the reason for the monitoring. We emphasized that the “how” of monitoring involves at least two important sources of uncertainty, spatial sampling and detectability. Spatial variation in state variables of interest dictates that sample units to be surveyed must be selected in a manner that permits inference about the sample units not selected. Detectability refers to the usual inability to detect all individuals in a sample area that is surveyed. Count statistics must be collected in such a way that the associated detection probability can be estimated.

Because of the difficulty of working with and viewing animals in trop-

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ical forests, remote camera-traps provide an attractive means of sampling animals. If abundance of animals is the state variable of interest and if the animals possess natural marks permitting individual identification, full-fledged capture-recapture models can be used to estimate abundance. The count statistics are the numbers of different animals detected, and the detection histories of individual animals provide the data needed to draw inferences about detection probability, and hence abundance.

In some cases, it may be reasonable to use habitat occupancy as the state variable of interest. In this case, the count statistic is the number of patches or sample units at which the mammal species of interest is detected, and detection histories of the sample units are used to draw inferences about detection probability.

In community-level studies of mammals, the state variable of interest may be the number of animals (species richness) in a certain size class or guild or taxonomic group. In such studies, the count statistic is the number of different species detected, and detection probability is estimated using detection histories of the different species.

For each of the above three possible state variables, if sampling is conducted at approximately the same time for each of a number of years or seasons, it is possible to use robust design approaches (Pollock 1982) to estimate not only the state variable of interest but also the vital rates governing changes in the state variable.

Camera-trap surveys of elusive mammals usually involve heavy investments of resources and effort. However, many camera-trap survey protocols currently being implemented or recommended appear to be based on ad hoc considerations (e.g., Fonseca et al. 2003) that are unlikely to yield scientifically defensible results. We believe that scientific and conservation values of camera-trapping studies of elusive tropical mammals can be enhanced substantially by paying closer attention to issues covered above.

REFERENCES

- Barbraud, C., J. D. Nichols, J. E. Hines, and H. Hafner. 2003. Estimating rates of extinction and colonization in colonial species and an extension to the metapopulation and community levels. *Oikos* 101:113–126.
- Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 1998a. Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proceedings of the National Academy of Sciences, U.S.A.* 95:7497–7501.
- Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology* 82:1159–1169.

Photographic Sampling of Elusive Mammals in Tropical Forests 245

- Boulinier, T., J. D. Nichols, J. R. Sauer, J. E. Hines, and K. H. Pollock. 1998b. Estimating species richness: The importance of heterogeneity in species detectability. *Ecology* 79:1018–1028.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, United Kingdom.
- Burnham, K. P., and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 62:625–633.
- Cam, E., J. D. Nichols, J. E. Hines, J. R. Sauer, R. Alpizar-Jara, and C. H. Flather. 2002. Disentangling sampling and ecological explanations underlying species-area relationships. *Ecology* 83:1118–1130.
- Carbone, C., S. Christie, K. Conforti, T. Coulson, N. Franklin, J. R. Ginsberg, M. Griffiths, J. Holden, K. Kawanishi, M. Kinnaird, R. Laidlaw, A. Lynam, D. W. MacDonald, D. Martyr, C. McDougal, L. Nath, T. O'Brien, J. Seidensticker, D. Smith, M. Sunquist, R. Tilson, and W.N. Wan Shaharuddin. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation* 4:75–79.
- Champion, F. W. 1927. *With a Camera in Tiger Land*. Chatto and Windus, London.
- Cochran, W. G. 1977. *Sampling Techniques*, 3rd ed. Wiley, New York.
- Cutler, T. L., and D. E. Swann. 1999. Using remote photography in wildlife ecology: A review. *Wildlife Society Bulletin* 27:571–581.
- Doherty, P. F., Jr., G. Sorci, J. A. Royle, J. E. Hines, J. D. Nichols, and T. Boulinier . 2003. From the cover: Sexual selection affects local extinction and turnover in bird communities. *Proceedings of the National Academy of Sciences, U. S. A.* 100:5858–5862.
- Eisenberg, J. F. 1981. *Mammalian Radiations*. University of Chicago Press, Chicago.
- Fonseca, G., T. E. Lacher, P. Batra, J. Sanderson, S. Brandes, A. Espinel, C. Kuebler, A. Bailey, and J. Heath. 2003. *Tropical Ecology, Assessment, and Monitoring: Camera Trapping Protocol* (Electronically published report). Center for Applied Biodiversity Science, Conservation International, Washington, D.C. Available from <http://teaminitiative.org> (accessed October 15, 2003).
- Griffiths, M., and C. P. van Schaik 1993. The impact of human traffic on the abundance and activity periods of Sumatran rainforest wildlife. *Conservation Biology* 7:623–626.
- Gysel, L. W., and E. M. J. Davis. 1956. A simple automatic photographic unit for wildlife research. *Journal of Wildlife Management* 20:451–453.
- Hilborn, R., and M. Mangel. 1997. *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, New Jersey.
- Hines, J. E., T. Boulinier, J. D. Nichols, J. R. Sauer, and K. H. Pollock. 1999. COMDYN: Software to study the dynamics of animal communities using a capture-recapture approach. *Bird Study* 46:S209–S217.
- Jenelle, C. S., M. C. Runge, and D. I. MacKenzie. 2002. The use of photographic rates to estimate densities of tigers and other cryptic mammals: A comment on misleading conclusions. *Animal Conservation* 5:119–120.
- Karanth, K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation* 71:333–338.
- _____. 2002. Nagarahole: Limits and opportunities in wildlife conservation. pp. 189–202 in J. Terborgh, C. P. Van Schaik, L. Davenport, and M. Rao, eds., *Making Parks Work: Strategies for Preserving Tropical Nature*. Island Press, Washington, D.C.

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- Karanth, K. U., N. S. Kumar, and J. D. Nichols. 2002. Field surveys: Estimating absolute densities of tigers using capture-recapture sampling. pp. 139–152 in K. U. Karanth and J. D. Nichols, eds., *Monitoring Tigers and Their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia*. Centre for Wildlife Studies, Bangalore, India.
- Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- _____, eds. 2002. *Monitoring Tigers and Their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia*. Centre for Wildlife Studies, Bangalore, India.
- Karanth, K. U., J. D. Nichols, N. S. Kumar, and J. E. Hines. In preparation. Assessing tiger population dynamics using photographic capture-recapture sampling.
- Karanth, K. U., J. D. Nichols, N. S. Kumar, W. A. Link, and J. E. Hines. 2004. Tigers and their prey: Predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences, U.S.A.* 101:4854–4858.
- Karanth, K. U., J. D. Nichols, J. Seidensticker, E. Dinerstein, J. L. D. Smith, C. McDougal, A. J. T. Johnsingh, R. Chundawat, and V. Thapar. 2003. Science-deficiency in conservation practice: The monitoring of tiger populations in India. *Animal Conservation* 6:141–146.
- Kawanishi, K. 2002. *Population Status of Tigers in a Primary Rainforest of Peninsular Malaysia*. Ph.D. Dissertation, University of Florida, Gainesville.
- Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. pp. 215–253 in T. Bookhout, ed., *Research and Management Techniques for Wildlife and Habitats*. The Wildlife Society, Bethesda, Maryland.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- McDougal, C. 1977. *The Face of the Tiger*. Rivington Books, London.
- Nichols, J. D. 2001. Using models in the conduct of science and management of natural resources. pp. 11–34 in T. M. Shenk and A. B. Franklin, eds., *Modeling in Natural Resource Management: Development, Interpretation, and Application*. Island Press, Washington, D.C.
- Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998. Estimating rates of local extinction, colonization and turnover in animal communities. *Ecological Applications* 8:1213–1225.
- Nichols, J. D., and K. U. Karanth. 2002. Statistical concepts: Estimating absolute densities of tigers using capture-recapture sampling. pp. 121–137 in K. U. Karanth and J. D. Nichols, eds., *Monitoring Tigers and Their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia*. Centre for Wildlife Studies, Bangalore, India.
- O'Brien, T., M. Kinnaird, and H. T. Wibisono. 2003. Crouching tigers, hidden prey: Sumatran tigers and prey populations in a tropical forest landscape. *Animal Conservation* 6:1–10.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1–135.

Photographic Sampling of Elusive Mammals in Tropical Forests 247

- Pearson, O. P. 1959. A traffic survey of *Microtus-Reithrodontomys* runways. *Journal of Mammalogy* 40:169–180.
- _____. 1960. Habits of *Microtus californicus* revealed by automatic photographic recorders. *Ecological Monographs* 30:231–249.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:757–760.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference from capture-recapture experiments. *Wildlife Monographs* 107:1–97.
- Pollock, K. H., J. D. Nichols, T. R. Simons, and J. R. Sauer. 2002. Large scale wildlife monitoring studies: Statistical methods for design and analysis. *Environmetrics* 13:1–15.
- Rexstad, E., and K. P. Burnham. 1991. *User's Guide to Interactive Program CAPTURE*. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins.
- Robinson, J. G., and E. L. Bennett, eds. 2000. *Hunting for Sustainability in Tropical Forests*. Columbia University Press, New York.
- Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84: 777–790.
- Terborgh, J. 1992. *Diversity and the Tropical Rainforest*. Freeman, New York.
- Thompson, S. K. 1992. *Sampling*. Wiley, New York.
- Thompson, W. L., G. C. White, and C. Gowan. 1998. *Monitoring Vertebrate Populations*. Academic Press, San Diego.
- Trolle, M., and M. Kéry. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *Journal of Mammalogy* 84:607–614.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. *Capture-recapture and Removal Methods for Sampling Closed Populations*. USDOE Report Number LA-8787-NERP, Los Alamos National Laboratory, Los Alamos, New Mexico.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival rate estimation from both live and dead encounters. *Bird Study* 46:S120–S139.
- White, G. C., and R. A. Garrott. 1990. *Analysis of Wildlife Radiotracking Data*. Academic Press, San Diego.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and Management of Animal Populations*. Academic Press, San Diego.
- Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy* 66:13–21.
- WCMC (World Conservation Monitoring Center). 1992. *Global Biodiversity: Status of the Earth's Living Resources*. Chapman and Hall, London.
- Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution* 16:446–453.

An ecology-based policy framework for human–tiger coexistence in India

K. ULLAS KARANTH AND RAJESH GOPAL

INTRODUCTION

Carnivores are in decline across the world for a variety of reasons, among which conflict with humans is the most predominant (Woodroffe 2000). This conflict takes varied forms and involves several carnivore species (see Treves and Karanth (2003) for a recent review). Mitigation of such conflicts should be the most important part of any conservation agenda that strives for continued coexistence of carnivores and humans. Among carnivore taxa, felids in the genus *Panthera* appear to be particularly conflict-prone (Rabinowitz 1986; McDougal 1987; Mishra et al. 2003; Ogada et al. 2003). How conservationists can promote the coexistence of *Panthera* cats and humans in densely populated countries such as India, or can generate potentially useful models for other regions of the world where human population densities and habitat fragmentation levels are relatively lower, but rising rapidly, are urgent problems.

The tiger (*Panthera tigris*) is a felid species of global concern because of its cultural and ecological significance (Jackson 1990; Karanth 2001; Thapar 2002). Over the last three decades, the Indian government has used the tiger as an effective flagship species to protect a wide range of biodiversity. Special tiger reserves have been established in different biomes across India covering mangrove swamps, alluvial grasslands and forests of the deciduous, semi-deciduous and evergreen types. However, India's wild tiger populations are still under serious threat from human impacts such as prey depletion, poaching, habitat loss and fragmentation (Karanth and Stith 1999; Seidensticker *et al.* 1999; Karanth 2003). Such proximate causal factors of tiger decline are ultimately driven by human demographic and resource consumption patterns that fuel expanding economic development.

Tigers are obligate predators of ungulates in the 20–1000-kg body mass category (Sunquist *et al.* 1999; Karanth 2003). Consequently, wherever wild tiger populations survive and interface with landscapes dominated by humans, they pose a threat by preying on livestock, and, less commonly, on people. Although the traditional social ethos in most parts of India is remarkably tolerant of wildlife damage compared with elsewhere (Rangarajan 2001), in conflict situations, local antagonism against tigers often erupts into a serious management problem.

Paradoxically, given the key demographic traits of tigers such as early reproduction, high fecundity, wide-ranging movements and territorial land tenure system (Sunquist 1981; Smith 1993; Chundawat *et al.* 1999; Karanth and Stith 1999; Karanth 2003), conflict with humans becomes an inevitable consequence of successful tiger population recoveries. Because of the tiger's endangered status, mitigation of these conflicts through traditional lethal control has become increasingly problematic.

A tiger management policy that aims to mitigate human–tiger conflicts must necessarily consider situation-specific details of how the needs of humans and tigers clash. How can one address the broader question of coexistence between people and tigers in India? Which of the two competing conservation paradigms (Robinson 1993) – ‘preservation’ or ‘sustainable use’ – is more appropriate for effectively addressing this issue? Among the wide array of conflict-mitigation tactics available to managers (Treves and Karanth 2003) – ranging from lethal control to strict preservation – which ones are most relevant to resolving conflicts in specific ecological and social contexts?

We explore the above questions in this case study. Our goal is to generate a policy framework to maintain demographically viable meta-populations of wild tigers across India's conservation landscapes, while trying to keep human–tiger conflicts within socially acceptable limits. In generating this policy framework, we have deliberately avoided delving into the political question of who should manage India's wildlife reserves: the official machinery as at present, or an alternate localized power structure (Kothari *et al.* 1995). We argue that, whoever is responsible for managing human–tiger conflicts, the factors we consider in our analysis are still relevant to promoting coexistence of humans and tigers.

PARADIGM SHIFTS IN TIGER MANAGEMENT

India's geographical area of 3.05 million km² supports a human population of over 1 billion. About 70% of this population is rural, with a majority depending on agriculture, animal husbandry and related occupations. Over

half the rural people are classified as poor, with typical wage rates being less than a US\$1 per day. Because of various cultural and social reasons, rural India supports about 450 million livestock – a large proportion of which are unproductive animals grazed on public lands for the primary purpose of producing dung applied to fertilize crops. Rural domestic energy needs are primarily met by burning wood, animal dung or other biomass. The collection of firewood from forests for sale in nearby villages and towns is a dominant form of rural occupation in many forested parts of the country (Agarwala 1985). All such extractive pressures have been driving the degradation of tiger habitats (Gee 1964; Schaller 1967; Karanth 2001; Madhusudan and Mishra 2003).

Consequent to the rapid expansion of agricultural areas, the remaining tiger habitat has shrunk and fragmented continuously over the last few centuries (Karanth 2001, 2003). In more recent times, economic development projects such as dams for irrigation and power generation, mines, and road and rail transportation have increased levels of fragmentation and facilitated the penetration of forces of modern commerce into relatively remote tiger habitats. At present forests potentially suitable for tigers cover about 300 000 km² (Wikramanayake *et al.* 1998) of India's land area, with perhaps half that extent actually harbouring tigers. This potential tiger habitat is patchy and restricted primarily to blocks of forests in the southwestern, central and northeastern parts of the country (Fig. 23.1).

Historically, tigers were widely distributed and viewed as threats to expansion of agriculture and rural livelihood (Karanth 2001; Rangarajan 2001) because of persistent tiger predation on humans and livestock. A compilation by McDougal (1987) showed that tigers killed 798 people in 1877 and 908 people in 1908 in the British-administered provinces of India. Consequently, tigers were simultaneously targeted both as dangerous vermin and desirable trophies (Rangarajan 2001).

The preferred mode of dealing with human–tiger conflicts was lethal control through intensive bounty and sport hunting. The scale of this lethal control effort can be gauged from examples such as the lifetime tallies of tigers hunted by 'sportsmen' like kings of Surguja and Udaipur that exceeded 1000 tigers (Schaller 1967). Even ordinary government officials shot tigers by the thousands. Such 'sportsmen' operated simultaneously with the even more numerous 'native poachers' using an array of devices such as muzzle-loaders, spears, nets, traps, snares and poisons to virtually eradicate wild tigers from large regions of India during the nineteenth and twentieth centuries. Rangarajan (2001) estimates that about 80 000 tigers were killed in India between 1875 and 1925.

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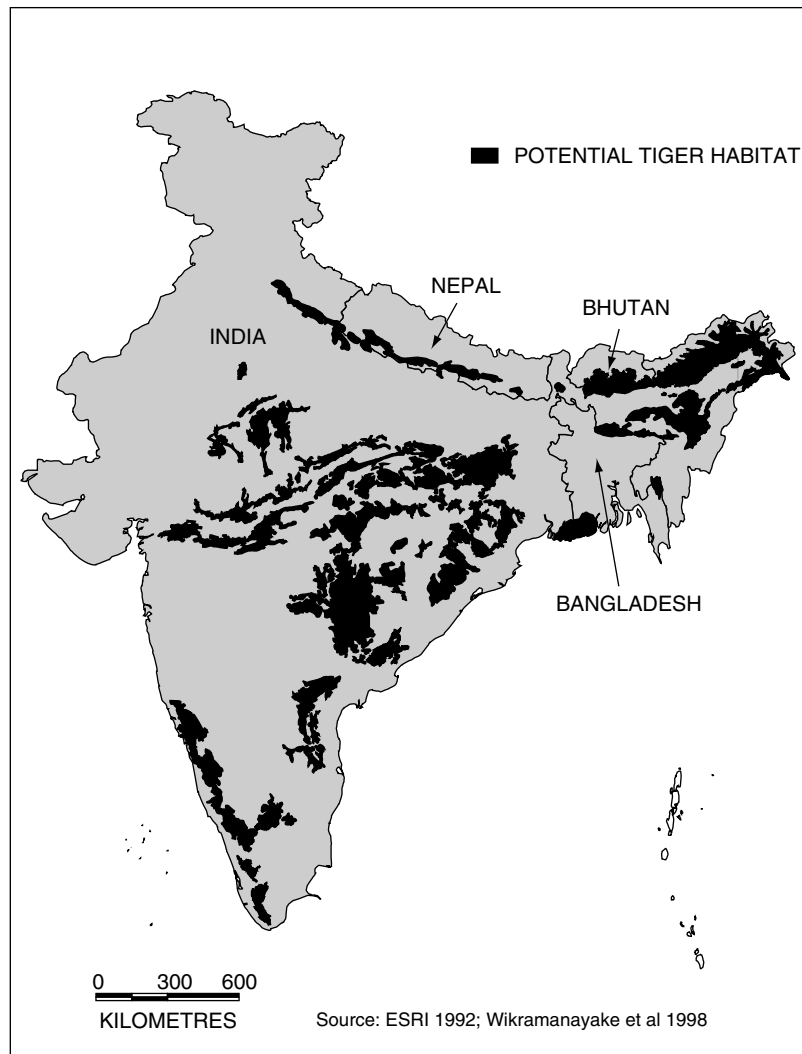


Figure 23.1. Potential tiger habitat in the Indian subcontinent.

By the late 1960s tigers were on the verge of extirpation in the remaining areas (Gee 1964; Schaller 1967). However, a remarkable policy turnaround occurred in the early 1970s, driven by pressure from conservationists. A committed political leadership introduced new initiatives that proscribed tiger hunting and established special protected reserves (Jackson 1990; Karanth 2001, 2003). The core of this new 'preservationist' strategy implemented within protected reserves included active patrolling to deter hunting

of tigers and their prey species, as well as habitat recovery measures such as curbs on human-induced forest fires, livestock grazing and harvest of forest products. In some cases, human settlements were also relocated from protected tiger reserves. Effective implementation of such measures in several reserves across the country led to significant recoveries of tiger populations in the 1970s and 1980s (Panwar 1987; Karanth *et al.* 1999; Karanth 2003).

After the 1990s, although the protectionist laws remained in place, their implementation slackened significantly because of several social factors (Karanth 2002, 2003). Driving this change was a shift from earlier ‘exclusionary’ conservation policies towards more ‘inclusive’ policies that de-emphasized law enforcement in favour of community development activities around tiger reserves (Mackinnon *et al.* 1999). *Prima facie*, these new approaches appear to have failed either to make conservation gains or to reduce local antagonism towards protected reserves (Karanth 2002; K. U. Karanth unpubl. data).

THE CURRENT STATUS OF HUMAN–TIGER CONFLICT

Although the extent of potential tiger habitat in India is still around 300 000 km² (Wikramanayake *et al.* 1998) (Fig. 23.1), the proportion of the habitat that can support adequate reproduction is perhaps only about 10% of this area, and lies mostly within protected nature reserves. Inside such reserves, superior habitat productivity, combined with reduced human impacts, has resulted in ungulate prey attaining high densities of 15–70 animals/km². Consequently, tiger densities are also high (5–20 tigers/100 km²: Karanth and Nichols 1998; Karanth *et al.* 2004). Stochastic simulation models of tiger populations (Kenny *et al.* 1995; Karanth and Stith 1999) show that such clusters of 12–25 breeding tigresses are demographically viable and may produce 10–15% annual ‘surpluses’.

The present distribution of tigers in India (Fig. 23.1) comprises several discrete meta-populations, embedded within larger landscape matrices made up of protected reserves, multiple-use forests and agricultural and urban areas (Karanth 2003). The protected reserves are essentially ‘sources’ for dispersing tigers that may survive for brief periods in the surrounding landscape matrix, before perishing from poaching or prey depletion. However, because of the tiger’s habitat specificity (requirements of cover, water, prey) even such transient tigers cannot survive over large parts of the country. As a consequence, conflict with humans is largely restricted to the edges of protected reserves, and some multiple-use forests or plantation crop areas.

Given the pattern of human population densities across India (Guha 2001) and the highly clumped distribution of tiger populations (Wikramanayake *et al.* 1998) (Fig. 23.1), the extent of area of conflict is relatively small. Such conflict zones perhaps cover less than 1% of India's geographical area, and involve an even smaller fraction of its human population. Therefore, in a macro-ecological sense, human-tiger conflict is a relatively localized management problem. However, by its very nature, the conflict poses a serious dilemma for conservationists trying to promote human-tiger coexistence. The conflict assumes the forms of killing of livestock, accidental killing of humans and even persistent predation on humans by tigers, all of which lead to retaliatory killings of tigers.

Tigers readily kill domestic ungulates (Table 23.1). Most such predation takes place inside government-owned forests or common pasturelands,

Table 23.1. Depredation on livestock by tigers and monetary compensation paid around Kanha tiger reserve, Madhya Pradesh, Central India between 1977 and 2001

Year (April to March)	Number of cattle kills	Compensation (current US\$)
1977-78	4	10
1978-79	7	41
1979-80	21	149
1980-81	26	307
1981-82	26	295
1982-83	22	242
1983-84	61	698
1984-85	80	1094
1985-86	45	545
1986-87	109	1419
1987-88	122	1483
1988-89	107	1009
1989-90	71	703
1990-91	63	859
1991-92	60	816
1992-93	38	425
1993-94	33	373
1994-95	22	360
1995-96	52	742
1996-97	40	570
1997-98	58	907
1998-99	131	2234
1999-00	117	2418
2000-01	129	4467
Total	1444	2216

where large numbers of livestock are grazed legally. Usually such livestock kills are not fully consumed by tigers, because herders intervene. In most multiple-use forests, densities of wild prey are low because of hunting and competition with livestock (Madhusudan and Karanth 2002; Madhusudan and Mishra 2003). In such situations tigers may take as much as 12% of the livestock herds annually (Madhusudan 2003).

Tiger depredations lead to retaliation through poisoning of carcasses and other forms of unsanctioned lethal control (Karanth 2003; Madhusudan and Mishra 2003). Organized criminals involved in the illegal trade in tiger body parts (Kumar and Wright 1999) exploit such conflicts by distributing poisons and traps to villagers, and buying tiger body parts from them. As a result, retaliatory killings often escalate into deliberate, market-driven poisoning of both natural and domestic animal kills. Kumar and Wright (1999) reported 123 tiger poaching cases in 44 months between 1994 and 1997. More recent data show that at least 41 tiger-poaching cases were detected during the year 2001. Both these figures are based on law-enforcement records, and total levels of poaching are probably much higher.

In most places, tigers are wary of human beings and avoid encounters. Accidental mauling or killing of humans by tigers is rare, and usually occurs when irate mobs surround tigers that enter human settlements to take livestock. Very rarely, tigers may maul or kill humans they unexpectedly encounter, and the tiger may sometimes eat a part of the cadaver. However, by no means all such encounters lead automatically to persistent predation on humans; hence many incidents may require no further management intervention than compensating the victim's relatives.

In rare cases, individual tigers begin to view human beings as a 'prey species' and persistently stalk them. Such man-eating behaviour, although rare, has been historically documented in several parts of India (McDougal 1987; Daniel 2001). The ecological and social factors that lead to man-eating are unclear, but appear to be influenced by scarcity of natural prey, injuries, transmission of man-eating behaviour from parent to offspring and the lack of effective retaliation following initial attacks on humans (McDougal 1987; Karanth 2001).

Man-eating behaviour is exhibited in an unusually persistent form among the tigers of the Sundarban delta of India and Bangladesh (McDougal 1987; Sanyal 1987; Daniel 2001). In these roadless mangrove forests partially submerged under tidal waters, thousands of people intrude on foot or in boats to collect a variety of forest products, wild honey and fish. Tigers of Sundarban opportunistically kill and eat these people, particularly when they are alone, in small groups or sleeping inside boats at night. Although no scientific data exist, tiger predation on humans in Sundarban

Table 23.2. *Incidental tiger attacks on humans (Kanha tiger reserve, Madhya Pradesh), typical of most areas of India, and records of persistent tiger predation on humans (Sundarban tiger reserve, Bengal) from 1985 to 2001*

Year (April–March)	Kanha			Sundarban		
	Injuries	Deaths	Total attacks	Injuries	Deaths	Total attacks
1985–86	0	0	0	6	32	38
1986–87	0	1	1	6	25	31
1987–88	1	1	2	7	21	28
1988–89	2	5	7	3	14	17
1989–90	1	2	3	2	9	11
1990–91	3	6	9	8	43	51
1991–92	3	3	6	7	38	45
1992–93	1	1	2	5	34	39
1993–94	1	0	1	4	31	35
1994–95	1	1	2	0	5	5
1995–96	1	0	1	0	4	4
1996–97	5	0	5	1	3	4
1997–98	1	0	1	2	5	7
1998–99	0	1	0	2	2	4
1999–00	3	0	3	0	13	13
2000–01	2	1	3	4	15	19

does not appear to be restricted to aberrant individuals as in other parts of tiger range. A substantial proportion of the tiger population appears prone to opportunistic predation on humans.

Sanyal (1987) reported that tigers killed 318 people in Indian Sundarban between 1975 and 1981. Although country-wide records of human fatalities caused by tigers are not available, we provide some data on accidental killings around Kanha reserve in Central India and persistent tiger predation on humans in Indian Sundarban in recent years (Table 23.2). These official figures may be underestimates, because of underreporting of the killing of persons engaged in clandestine activities, and of livestock being grazed illegally.

MITIGATING CONFLICT, FOSTERING COEXISTENCE

Wildlife management in India is carried out under legal provisions of the Wildlife Protection Act of 1972. This law was originally introduced to counter destruction of wildlife occurring in the absence of weak regulations, and is therefore strongly preservationist in its basic thrust. The Act makes it virtually illegal to kill or capture wild animals even when problem animals

are involved in severe conflict situations. Only government officials or agents authorized by the Chief Wildlife Warden of the state government can authorize such killings or captures. In case of endangered species like tigers, the necessary authorizations can only be issued by the Director-General of Wildlife Preservation in Delhi, based on an application made by the state Chief Wildlife Warden. While admirable in their intent, these strict legal provisions make it very difficult for local wildlife managers to deal effectively with urgent, life-threatening situations of human–tiger conflict.

Following Karanth and Madhusudan (2002), we classify the strategies employed for mitigating human–tiger conflicts into two basic categories: reacting to the conflict in ecological settings where conflict is inevitable, or preventing the conflict by altering the ecological setting itself. In the following analysis, we evaluate the utility of different conflict-mitigation approaches in terms of their value for tiger conservation, technical feasibility and social practicality. We employ the term ‘problem tiger’ for any animal that is persistently preying on domestic livestock, or has either killed human beings, or is potentially likely to do so immediately.

Lethal control

Killing of problem tigers through shooting, poisoning of livestock kills and less commonly using techniques such as electrocution, snaring and trapping has been the traditional method of conflict mitigation. Killing of ‘problem’ tigers has been widely accepted and practised by local people in India (Daniel 2001; Karanth 2001). Often, in situations involving tigers cornered by uncontrollable mobs, with the imminent prospect of human deaths, or with injured tigers, lethal control is the only practical option (Karanth and Madhusudan 2002).

However, urban advocacy groups often oppose such tiger killings on the grounds of either conservation or animal welfare. In the case of tigers straying out from small ‘source’ populations, repeated application of lethal control in the surrounding landscape may eventually lead to population extirpation (e.g. see Woodroffe *et al.*, Chapter 1). Furthermore, in a free-ranging population, it is very difficult to specifically target the individual problem tiger: several tigers may have to be killed before the problem animal gets eliminated. In such situations, local wildlife managers are often unfairly criticized, based on the unrealistic, anthropocentric expectation that only the ‘guilty’ tiger should have been punished. While lethal control is abhorrent to some conservationists and most animal welfare advocates, unfortunately it is the only practical option open to wildlife managers in many actual cases of human–tiger conflict (see also Treves and Naughton-Treves, Chapter 6).

Capture and removal of 'problem tigers'

Sometimes managers attempt to capture a problem tiger and move it away from the spot of the conflict because this approach has wider social acceptability among conservationists and animal welfare groups. In case of individual tigers of dispersal age (Smith 1993), moving the animals back to the source population may even be justifiable. However, such translocations are rarely practical, and may not have satisfactory conservation outcomes. In a free-ranging tiger population it is rarely possible to identify the individual problem animal for removal, unless it enters human settlements or is injured. Furthermore, safe chemical capture (or driving away) of tigers is usually rendered difficult because of crowd-control problems, injuries to the animal, lack of technical skills, scarcity of resources and other logistical problems (Karanth and Madhusudan 2002; K. U. Karanth, pers. obs.).

Even after safe capture, the problem tiger has to be permanently housed in captivity or relocated into the source population from which it came or into a new habitat. There are severe constraints on all three options. Wild tigers do not adapt well to life in captivity, and the capacity of Indian zoos to hold tigers is already saturated. Most zoos simply cannot afford to house an ever-increasing number of problem tigers.

Most problem tigers that undergo capture and handling are injured in the process, particularly by losing their canine teeth in steel transport cages that are commonly used. Many are either old or weak animals evicted from their ranges by more vigorous rivals (Smith 1993). Such tigers are unfit for relocation into the wild.

There are several ecological arguments against translocation of even healthy problem tigers into new habitats. First, most such relocations simply result in transfer of the problem to a new location leading to a new situation of conflict, because high-quality tiger habitats devoid of conflict potential are scarce. Second, even after translocation into a large reserve with an adequate prey base, the introduced animal will compete for space and prey with other individuals in the local tiger population. Because tigers are territorial animals (Sunquist 1981; Smith 1993) and their numbers are limited by prey densities (Karanth and Nichols 1998; Karanth 2003; Karanth *et al.* 2004), intraspecific competition is likely to lead to elimination of either the introduced tiger or of another individual from local population. Tiger populations normally go through increased rates of infanticide and mortalities during periods of social instability, which follow natural turnovers of male resident breeders (Sunquist 1981; Smith 1993). Periodic release of new tigers into wild populations may further aggravate such instability, causing more 'problem tigers' to disperse out of the population.

Guarding, barriers and aversive conditioning

A reasonably effective traditional approach involves employing human herders to guard livestock grazing in tiger habitats, wherever such labour is available and inexpensive.

Since most tiger attacks on livestock and humans occur under free-ranging conditions, mechanical barriers like stockades have limited utility. However, barriers made of wooden poles, wire mesh and nylon netting are being used to prevent tigers from entering villages in Sundarban. In the same region, aversive conditioning of tigers using electrified ‘human dummies’ has been tried out. Another technique used in Sundarban involves attaching backward-facing masks behind the heads of potential victims. The mask is expected to deter tigers, which are behaviourally attuned to avoid frontal attacks on prey. Success has been claimed for both these interesting innovations developed by local wildlife managers (Sanyal 1987). However, their use has been sporadic and irregular with no rigorous experimentation to test their efficacy.

The advanced – and expensive – non-lethal aversive conditioning techniques occasionally used for deterring carnivore attacks in developed countries (Treves and Karanth 2003; Shivik *et al.* 2003; Breitenmoser *et al.*, Chapter 4) do not appear to be very relevant to the technology and resource-scarce social context in which most human–tiger conflict occurs in India.

Compensatory payments

In cases of human predation by tigers, financial aid can never fully compensate the loss suffered by the victim’s families. However, prompt delivery of such assistance may help mitigate local hostility towards tigers to some extent (see also Nyhus *et al.*, Chapter 7). Given the relative rarity of tiger attacks on humans (except in Sundarban) and the public pressures that such attacks generate, government schemes for compensating for human lives lost to tigers seem to be working reasonably well.

However, payment of compensation for livestock predation – particularly in multiple-use forests with grazing rights – is problematic (Madhusudan 2003). Livestock compensation schemes fail for a variety of reasons: the massive scale of the problem; the low value of livestock in relation to the expenses involved in getting claims verified; corruption in the official machinery and among claimants; and a general lack of rural financial mechanisms enabling quick transactions (see also Nyhus *et al.*, Chapter 7).

Although compensation schemes of the government (and occasionally non-governmental agencies) have long existed over most parts of India, they

do not appear to be highly effective (Karanth and Madhusudan 2002; Madhusudan and Mishra 2003). Furthermore, no systematic evaluation of these schemes appears to have been undertaken during the last 30 years. We note that Indian herders appear to tolerate some degree of carnivore predation as price they are willing to pay for access to resources in public forests (Sekhar 1998; Madhusudan 2003).

Preventing conflict: relocation of human settlements

All the techniques described earlier are essentially components of an overall 'reactive' mitigation strategy, which tries to deal with the conflict generated by the interspersed human settlements and tiger habitats. In such settings, conflict is driven by ecological competition because tigers are large, obligate predators (Madhusudan and Mishra 2003).

On the other hand, relocation of human settlements is a proactive strategy that tries to alter the ecological setting, and thus prevent conflict rather dealing with it after the fact (Karanth 2002, 2003; Karanth and Madhusudan 2002). This strategy has been implemented under the Indian government's wildlife conservation schemes since the early 1970s. As a tool for promoting long-term human–tiger coexistence at the landscape level beyond reserve boundaries, the relocation strategy has several important advantages.

For most tiger populations in India (Fig. 23.1) survival prospects are bleak in the face of escalating habitat fragmentation and resulting conflict with human interests (Karanth 2001, 2003). Relocation of human settlements arrests ongoing conflicts and prevents their escalation. Relocation has been a critical tool in reducing habitat fragmentation and in driving the recovery of many wild tiger populations from the brink of extirpation in several Indian reserves (Karanth *et al.* 1999; Karanth 2002, 2003). When long-term social and economic costs of dealing with perennial human–tiger conflict are considered, relocation appears to be an attractive preventive option.

However, despite their ecological desirability and cost-effectiveness, resettlement projects face many practical hurdles. If the relocation process is not transparent, incentive-driven and fair, it can lead to hardship and resentments (Kothari *et al.* 1995). Scarcity of alternate land, lack of adequate financial resources or other social and cultural factors can also lead to setbacks to resettlement schemes (Karanth *et al.* 1999; Karanth 2002). Relocation schemes are unlikely to work well for large areas under multiple-use forests that support high human population densities, or situations where alternate land is scarce. They are not very relevant for dealing with conflicts that occur at the hard edge between strictly

protected tiger reserves and the extensive agricultural landscapes outside. Therefore, the relocation strategy is of primary relevance only for enclaves of human settlements within important tiger habitats, or critical corridors that connect insular tiger populations. Fortunately, in many such situations, there seems to be an incipient local demand for relocations, driven by changing social traditions and economic aspirations of the local people (Karanth 2002). In the light of these ongoing social changes and the escalating costs of delivering economic development and social services to remote settlements, incentive-driven relocation may emerge as a key strategy in India to ensure coexistence of humans and wild tigers at the landscape level.

THE FUTURE OF COEXISTENCE: AN ECOLOGY-BASED POLICY FRAMEWORK

Wildlife managers in India now employ a mix of conflict mitigation strategies. However, this strategic mix is largely *ad hoc* and not guided by clear policy prescriptions based on the aspects of tiger ecology and human social factors discussed earlier. Wildlife managers are severely handicapped by stringent legal requirements, lack of financial resources and technical skills, as well as by social pressures generated locally in conflict situations. A clear policy framework would enable them to avoid *ad hoc* responses and deal with conflict situations much more logically and effectively.

The framework we propose for managing conflict is shaped by the ecological reality that effectively protected breeding tiger populations are restricted to around 1% of India's geographical area and are further losing ground. Clearly, if the societal consensus is that wild tigers must survive in viable numbers in India, it is necessary to ensure that their ecological needs are central to any policy framework for reducing conflict and promoting coexistence.

Therefore, the long-term vision underlying our proposal involves increasing the area that supports demographically viable tiger populations (Karanth and Stith 1999) to at least one-third of the estimated potential tiger habitats in India (about 100 000 km²). This effort will involve maintaining 50–100 insular or tenuously connected wild tiger populations, each containing 12–50 breeding female ranges. If successful, such a strategy will require the management of tiger populations at average densities of 5–15 animals/100 km² with an overall size of 5000–15 000 wild tigers. These populations will naturally produce an annual 'surplus' of 500–1500 dispersing transient tigers that will come into conflict with people in the human-dominated landscapes around them.

We expect that the breeding tiger populations visualized above will be largely confined to protected areas, which will interface with either hard-edge agricultural landscapes or multiple-use forests, both riddled with conflict-prone land uses. Therefore, the above tiger conservation scenario has the potential for substantially escalating the present levels of conflict. Paradoxically, successes in tiger conservation will lead to higher levels of conflict that can only be mitigated by a proactive policy mix of conflict prevention and mitigation, rooted in sound science and practical experience (see Bangs *et al.*, chapter 21). Tactics ranging from lethal control of tigers at one end of the spectrum to relocation of human settlements at the other would have to be part of the mix.

We suggest the contours of an ecology-based policy matrix to guide future management of human–tiger conflict (Table 23.3). Our two-way

Table 23.3. A policy framework for human–tiger coexistence in India^a

Land Use	Conflict type		
	Livestock predation	Accidental killing of humans	Persistent predation on humans
Protected area for tiger conservation	Toleration Relocation	Compensation Relocation	Compensation Relocation Lethal control?
Tiger habitat in multiple-use public forest or extractive reserve	Toleration Compensation?	Compensation	Compensation Lethal control
Tiger habitat in privately owned land	Compensation	Compensation Capture–captivity	Compensation Lethal control
Unsuitable tiger habitat in public or private land	Compensation Translocation	Compensation Translocation Lethal control	Compensation Lethal control
Human habitations, livestock enclosures	Compensation Translocation Barriers?	Compensation Translocation Capture–captivity Lethal control	Compensation Lethal control

^aThe management context (each cell in the matrix) is defined by the nature of the conflict (columns) and the priority land use at the site of the conflict (rows). The suggested conflict mitigation tactics (not mutually exclusive) are listed in order of priority within each cell. These tactics include: passive toleration of conflict, financial compensation, tiger capture followed by translocation into the source population or captivity, lethal control of tigers, and incentive-driven relocation of human settlements.

matrix considers the type of conflict and the land-use priority at the site of the conflict, as the basis for management actions listed in order of priority within each cell – a form of zoning (Linnell *et al.*, Chapter 10). This framework prioritizes the need to keep tigers spatially separated from incompatible human land uses at the scale of protected reserves, while at the same time aiming to mitigate conflicts by prioritizing human needs at larger landscape scales. Robinson's (1993) conservation paradigm of establishing 'sustainable landscapes' provides a more appropriate conceptual template for implementing the proposed policy framework than the alternatives of 'sustainable' human use of all tiger habitats favoured by social advocacy groups in India (Kothari *et al.* 1995), or the 'don't kill a single tiger' approach favoured by some votaries of animal rights. We believe that as human populations and resource consumption levels increase, similar policies will be essential for enabling the continued coexistence of all big cat species with human societies in most parts of the world.

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