EVALUATING METHODS TO MONITOR TIGER ABUNDANCE AND ITS PREY IN INDIAN SUNDERBANS

A THESIS
Submitted by

MANJARI ROY

for the award of the Degree of

**DOCTOR OF PHILOSOPHY
IN
WILDLIFE SCIENCE**

Under the guidance of

K. SANKAR & Q. QURESHI

Wildlife Institute of India

**Saurashtra University
Rajkot – 360 005**

JULY 2019

Declaration by the Candidate

I declare that the thesis entitled **Evaluating methods to monitor tiger abundance and its prey in Indian Sunderbans** submitted by me for the degree of Doctor of Philosophy is the record of research work carried out by me during the period from **2012 to 2019** Under the guidance of **K. Sankar and Q. Qureshi** and has not formed the basis for the award of any degree, diploma, associate ship, fellowship, titles in this or any other University or other institution of higher learning. I further declare that the material obtained from other sources has been duly acknowledged in the thesis. I shall be solely responsible for any plagiarism or other irregularities, if noticed in the thesis.

Signature of the Candidate:

Place: Dehradun

Date : 23rd$^{\text{th}}$ July 2019

SAURASHTRA UNIVERSITY

Original

Regi.No.4876

Re-Accredited **Grade B by** NAAC
(CGPA 2.93)

CERTIFICATE OF REGISTRATION FOR Ph.D.

Name of the College / Institution Uni. Deptt. in which the student is to work for Ph.D. Degree is Wildlife Institute of India, Chandrabani, Dehradun

DATE OF REGISTRATION 1/1/2012 REGISTRATION No.4876

This is to certify that Shri/Smt./Kum. ROY MANJARI has been registered as a Post-Graduate student of the Saurashtra University working for the degree of the Ph.D. under the Guidance of Dr.K.Sankar in the faculty of Science and Subject Wildlife Science. The Title / Topic of the Thesis is "EVALUATING METHODS TO MONITOR TIGER ABUNDANCE AND ITS PREY IN INDIAN SUNDERBANS"

AND INTENDING TO FINISH HIS WORK IN THE MONTH OF (Month & Year of Submission of thesis January ' 2014)

Assistant Registrar
Saurashtra University
Rajkot

Assistant Registrar
SAURASHTRA UNIVERSITY
RAJKOT

Rajkot
Dt. 4 /07/2012

Self Attested
Manjari Roy
4/11/2020

Declaration by the Candidate

I declare that the thesis titled **Evaluating methods to monitor tiger abundance and its prey in Indian Sunderbans** submitted by me for the degree of Doctor of Philosophy is the record of research work carried out by me during the period from **2012 to 2019** Under the guidance of **K. Sankar and Q. Qureshi** and has not formed the basis for the award of any degree, diploma, associate ship, fellowship, titles in this or any other University or other institution of higher learning. I further declare that the material obtained from other sources has been duly acknowledged in the thesis. I shall be solely responsible for any plagiarism or other irregularities, if noticed in the thesis.

Signature of the Candidate:

Place: Dehradun

Date : 23rd July 2019

Certificate

This is to certify that the thesis titled "Evaluating methods to monitor tiger abundance and its prey in Indian Sunderbans" submitted for the award of the Doctor of Philosophy in Wildlife Science to Saurashtra University, Rajkot is a record of original and independent research work carried out by Ms. Manjari Roy under our guidance. No part of this thesis has been submitted to any other university or institution for the award of any degree and it fulfills all the requirements laid down by the Saurashtra University.

Dr. K. Sankar
(Supervisor)
Senior Professor and Scientist 'G'
Department of Habitat Ecology
Wildlife Institute of India,
Dehradun, Uttarakhand.

Shri. Qamar Qureshi,
(Co-Supervisor)
Senior Professor and Scientist 'G'
Department of Landscape Ecology
Wildlife Institute of India,
Dehradun, Uttarakhand.

Saurashtra University, Rajkot

Office of the Saurashtra
University, University Road,
Rajkot – 360 005
Gujarat (INDIA)

Re-Accredited Grade "B" by NAAC
[CGPA 2.93]

Phone: +91 281 2578501

Fax: + 91 281 2586983

CERTIFICATE FOR PRE PH.D. PRESENTATION

This is to certify that **Ms. Manjari Roy (Regd. No. 4876, 01.01.2012)** has made Pre Ph.D. presentation as per UGC Guide Line "University Grant Commission (Minimum Standard and Procedure for award of Ph.D. Degree) Regulation–2009" and Saurashtra University Ordinance for Ph.D. Programme (O.Ph.D. 6.2), on the research work titled **"Evaluating methods to monitor tiger abundance and its prey in Indian Sunderbans"** at the Wildlife Institute of India, Research Centre of Saurashtra University, Rajkot, on 23rd July 2019 before all faculty members and students of the Department for getting feedback and comments.

I also certify that the research work was appreciated by all who remain present and there was no comments made for this research work/comments made are incorporated in the thesis.

Place: **Dehradun**

Date: 23.07.2019

Guide: **Dr. K. Sankar**

Department/College:

Wildlife Institute of India
Chandrabani, Dehradun – 248 001
(Uttarakhand)

संकाय अध्यक्ष /Dean
भारतीय वन्यजीव संस्थान
Wildlife Institute of India
देहरादून / Dehradun

Qamar Qureshi
Scientist-G & Nodal Officer
IT, Remote Sensing and GIS
Wildlife Institute of India
Chandrabani, Dehradun-248001

SAURASHTRA UNIVERSITY, RAJKOT
CERTIFICATE OF PLAGIARISM CHECK

01	Name of the Research Scholar	MANJARI ROY
02	Title of the Thesis/Dissertation	EVALUATING METHODS TO MONITOR TIGER ABUNDANCE AND ITS PREY IN INDIAN SUNDERBANS
03	Name of the Supervisor	K. SANKAR & Q. QURESHI
04	Department/Institution/Research Center	WILDLIFE INSTITUTE OF INDIA
05	Similar Content (%) identified	12%
06	Acceptable Maximum Limit	15%
07	Software Used	iThenticate
08	Date of Verification	22-07-2019

Checked by (with Name designation & signature):

पुस्तकालयाध्यक्ष
Librarian
भारतीय वन्यजीव संस्थान, देहरादून
Wildlife Institute of India, D.Dun

Librarian,

Name & Signature of the Researcher: MANJARI ROY Manjari Roy

Name & Signature of the Supervisor:

Qamar Qureshi
Scientist-G & Nodal Officer
IT, Remote Sensing and GIS
Wildlife Institute of India
Chandrabani, Dehradun-248001

Name & Signature of the HOD (Co-ordinator of the Department Research Committee):

संकाय अध्यक्ष /Dean
भारतीय वन्यजीव संस्थान
Wildlife Institute of India
देहरादून / Dehradun

Similarity
Index 12%

Thesis

By: Manjari Roy

Sources:

1,837 words / 9% - Crossref
Manjari Roy, Qamar Qureshi, Dipanjan Naha, Kalyanasundaram Sankar, Rajesh Gopal, Yadvendradev Vikramsinh Jhala. "Demystifying the Sundarban tiger: novel application of conventional population estimation methods in a unique ecosystem", Population Ecology, 2015
199 words / 1% - Internet from 23-Jan-2015
12:00AM projecttiger.nic.in
125 words / 1% - Internet from 02-Oct-2018
12:00AM www.lifebonelli.org
92 words / < 1% match - Crossref
"Ecological Connectivity among Tropical Coastal Ecosystems", Springer Nature, 2009
17 words / < 1% match - Internet from 12-Aug-2016
12:00AM www.springerprofessional.de

पुस्तकालयाध्यक्ष
Librarian
भारतीय वन्यजीव संस्थान, देहरादून
Wildlife Institute of India, D.Dun

Qamar Qureshi
Scientist-G & Nodal Officer
IT, Remote Sensing and GIS
Wildlife Institute of India
Chandrabani, Dehradun-248001

ACKNOWLEDGEMENT

This dissertation was part of a larger project entitled "Population estimation and ecology of the tiger in Sundarban Tiger Reserve" under the supervision of the investigators Y.V. Jhala and Q. Qureshi. My project supervisor Y.V. Jhala deserves due credit and recognition for facilitating my work, mentoring me and in general being very patient with my ever-lasting thesis writing. He has helped me to not only push myself to be better at my work (though he gets often irritated by my insistence to be a perfectionist at every little thing!) but has also taught me the values of honesty and trust.

My project supervisor and co-guide Q. Qureshi has been the beacon of hope in many of my dark days both in field and while writing this thesis. He has always been very patient with my frequent complaining and has always tried to inspire me when at times I have been overcome with poor self-worth. Academic discussions with him would somehow always meander through unrelated topics which would at times leave me exasperated but in the end constantly forced me to think outside the box. I also enjoyed our many varied conversations ranging from academics to music to debates on communism and in my opinion he is one of the 'coolest' faculties that I know of. He will always have a special place in my heart whose mere acknowledgement of my work and individuality would brighten up my day.

I thank my dissertation guide, K. Sankar, who had given me a free reign and the space to explore my own ideas for my work. Alongside, I thank my colleague, Dipanjan Naha for helping me to collect data for my dissertation.

I heartily thank V.P. Uniyal for facilitating my registration extension and constantly keeping me on my toes to finish the thesis as fast as possible.

I thank my field staff, Nareshda, Goutamda, Srinivasda and the entire staff of boatmen, labourers who helped me in my field work. A special shout-out to my field assistant, Ranjitda. He is one of the best human beings I know and all my pleasant memories of Sunderbans are associated with him. He taught me age (he was 65 years old at the beginning of my field work) and lack of education has got very little to do with hard work, diligence and kind-heartedness. Being the only girl in boatful of men and all alone in the forest, he always went out of his way to ensure my safety. He and his family showered their affections towards me which made Sunderbans feel like my third home.

Shikha, Sudip, Anant and Indro have been the pillars of my life in Dehradun. They have been there for me when I needed them. We have had our fair share of bumps and tantrums yet without them, my little world in Dehradun would feel empty. Parties, breakups, pasta- we have done it all together! They have made me bored, they have made me laugh, they have made me cry, they have made me feel loved, they have made me livid with anger and hatred - yet at the end of the day, it is their company that I seek the most. It is impossible for me to describe the impact they have had in my life in this tiny space of 'Acknowledgements'!

I thank Sabujda for his mentoring and always lending me a helping hand whenever I got stuck be it in academics or in personal life. He has often helped me in clarifying and structuring my thoughts. I thank Sutirtha for helping me with my manuscript preparation and analysis of my sign-based chapter. His intelligence

combined with his sense of humour has never failed to entertain me. I thank Stotro for allowing me to push him around and yet he has always been ready to help me with shaping my abstracts from verbose garbage to succinct masterpieces. I thank Ayan for patiently listening to my academic rambles even when he did not feel like and his intelligence and understanding has always sparked new ideas in me. I thank Anindita for helping me to clear up my mark-recapture doubts and giving me the space and time to rant whenever I got angry. I thank Tapajit for pushing me to join this project and mentoring me during my Masters, which helped me ace the interview for this project in the first place! I thank Ujjwal for his willingness to help me whenever I asked, no matter how busy he might have been. I thank Amrita for taking care of me whenever I fell sick and going out of her way to help me get better. I thank Bhaskar, my closest and oldest friend who always kept me grounded with his sarcasm and pragmatism and his generous offer to house me if I never get a job! I thank Keshta for making me a better human being and always listening and trying to understand my scientific garble even though she is from the humanities background. I thank Sanath for enriching my weekends after a long week of work with delicious dishes of meat and sweets and always letting me use his washing machine to avoid the dreadful job of hand-washing clothes.

I thank Rashid bhai, Bipin, Ranjana, Nilanjan, Vishnu, Bopu, Divya, Dibyendu, Swati, for helping me whenever I got stuck be it analysis related or theoretical understanding or GIS related or just plain and simple threshing out ideas. I thank Srinivas, Manas, Ashok, Pritha for the fun filled hostel days. I thank Charles, Devlin,

Anup, Manendra, Rahul, Sougata and Urjit for their help in collecting data during field work. I thank Jayanta for the late-night printouts of my chapter.

I thank the staff of Sunderbans Forest Department and the staff of Wildlife Institute of India for helping me with the logistics.

I thank my parents who had nearly run out of patience yet kept it mostly under wraps with my never-ending dissertation writing. I cannot imagine a world without their presence and constant support.

Lastly I thank the Sunderbans tigers for not eating me!!

Table of Contents

List of Tables

List of Figures

SUMMARY

Anthropogenic pressure has lead to increasing fragmentation and disconnected tiger occupied forest patches all over Asia. Sanderson et al. 2006 outlined the future persistence of this species being dependent on conservation measures that are rooted in protecting ''representative, redundant, and resilient'' populations across the historical range over which it has evolved. Diverse habitats are likely to produce dissimilar ecological adaptations and dynamics. Hence for minimizing extinction risks, one is forced to adopt conservation strategies that focus not only on large tiger populations but the suite of unique adaptations of different populations. One such habitat, the mangroves, is exclusively represented by Sunderbans. It supports one of the largest tiger populations across India and Bangladesh. However, there is a lacuna of information on this tiger population due to its man-eating reputation and logistic difficulties of sampling in a mangrove ecosystem subjected to the vagaries of tide. In this thesis, I have attempted to test and evaluate different methods for estimating tiger and its prey population in Sunderbans that can be adopted as part of a monitoring programme.

Remote sampling cameras are currently used for studying many animal populations especially for species that are rare and/or elusive due to their morphology, habitat preference, behaviour or ecological aspects. Tigers with their unique individual markings are a prime example of how such data can be used to generate estimates of abundance and density that are critical for the species conservation and directing management actions. I applied the standard spatially explicit capture-recapture, tailored according to the local conditions to estimate tiger density in Sunderbans for three years.

Tiger densities were estimated at 4.08 (SE 1.51) in 2010, 5.81 (SE 1.24) in 2012 and 3.15 (SE 0.88) tigers/100 km^2 in 2014. The tiger abundance for my camera trapped study area generated through conventional mark-recapture was 11 (SE 2), 24 (SE 3) and 16 (SE 3) tigers for 2010, 2012, 2014 respectively.

In species like African forest elephant, chimpanzee, orangutan, gorilla index based technique is used to generate animal density on the basis of sign (dung, nest) density. Information on sign deposition rate and sign decay rate are used to convert the sign density to animal density. I tested this method to see if tiger density in Sunderbans could be derived from sign densities. The sign in this case was considered to be the crossings (set of the pugmarks) deposited on the mud strips along the banks of islands, when they cross channels. This method has never been applied in tiger science before, and I felt would be a novel alternate to estimating density through camera trapping. The tiger density was estimated at 3.34 (SE 1.44) tigers per 100 sq. km. while the tiger abundance in the study area was estimated as 25.88 (SE 11.2) tigers.

Ungulates occupy a primary position in the diet of tigers and a monitoring protocol for tiger should inherently include a component of prey base estimation. I used boat trasect based distance sampling to generate density estimates for four years. I could only do so for spotted deer as Sunderbans has very low prey species richness and poor detectability of other prey species such as wild pig and rhesus macaque. The individual densities of spotted deer were 4.94 (SE 2.68) in 2011, 6.68 (SE 1.81) in 2012, 5.6 (SE 1.48) in 2013, 3.2 (SE 0.84) spotted deer per sq.km. in 2014.

One of the core activities of conservation biology is ecological monitoring. Monitoring data are used for identifying endangered species trend. Power analysis is a tool often used to test the efficacy of any method to detect changes in the population. I tested for power on the spatially explicit capture-recapture, conventional mark-recapture, sign based method and distance sampling to see if they had the ability to detect negative trend in tiger and its prey in Sunderbans when these exercises are conducted regularly. I specifically used the datasets generated in 2014 for this analysis. Spatially explicit capture-recapture had a power of 82% to detect a decline of 45% in the population, while conventional mark-recapture had a power of 83% to detect a decline of 30 percent in tiger population. The sign based method had the lowest power (79% to detect a decline of 60% in the tiger population). Distance sampling had a power of 80% to detect a decline of 35% in the spotted deer population.

CHAPTER I - INTRODUCTION

Large carnivores have the potential to trigger cascading effects on ecosystem structure and functioning (Ripple et al. 2014). Through multiple food-web pathways these carnivores shape the ecosystem by predation on herbivores and intraguild competition with meso-carnivores (Ripple et al. 2013). They deliver ecosystem services indirectly, like increasing carbon storage, establishing native plant diversity, stabilising riparian systems, reducing disease prevalence and spill-over effects to agricultural livestock, through prey regulation (Terborgh et al. 2001, Packer et al. 2003, Beschta and Ripple 2012). Additionally, large carnivores gain prominence, due to their charismatic nature, providing direct economic benefits of tourism (Ripple et al. 2014). These large predators are characterised by their low population densities, low reproductive rates, and high energy requirements, and hence require extensive inviolate spaces for their survival (Cardillo et al. 2004). It is this juxtaposition of slow life-history traits and requirement of large areas that has placed carnivores at the vulnerable crossroads of human-animal conflict and persecution (Cardillo et al. 2004).

The global population of tigers (*Panthera tigris tigris*) has declined drastically, and has gone locally extinct at the extreme ends of its distribution in Asia (Tilson et al 2004). Poaching for trade in tiger parts, reduction of prey base, and habitat fragmentation has forced this species to a few isolated populations (Dinerstein 1997). Tigers serve as the umbrella species for many tropical systems (Wikramanayake et al. 2004) acting as the pulse of the changing forest. Their cultural and socio-economic role as a flagship species moreover, has attracted funding and wider conservation benefits

(Walpole & Leader-Williams. 2002). Yet this species remains endangered with the global wild population fewer than 3500 individuals (Joshi et al. 2016).

Ungulates occupy a primary position in the diet of tigers (Karanth et al. 2004). They also perform important ecological services such as dispersal of seeds (Prasad et al. 2006) and structuring of vegetation diversity (Adler et al. 2001). However, this group of mammals is under disproportionately high extinction risk due to commercial poaching and resource competition with domestic livestock especially in South-East Asia (Steinmetz et al 2010). This has led to large tracts of silent forests – intact yet empty forests due to locally extinct ungulate communities (Datta and Naniwadekar 2008). Such situations have obvious and serious implications for large carnivore conservation; as observed in case of tigers, in the absence of human-induced mortality, tiger disappearance is directly related to prey loss (Chapron et al 2008).

But, beyond such value associations of carnivores and their prey, 'wildlife' has an intrinsic right to exist independent of human notions of its worthiness or 'use' (Stevens et al. 1991).

In order to stall the perils threatening large carnivores like tigers and their prey base, implementation of monitoring strategies assumes a critical role (Marsh & Trenham 2008). Monitoring is the gathering of information on certain state variables such as population size, biomass or species richness at regular temporal intervals on specific/certain populations, communities or ecosystems (these being the systems of interest) respectively (Yoccoz et al 2001). Monitoring can be undertaken with either scientific or management objectives in mind. Scientific objectives aim to understand the dynamics of the monitored system, while management objectives seek to use such information for taking informed management decisions (Yoccoz et al 2001). In the recent past, scientists, governments and NGOs have increasingly recognized that monitoring should be a central and operational part of all conservation activities, because if one cannot measure and assess the impact of the actions on biodiversity conservation, one can never adapt the practices or improve their effectiveness. Hence, monitoring is an essential tool for adaptively managing conservation actions as conditions change (Marsh & Trenham 2008). While conducting monitoring exercises, one should keep in mind the two sources of error which can bias the interpretation of changes in the state variable – detection error (acknowledging that not all animals are visible at all times) and spatial/survey error (errors associated with the inability to survey large areas in an unbiased manner) (Yoccoz et al. 2001).

As mentioned afore, monitoring exercise describes a population (system of interest) and helps in assessing factors that may influence the population over time. One of the principal state variables used in such projects is population size. Population size helps to identify the effects of management actions, such as, whether targeted actions have a positive or neutral effect on certain endangered species population or if such actions are effective in controlling/decreasing populations of certain pest/invasive species (Williams et al. 2002). Emphasis on estimation of population size is also placed in studies on/of biological relationships that are sensitive to the number of individuals in a population such as density-dependent growth rates, prey-predator relationships, and models of competing populations (Williams et al. 2002). Population size can be described by both abundance, i.e., the number of individuals in a population occupying the same space at the same time, or by density where abundance is scaled by area. Density becomes especially useful when comparing different locations or across time (Caughley 1977).

Absolute abundance can be estimated broadly through two basic approaches. Census is the counting of all individuals or a complete count; however, such total counts are almost impossible to conduct on wild animal populations. An alternative method, sample survey, can further be categorised to two types – i. complete survey on sample units, where the unit represents a sample of the area/volume occupied by the population of interest, e.g., quadrat sampling or strip transect, and ii. incomplete counts on sample units which accommodate the probability of missing individuals in the unit, e.g., distance sampling, capture mark recapture, or removal methods (Williams et al. 2002).

For many species, direct counts may be impossible due to terrain complexity, rarity, nocturnal habits or time and money available for the survey. In such cases, animal signs such as footprints (pugmarks/hoofmarks), faecal deposits, nests/dens are used to estimate relative abundance or density, provided that such signs have a monotonic relationship with absolute abundance (Caughley 1977). Signs are also used occasionally to estimate absolute density relying on the availability of suitable correction factors (Schwarz & Seber 1999). However, since such applications often rely on a number of assumptions, some of which may be unsubstantiated, their usage remains controversial (e.g. Carbone et al. 2001, 2002; Jennelle et al. 2002). Nevertheless, indices (for relative or absolute abundance) remain a popular tool used to monitor populations (Nichols

2010, Jenks et al. 2011, Depraetere et al. 2012, Townsend et al. 2014, Cusack et al. 2015, Kays et al. 2017, Palmer et al. 2018).

Hence, 'why monitoring tiger and its prey is essential in Sunderbans?' Sanderson et al. 2010 outlined an effective conservation strategy where the limited resources should be directed at protecting ''representative, redundant, and resilient'' populations across the historical range over which it has evolved. Such selective conservation action seeks to preserve diverse habitats that are likely to produce dissimilar ecological adaptations and dynamics (Dinerstein 1997). One such habitat, the mangroves, is exclusively represented by Sunderbans that supports one of the largest tiger populations across India and Bangladesh (Jhala et al. 2011). Sunderbans tigers differ in morphology from their geographically closest conspecifics (*P. tigris tigris*, Linnaeus and *P. tigris corbetti*, Mazak) (Barlow 2009) and represent, at the least, an Evolutionarily Significant Unit (Singh et al. 2015).

The ambit of conserving Sunderbans extends beyond its charismatic species. Sunderbans has the distinction of being the largest (10,263 km^2) and most diverse mangrove forest in the world, spanning across India and Bangladesh (Chaudhuri and Choudhury 1994). These mangroves play a critical role in coastal ecology by buffering inlands from cyclones, stabilising sediments and aiding land maturation (Blasco et al. 1996). This tiger habitat is also in close proximity to one of the densest (1437.4 persons/km^2, Qureshi et al. 2006) and poorest (Kanjilal et al. 2010) human populations, where many local communities derive a substantial portion of their livelihood from harvesting forest products like fish, giant tiger shrimp (*Penaeus monodon*, Fabricius) and honey (Blair 1990; Rahman 2000; Islam and Wahab 2005).

However, Sunderbans faces a precarious future primarily due to rising sea levels, coastal squeeze (Loucks et al. 2010) and water pollution. Yet, rigorous scientific research on Sunderbans tigers and their prey base is scarce. This estuarine landscape is subjected to the daily vagaries of tides, where majority of the land gets inundated by brackish water twice daily, erasing animal pathways, forcing one to rethink established survey methods in a new light. This unique situation also inevitably leads to an increase in logistic cost and complexity. On top of that is the ever present threat of being killed by tigers, which makes any kind of field work a daunting task. The Sunderbans tiger is most known for its human killing. Human-tiger conflicts involving attack and killing by the tiger are more recurrent here than in any other tiger area of the world (Neumann-Denzau and Denzau 2010). Chakrabarti (1992) estimated that about 36 people were killed each year in the Indian Sunderbans. In the Bangladesh Sunderbans, Barlow et al. 2013 estimated a mean of 22 human deaths per year. Ironically, the infamous ''man-eating'' tiger, the archetypal symbol of this mangrove forest has been responsible for the continual survival of Sunderbans forests by minimizing overexploitation of forest resources (Roy et al. 2015).

These factors have led to a paucity of information on the basic ecology and population abundance of tigers. Past efforts of estimating tiger abundance in this region have reported unreliable densities ranging from as high as 23.5 individuals/100 km^2 (Barlow 2009) to as low as 0.7 individuals/100 km^2 (SD 1.67) (Karanth and Nichols

2000) while the reserve management (West Bengal Forest Department) claimed 250 tigers (a density of 20/100 km^2) (Mukherjee 2005). These discrepancies may further be attributed to less reliable exercises based on untested assumptions, and have in turn impeded the assessment of management efficacy towards conserving this population.

Hence, it becomes imperative to test and evaluate different methods for estimating tiger and its prey population, and develop a protocol that has both the power of detecting changes and is logistically cost-effective. To address this exigency, my thesis proposed the following objectives-

1. Estimating tiger abundance

    a. Estimation using camera trap based mark-recapture technique

Camera trap based mark-recapture (CTMR) (Karanth & Nichols 1998) estimation of tigers becomes particularly challenging in Sunderbans. This is due to the i) non-detectability of animal trails inside the forest, ii) restricted accessibility due to water channels, iii) inundation of land by the brackish water during high tides twice daily, and iv) risk of attack from tigers. Hence, I sought to test the feasibility of camera trapping in such a unique landscape by tailoring it to the local conditions.

    b. Estimation from sign decay and deposition rates

I proposed a novel sign deposition-decay based abundance estimator in this study as a parallel method for estimating tiger abundance. This approach has never been applied for estimating carnivore populations before and the stochasticity of the study system made this experimental set-up open to both success and failure.

2. Developing a monitoring protocol for Sunderbans tiger

I wanted to test the applicability of both of the above mentioned methods in terms of their precision and cost-benefit ratios. A number of complications arise from sign based technique. Consequently it is important to rigorously test the accuracy, bias and power of index based methods against the "true" population estimate before we can conclusively use them in monitoring. For Sunderbans, density generated from CTMR was used to assess the viability of sign generated estimates.

3. Developing a monitoring protocol for prey

In case of prey, I tested the applicability of distance sampling based boat transects to develop an effective monitoring tool for prey.

CHAPTER II – STUDY AREA

The concept of 'Tiger Conservation Landscape' or TCL seeks to prioritise and allocate funds and logistics to those places which will provide the greatest ecological returns in terms of species survival (Dinerstein 1997). It shifts the focus from concentrating efforts on single undifferentiated tiger populations to ecologically distinct populations covering the range of adaptations occurring across the different habitats in which it has evolved (Sanderson et al. 2010). Sunderbans, a class I TCL is the only mangrove habitat in the global priority category which harbours tigers. As mentioned in the Chapter I, Sunderbans tigers are unique in their size, behavior and reputation. These mangrove forests are the largest in the world spanning across India and Bangladesh and hold immense ecological as well as economic values. Such a landscape warrants a detailed description of its distinctiveness. The following focuses on the Indian Sunderbans as the two parts (India and Bangladesh) differ substantially in the nature of conservation, management and the level of human exploitation (Gopal and Chauhan 2006).

2.1 LOCATION

Sunderbans is the world's largest contiguous halophytic mangrove habitat covering an area of 10,000 sq. km. approx shared between two political boundaries, with 66% of the landscape in Bangladesh and 34% in India (Naskar & Mandal 1999). The Indian Sunderbans covers an area of 4,266.6 sq. km (Naskar & Guha Bakshi 1987) situated within 21°31' N - 22°30' N latitudes and 88°10' E - 89°51' E longitudes in the coastal district of South 24 Parganas, West Bengal.. The sea-land inter-phase comprises of about 55% forest land (2,300 sq. km area, Naskar & Guha Bakshi 1987) and 45% water (1,750 sq. km area, Naskar and Mandal 1999). The land area consists of 56 forested islands.

2.2 GEOLOGY

The entire land mass of Sunderbans is of very recent origin. The Himalayan orogenesis, carriage of world's largest sediment load to the sea by rivers Ganga and Brahmaputra and tectonic movement of the continental plates have built the unique geological characteristics of Sunderbans (Morgan and McIntire 1959, Milliman et al. 1995). Neotectonic movements induced an easterly tilt in the Bengal Basin in the 12-15th AD (Morgan and McIntire, 1959). In the 16th century, Ganga shifted its course eastward to join Brahmaputra (Snedaker 1991). These two combined rivers then further shifted their course to join river Meghna (Snedaker 1991). These constant shifts due to the tectonic movements leading to changing sedimentation patterns have greatly influenced the hydrology of Sunderbans (Gopal & Chauhan 2006). Sunderbans is shaped into hundreds of islands crisscrossed by a maze of tidal rivers, estuaries and creeks formed by the regular tidal action and the dominant geomorphic agent, the mangroves (Gopal & Chauhan 2006).

The mangrove ecology is highly influenced by the natural phenomena of tidal cycles (Thom 1967). A tidal cycle is defined as the time of one phase of the tide to the recurrence of the same phase (Nagelkerken 2009). There are two different tidal phases-high tide and low tide. High tide is defined as a rising of the water level or the incoming tide whereas low tide is the fall of the water level i.e. ebb tide or outgoing tide. The point at which speed and direction of the water are at zero and the tide turns from one phase to another is known as slack water (Nagelkerken 2009). Sunderbans is subjected to semidiurnal tide where two tide cycles in a day, each of 12 hrs 25mins duration (Nagelkerken 2009). The tidal range changes with the lunar cycle. Tides are classified as spring or neap depending on the phase of the moon and to a lesser extent, the position of the sun. Spring tide occurs at new or full moon when the sun, earth and moon are collinear. At spring tides, the tidal ranges and water speed reach a maximum (Barnes-Svarney and Svarney 1999). The water level at slack high tide is extremely high while at the slack low tide is extremely low (Kvale 2006). Neap tides occur at the first and third quarter moon phases, when the sun, earth and moon are perpendicular to each other (Barnes-Svarney and Svarney 1999). During neap tide, tidal ranges are significantly reduced and water speeds are much weaker (Kvale 2006). Most of the Indian Sunderbans is polyhaline (Gopal & Chauhan 2006).

2.3 CLIMATE

The climate is characterized by high temperature and high humidity (over 80%) throughout the year (Gopal & Chauhan 2006). There are three distinct seasons in Sunderbans viz., summer extending from March to June, monsoon from July to October and winter from November to February. The mean maximum and minimum temperatures are 29°C (June-July) and 20°C (December-January), respectively. The annual rainfall is as much as 2,790 mm on the outer coast, and 1,650-1,800 mm in the central and northern areas. Thunderstorms known as nor'westers or Kalbaisakhi are common during April and can often be accompanied by tidal waves as high as 7.5m (Seidensticker & Hai 1983).

2.4 BIODIVERSITY

2.4.1 Floristic diversity

The vegetation of this region is influenced by several factors like salinity levels, soil composition and structure, silt deposition rates and rates of humus formation. Interestingly, the Sunderbans supports fewer species than other mangrove areas in India and Southeast Asia. This area is home to around 35 true mangrove species and 117 other halophytic mangrove associates (Qureshi et al. 2006). Altogether, about 350 vascular plant species belonging to 254 genera are found here (Chakrabarti 1980). The Sunderbans forests are classified under the sub-group 4B Tidal Swamp forests with sub-divisions of Mangrove type (4B/TS1 and 4B/TS2), Salt water type mixed forest (4B/TS4), Brackish type (4B/TS4), AND Palm swamp type (4B/E1) (Champion and Seth 1968). Dominant tree species include *Avicennia alba* (Piara Baen), *A. marina* (Kala Baen), *Aegiceras carniculatum* (Khalsi), *Bruguiera sexangula* (Kankra), *Ceriops decandra* (Goran), *Exocoecaria agallocha* (Genwa), *Nypa fruticans* (Golpata), *Phoenix paludosa* (Hental), *Rhizophora apiculata* (Gorjan), *Sonneratia apetala* (Keora), *Xylocarpus granatum* (Dhundul) and *Xylocarpus mekongensis* (Pashur). Besides these, there are many species of climbers, grasses and herbs as well.

2.4.2 Faunal diversity

The tiger is an integral part of Sunderbans. This area attracts publicity largely for the claimed highest number of tigers in the world along with a high prevalence of man-eaters amongst them. While the former claim is under scientific deliberation, the latter remains a mystery. Mangrove habitats are amongst the most productive ecosystems, however, most of the productivity is confined to aquatic systems with terrestrial species being low in numbers. Thus, the ability of this region to sustain large mammals is restricted. The main prey of tiger in the region comprises of chital (*Axis axis*), wild pig (*Sus scrofa*) and Rhesus macaque (*Macaca mulatta*) and lesser adjutant stork (*Leptoptilos javanicus*) (Khan 2004). Other purported native fauna of the region which included Javan rhinoceros (*Rhinoceros sondaicus*), swamp deer (*Rucervus duvaucelii*), water buffalo (*Bubalus bubalis*), gaur (*Bos frontalis*), hog deer (*Axis porcinus*) and marsh crocodile (*Crocodilus palustris*) are now extinct from this area (Chakrabarti 1980). Estuarine crocodile (*Crocodylus porosus*), water monitor (*Varanus salvator*), northern river terrapin (*Batagur baska*), softshell turtle (*Pelochelys bibroni*), green sea turtle (*Chelonia mydas*), along with the Irrawaddy dolphin (*Orcaella brevirostris*) and Gangetic dolphin (*Platanista gangetica gangetica*) are some of the rare and endangered species found in Sunderbans. This landscape supports about 300 species of birds, 7 species of amphibians, 59 species of reptiles, 165 species of fishes, 110 species of molluscs, 64 species of crabs (Working Plan of Sunderbans Tiger Reserve). Sunderbans is a very important nursery for many estuarine and coastal marine fishes. Crustaceans form the largest proportion of animal biomass (Hendrichs 1975).

2.5 MANAGEMENT

In recognition of its ecological and cultural significance, Sunderbans has been recognized as a World Heritage Site and a biosphere reserve. It has further been brought under legal framework as a tiger reserve which encompasses a wildlife sanctuary, a national park and its buffer zone designated as a multiple use zone for regulated harvest of resources for meeting local needs. Sunderbans Tiger Reserve is further divided into 15 management sub-zones or 'blocks' which have further been divided into 70 'compartments' (Working Plan of Sunderbans Tiger Reserve).

2.6 THREATS

The biggest peril to this landscape, given the comparatively lower risk of direct habitat destruction by humans, is the rising sea level due to climate change which threatens to submerge 96 % of the landmass (Loucks et al. 2010). This will not only lead to the loss of a unique landscape, but also increased tiger movement into the surrounding villages leading to escalated human-animal conflict. Additionally, Rahman et al 2011 found that in the recent years the accretion rate has declined while, the erosion rate has been relatively high. A direct result of this is the loss of 170 km^2 of coastal land in 37 years (1973 to 2010).

Poaching of tigers and their prey are a major concern for tiger conservation globally, Sunderbans being no exception. Law enforcement is especially difficult in the Sunderbans due to its hostile habitat and porous borders. Smuggling of wildlife especially tiger parts and products becomes relatively easy.

Another threat to this landscape is the usage of water channels inside this forest as conduit for commercial boat traffic. Over 200 vessels ply everyday through the Sela river and Passur river located in and near the Chandpai-Sarankhola range of Bangladesh Sunderbans respectively. This constant movement of boats can become potential barriers to dispersal between islands leading to fragmented and isolated tiger populations within Sunderbans. The 1320 MW coal based thermal power plant at Rampal and proposed exclusive economic zone in Mongla, a collaborative effort between India and Bangladesh, would only further exacerbate this problem.

Pollution is also one of the major threats to this landscape. The vessels plying inside Sunderbans often carry cargo like oil, fly-ash, cement, fertiliser etc. These vessels are veritable 'mobile bombs' as attested by the massive oil spillage in December 2014, when the ship Southern Star-7, ran aground and dumped 358,000 liters of Heavy Fuel Oil in the Sela river. Unfortunately this is not an isolated event, as ships before and after the incident had run aground and emptied their entire cargo in the highly sensitive mangrove system. Additionally, with Sunderbans located at the estuarine phase of Ganga, Brahmaputra and Meghna, it becomes a veritable catchment area for the garbage of entire northern India and major parts of Bangladesh.

I conducted my fieldwork in the West Range of the national park inside the Sunderbans Tiger reserve in 2010-2013. For 2014, I extended my study area to include the Sajnekhali Range, the wildlife sanctuary of the Sunderbans Tiger Reserve. I was able to expand the area in 2014 due to greater logistic support in terms of fund and research personnel from the All India Tiger Monitoring Project 2014. The extent of the study area is given in the Figure 2.1.

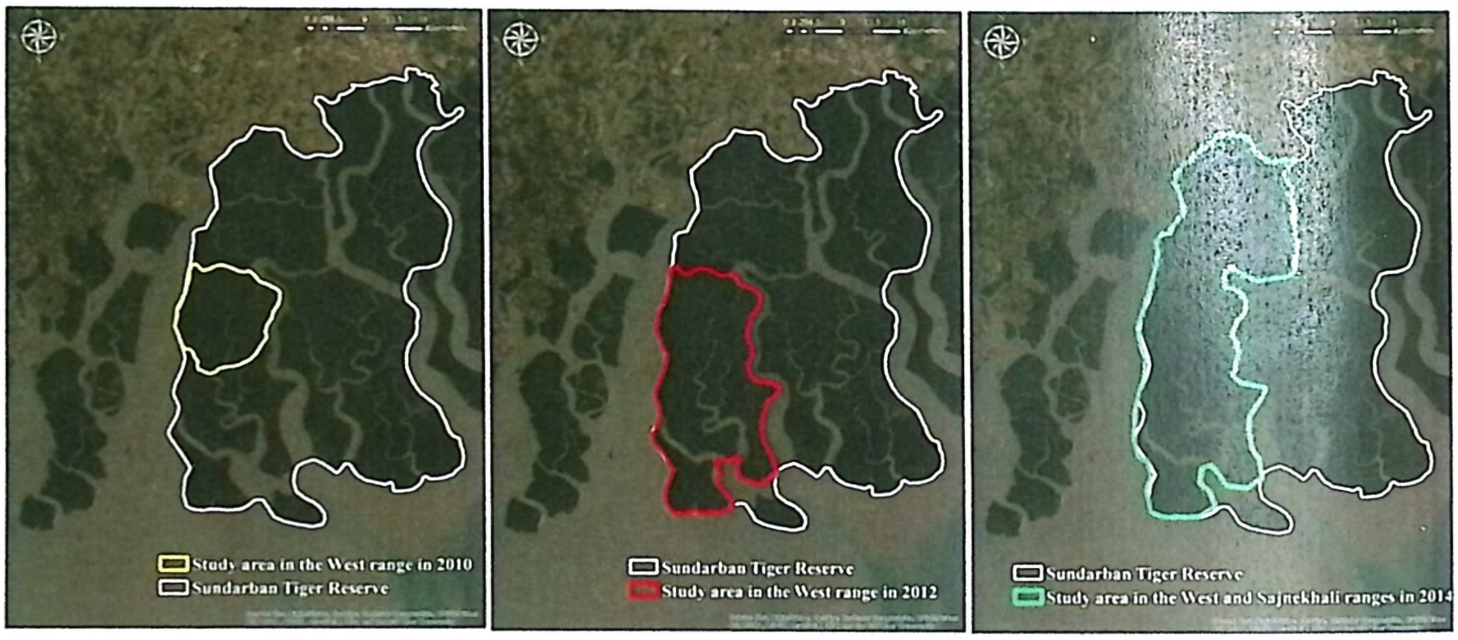


Figure 2.1 : Study area for 2010, 2012 and 2014 in Sunderbans

CHAPTER III - APPLICATION OF CAMERA TRAP BASED MARK RECAPTURE FOR ABUNDANCE ESTIMATION OF TIGERS

3.1 INTRODUCTION

For many animals that are not easily detectable in the wild, either because of their morphology, habitat preference, behaviour or other ecological aspects, mark-capture-recapture is a suitable method for estimating their abundance (Sutherland 2006). This method entails that we capture individuals from the population that we wish to study, mark them, release them back; after allowing sufficient time for thorough mixing of the marked animals into the population, we again capture individuals in which some are marked and some unmarked, we again mark these new unmarked individuals and release all back into the population. This procedure then continues for multiple capture sessions or 'occasions' (Otis et al. 1978). The marks used to identify individuals should be unchanged throughout the study to preserve the history of captures (Otis et al. 1978). As the number of occasions increase, the number of unmarked or new individuals in each subsequent captures reduces till almost no new individuals are captured. Thus, in effect we have counted almost all the individuals in a population.

But this 'almost total count' census is possible only if we assume that the population is closed and every individual has an equal chance of being captured. Since, basic population estimation models were conceptually based on classical urn models (Feller 1950), we have to assume that there are no deaths, births i.e. no demographic change/closure and no emigration or immigration i.e. a population having geographic barriers. However, no biological population is indefinitely closed, so such surveys are conducted over a short period of time during which such changes are negligible. Hence, effectively, we get to sample only part of the population or 'M_{t+1}' (i.e. the total number of uniquely marked individuals at $t+1$th time) within a given time 't'; each of the marked individual have a unique 'capture history' or encounter history, made up of a combination of finite 0s (not captured) and 1s (captured). We can then use this information of outcomes (summarised over all the individuals) to arrive at the total number of individuals (N) in a population by using a maximum likelihood framework (Otis et al. 1978). We assume that the particular set of histories occur due to an underlying detection or the 'detection probability' i.e. 'p' which is a function of a binomial or multinomial distribution; in the simplest case this 'p' is similar across animals and time. Practically, however, equal catchability is unlikely to be true for many wild animal populations. Some individuals may have a higher probability of being captured by virtue of their sex, age, proximity of home range to traps etc. Variation in catchability might also arise from differential trap response of the animals (trap-shy or trap happy) known as the 'contagion of catchability' (Otis et al. 1978) or varying methods of capture or varying weather conditions during the study period (Otis et al. 1978). In fact, keeping these sources of variation in mind, various models that provide for unequal probabilities have been developed to estimate population abundance.

Coming back to the closure assumption, a number of tests for closure are available (Robson and Regier 1968, Pollock et al. 1974). However, most of the time, these tests fail as they implicitly assume equal catchability and unless there is a distinct departure from closure in large samples (Otis et al. 1978). So, instead of using statistical tests, closure must largely be determined by an empirical biological reasoning. Lastly, for this methodology to succeed, no tag/mark should be lost as losses lead to overestimation of the abundance (Otis et al. 1978).

Marks can be artificially applied - metal bands (bats), colour bands (birds), ear tags (mammals), toe clip combinations (lizards), pen markings (invertebrates) or radio tags or they can be natural - stripe pattern of a tiger, or markings on fins of cetaceans (Lettink & Armstrong 2003). Historically, physical "traps" such as live traps, mist nets, pitfall traps have been widely used to sample animal populations (Royle et al. 2013). Advancement in technology has removed the need for such physical capture, enabling the study of many species that are otherwise difficult to capture/observe. Remotely operated cameras have been widely used for species that have unique pelage patterns such as tigers (Karanth 1995), ocelots (*Leopardus pardalis*; Trolle and Kéry 2003), leopards (*Panthera pardus*; Chapman and Balme et al. 2010), bobcat (*Lynx rufus*; Alonso et al. 2015), common genets (*Genetta genetta*; Sarmento et al. 2009), jaguars (*Panthera onca*; Silver et al. 2004), snow leopards (*Uncia uncia*; Jackson et al. 2010) and many other cat species. Such "camera traps" have also been used for species that are less easy to uniquely identify individuals such as wolverines (*Gulo gulo*; Royle et al. 2011), mountain lions (*Puma concolor*; Sollmann et al. 2013) and coyotes (*Canis latrans*; Kelly et al. 2008). Mark-recapture can also be used with DNA fingerprinted faeces from which individuals can be identified (Solberg et al. 2006, Prugh et al. 2005). Hair snares and scent sticks, giving individual DNA information, have been widely used to study black bear (Ursus americanus; Gardner et al. 2010), grizzly bear (Ursus arctos; Mowat and Strobeck 2000), argali (Ovis ammon; Harris et al. 2010). Mark recapture using acoustic detectors, that can be used to indentify at individual level, have been used to study birds (Dawson and Efford 2009), bats, Blainville's beaked whale (Mesoplodon densirostris; Marques et al. 2009) and bottlenose dolphins (Tursiops truncates; Speakman et al. 2010). Search-encounter methods that employ manual searches of geographic sample units such as quadrats, transects or road or trail networks have been used in mark recapture studies of martens (Martes pennant; Thompson et al. 2012), lynx, coyotes, birds (Royle et al. 2013), box turtles (Hall et al. 1999), desert tortoises (Zylstra et al. 2010), lizards (Royle and Young 2008).

Remotely operated cameras can be used as an efficient tool for 'capturing' naturally marked individuals. Using a trip wire and a flash system, George Shiras was the first to design a contraption which let wild animals photograph themselves in the 1890s (O'Connell et al. 2010). The first scientific attempt to record species presence using remote photography was carried out by Frank M. Chapman in Panama (O'Connell et al. 2010). The first successful attempt to use remote photography and population abundance estimation of tigers was conducted by Karanth in Nagarahole (Karanth 1995). Advancements in photographic equipment have made it increasingly possible to use these remotely operated camera traps for addressing a wide range of questions. Camera trap based mark-recapture framework can be used to estimate population abundance and density for individually identifiable animals. This data can further be used for understanding spatio-temporal dynamics of populations (Karanth et al. 2006).

For animals which can’t be individually identified, camera traps can be used to develop indices of relative abundance (Carbone et al. 2001). Camera traps can also be used in studies of community ecology to draw inferences about species richness (Nichols and Conroy 1996). Furthermore, camera trapping exercises can be used for management of rare and elusive species.

With easy availability and affordability, camera traps have become a mainstream tool in tiger conservation and understanding its ecology. Camera traps have been employed to estimate tiger population parameters almost throughout its range countries (O'Brien et al. 2003; Kawanishi & Sunquist 2004; Johnson et al. 2006; Simcharoen et al. 2007; Lynam et al. 2009; Wang et al. 2009; O'Kelly et al. 2012; Karki et al. 2015), with the bulk of the studies occurring in India (Karanth 1995; Datta et al. 2008; Harihar et al. 2009; Royle et al. 2009; Gopal et al. 2010; Sharma et al. 2010; Jhala et al. 2011; Kalle et al. 2011; Singh et al. 2013; Jhala et al. 2014; Sadhu et al. 2017). The only published study on tigers in Sunderbans by camera trap based mark-recapture framework was carried out by Karanth & Nichols (2000). However the statistical inferences made from this study were not robust due to factors discussed in the Discussion section (Section 3.4).

In 2010 I conducted a pilot study on the applicability of camera trap based photographic capture recapture to estimate abundance of Sunderbans tigers. The study was carried out in an area of 270 km^2 in West Range of Sunderbans Tiger Reserve. After a successful implementation of this exercise, the camera trapped area was enlarged in 2012 to 518 km^2 in the West Range. The exercise was repeated in 2014 in the 518 km^2

area of the West Range and in an additional area of 347 km^2 in Sajnekhali Wildlife Sanctuary (Figure 3.1).

Figure 3.1 : Camera trapped areas of 2010, 2012 and 2014

This chapter thus addresses the challenges and possible solutions for the camera trap based mark recapture exercise and ultimately estimation of the population size of tigers in Sunderbans.

3.2 METHODS

3.2.1 Field Methods

Camera trap placement largely determines the success of any study designed to estimate abundance as it affects the detection probability. Camera traps should be placed in a way such that they seek to maximise the detection of individuals (Otis et al. 1978). When traps are spaced too far apart, there is a greater chance of missing an individual completely, as the areas in between might be large enough to contain one individual's home range (Karanth & Nichols 2000). On the other hand closer trap spacing does increase the probability of detecting individual animals; however it often reduces the sample area coverage, resulting in fewer individuals being available for sampling ((Karanth & Nichols 2000) and also leads to logistic wastage. Hence, spacing of camera traps should be determined by habitat use and space usage of target species as well as logistic constraints. For tigers, typically, traps are set at about 2-10 km distance apart depending on the female home range as breeding females have the smallest home ranges (Smith 1993). This automatically ensures that transients as well as adult males have multiple traps operating in their movement paths/ranges. Barlow (2009) observed that the home ranges of the two females that they had collared in Bangladesh Sunderbans, between 2004 and 2006, were 12.3 km^2 and 14.2 km^2. However, these females were from a higher than average productive area, hence extrapolating these areas to be the average female home range sizes in Sunderbans would be misleading. Information on female home ranges in low to medium prey density areas is lacking. Areas like Royal Chitwan, Nepal and Nagarahole with high prey density have recorded female home range sizes to be about 16 km^2 (Sunquist 1981) and 16.5 km^2 (Karanth & Sunquist 2000) respectively. Considering the lacuna of information, I could at best use these numbers to delineate the minimum inter-trap distances. Hence, in my camera trapping exercise, in the first two years, I ensured that the minimum distance between adjacent camera stations was 2 km while the maximum distance was 4 km, as dictated by the assumed home range radius of the females and logistic constraints. In 2014, due to greater logistic support from the All India Tiger Monitoring Programme, I had a more extensive coverage following a cellular grid design. I overlaid a 5 sq. km. grid onto the study area and maximised camera trap locations by covering almost all (>80%) grids.

Tigers naturally occur at low densities and chances of encountering them are quite low. Therefore, in most places, camera traps are set on trails and paths that are most likely to be frequented by tigers, in order to maximise capture-recapture probabilities. However, it was not feasible to conduct extensive foot surveys due to the threat from tigers and lack of trails due to tidal effects in Sunderbans. Hence, I located trapping stations by boat in accessible areas with ample visibility to minimize chances of lethal encounters with tigers. I instead lured tigers to my camera stations with food (meat—2 to 5 kg) and fresh water as bait and a concoction of rotten eggs, fish and chicken liver as lure to maximise photo-capture rates. I also oriented tigers to approach baits using nets and cut vegetation so as to obtain both flank pictures for individual identification. Trapping stations comprised of two cameras, set at a height of 40–45 cm from the ground, facing each other across a maximum distance of 8 m to capture both flanks of the animal (Roy et al. 2015). I used passive infra-red Moultrie Game Spy D—40 Digital Game cameras (Moultrie Feeders, Alabama, USA) in 2010, 2012 and 2014 and whiteflash Cuddeback Ambush - Model 1170, cameras (Cuddeback, Wisconsin, USA) in 2014 (Table 3.1).

Year	Location	Effective trapping area (in km^2)	Number of camera traps	Trap nights
2010	West Range	270 (SE range 251–291)	11	407
2012	West Range	518 (SE range 500–535)	29	1073
2014	West Range	518 (SE range 498-537)	76	2763
	Sajnekhali Range	347 (SE range 328-366)	40	960

Table 3.1 : Sampling details of camera trapping exercise 2010-2014

For the first two years, to minimize possibilities of damage to cameras and food rewards getting washed away, due to submergence during spring high tide, I deployed the entire trap set-ups for 9–10 neap tide days when the high tide water levels were low, and removed them for the next 4–5 spring tide days when water levels reached maximum height, continuing this cycle for a maximum of 55 days in both years. In 2014, I built platforms 45-50 cm high, made of mud and leaves for the meat and the fresh water. I placed the cameras then accordingly 90-100 cm high from the ground facing the platforms. By ensuring that the tidal water wouldn't touch the cameras or the baits and lures, I camera trapped continuously even during spring tides in 2014. I sampled for 32 days in West range while in Sajnekhali range the sampling was for 23 days. I inspected the camera trap stations after every alternate day to ensure proper functioning of cameras and replenishing the baits to minimize spatiotemporal heterogeneity in tiger visitation among stations (Gerber et al. 2012).

3.2.2 Analytical Methods

As mentioned earlier, one of the basic premises of population size estimation through mark-recapture is that the population remains constant in size and composition during the sampling period, i.e. a closed population. However, tiger populations have high mortality, recruitment and turnover rates (Karanth et al. 2006). To counteract these violations of closure, it has been suggested that trapping period for a closed population study of tigers can extend till a maximum of 45-60 days (O'Connell et al. 2010). I tested this specification by using the apparent annual survival rate of tigers (0.72) from one of the densest populations, i.e Corbett Tiger Reserve (Bisht et al. 2019). This annual survival rate can be converted to daily survival rate i.e. 0.68^(1/365). [1 - (daily survival rate)^45-60 days] will then give the mortality and emigration rate (since this survival rate obtained in that study was through intensive camera trapping for 365 days and hence was confounded by both these processes) over 45-60 days which was estimated at 0.04-0.05. I believe that the 45-60 days requirement is justified in light of - a. it is never possible to ensure complete closure, however a 6% mortality is within tolerable limits and b. if the high density population of Corbett with lower survival is closed during the stipulated time, then the same should be applicable for low density population of Sunderbans. Hence, I can assume that the selection of 55 days of trap operation had not violated closure in terms of apparent mortality.

Selection of particular age class or cohort further minimise closure violation. I used photographs of individuals more than 1 year of age for analysis as younger animals rarely accompany mothers on foraging trips and are underrepresented in camera trap studies (Karanth and Nichols 1998). They are also the most vulnerable cohort to mortality events in the short term. This way, I accounted for demographic closure. On the otherhand, a geographically closed area removes the uncertainty associated with inherent mobility of tigers (O'Connell et al. 2010). In most cases, however, since the trapping area is a sample of a larger area, from where animals move in and out, it becomes difficult to say which area is actually being trapped (Lettink & Armstrong 2003). In such cases, post hoc analytical operations are conducted to address this violation of geographic closure. However, in my case, I was able to use the information from our four radiotagged individuals (one female and three males) with GPS PLUS Iridium satellite collars (VECTRONIC Aerospace GMbH, Berlin, Germany) beforehand to delineate the trapping area . I found that tigers rarely crossed channels greater than 1 km width (Naha et al. 2016). Therefore, in all the three years of sampling, I chose trapping areas, that were bound on almost all sides by 1 km wide channels to minimise the uncertainty associated with immigration/emigration of individuals. The selected study areas were also representative of the various major habitat types found in Sunderbans that potentially influence tiger movement and usage (Naha et al. 2016).

For analytical purpose, the data obtained, is formatted in a standard "X matrix" (Otis et al. 1978). This format summarises the capture history of each individual by specifying whether the *i*th individual was encountered on the *j*th sampling occasion, consisting of a contiguous series of '1's (animal was captured/recaptured) and '0's, (animal was not recaptured) (Cooch et al. 2006). I identified individual tigers by their stripe patterns and summarized their detection history across occasions into the X matrix where each discrete sampling occasion was defined as a 24-h period starting at 0000 hrs.

After obtaining the summarised capture history we then use a multinomial maximum likelihood technique to estimate the detection/capture probability or 'p' and ultimately the abundance or 'N'. We try to find the value of p and N at which the likelihood of getting that particular X matrix (i.e. the various outcomes or combinations of 1s and 0s and the frequency of each of these outcomes) is maximised (Otis et al. 1978). For computational ease, likelihood models are generally transformed to log likelihoods estimators. We can execute this exercise with two different approaches- a. full likelihood approach wherein missing individuals are also part of the maximum likelihood assumption (Otis et al. 1978) or, b. conditional likelihood approach wherein detection is entirely modelled on individuals detected at least once and missing individuals or rather N is a derived estimate (Huggins 1989). In either scenario, p can be modelled accordingly using different assumptions of variations in catchability. The most general model where capture probability varies across occasions, differential response to the traps and across individuals is the M_{tbh} model; however, this is more of a theoretical model as there are too many parameters to be estimated from too few sufficient statistics making it an unidentifiable model (Otis et al. 1978). On the other extreme, is the specialised M_o model, where capture probabilities are similar/equal across time, individuals and trap response (Otis et al. 1978). We can model capture probabilities on the assumption that animal's initial capture probability changes in subsequent recaptures as a response to the traps. The model M_b is based on removal models and allows the trap shy or the trap happy behaviour to be modelled out of the abundance estimation as a nuisance parameter and assumes all animals to have similar response to the traps (Otis et al. 1978). Model M_t allows captures probabilities to vary over time and this variation can either be due to different weather conditions (eg. stormy on one occasion and sunny on another which could possibly influence/limit animal movement) or due to usage of different types of traps. We also note that capture probabilities can vary across individuals due to factors like weight, gender, age, social hierarchy etc. Such heterogeneous detection can be modelled using Model M_h, in which, populations are assumed to comprise of latent mixtures or groups of individuals where detection remains the same within a group but differs across groups and these groupings can be attributed to some known or unknown variable (Norris and Pollock 1996). Lastly, the capture probabilities can be further modelled as a combination of these three sources of variation.

I formulated the variation in capture probabilities by considering models M_o, M_b, M_h and M_{bh} (where capture probabilities are influenced by both trap response and individual heterogeneity) since I believe our usage of baits and lures could have an effect on the response of tigers (*viz.* trap happy) and individual heterogeneity is inherent in any given population. Other models like M_t, M_{th}, M_{tb} (where capture probabilities are influenced by time, time and heterogeneity and time and trap response, respectively) were not postulated as similar camera traps were used and there was no marked difference in the daily weather/temperature conditions during the study period. I used both full likelihood as well as conditional likelihood estimators in program MARK v 6.2

(White and Burnham 1999) to estimate the population abundance within the trapped area. The primary difference between the two approaches is the inclusion and exclusion of the missing individuals (individuals with only 0s in their capture histories) respectively. In conditional likelihood the missing individuals are removed by adjusting or conditioning the probabilities of each of the different outcomes (barring not captured even once) by dividing them by the probability of detecting an individual least once, i.e. $[1-(1-p_1)(1-p_2)....(1-p_t)]$. In both the approaches, during computation the p's or detection probabilities are transformed to betas or 'ß' using a type of a link function as maximum likelihood operates best with unbound parameters and p is constrained and bound between 0 to 1. In full likelihood, the p is linked to ß by a sine function while in conditional likelihood it is linked by a logit function. For full likelihood, the missing individuals or 'f_{000}' is also transformed to a beta through a log function to bind it between positive integers. A literature review of the theory of maximum likelihood based mark-recapture (Otis et al. 1978) shows that it was primarily designed for abundant species with each unique encounter history having multiple replicates. In my case with such low number of captured individuals, with each having mostly unique outcomes over such long number of occasions, such data intensive technique often failed to arrive at plausible estimates (Gerber at al. 2014) and lead to lack of convergence more often than not. The difference between the two (full likelihood and conditional likelihood) however is more from a technical statistical point of view. Hence I reported full likelihood estimates where possible and conditional likelihood estimates where the former failed.

I had a low sample of photo-captured individual tigers (n=10) in 2010. I conjectured that since I had used the same methods in the same area in 2010 and 2012, the detection probability of tigers would likely be the same between the years. Hence, I computed the individual years' estimates by combining and borrowing information on detection probability (Lebreton et al. 1992; Williams et al. 2002) from the two years, for greater robustness. I computed abundance estimates of 2014 separately. I selected the model with minimum Akaike Information Criteria corrected for sample size (AICc, Akaike 1974) for inference.

Mark-recapture studies can also be used to estimate absolute densities (D). In most studies, the trapping area is a sampled area that is representative of and contiguous with the larger area occupied by the population. However, in attempting to estimate this density, we realise the problem of identifying the area actually used by the trapped animals (Williams et al. 2002). Animals will inevitably be moving in and out of the camera trapped area, especially near the edges of our trapped area creating an "edge effect" (Williams et al. 2002). This makes it difficult to say what area is actually being trapped, and biases the density. Traditionally, a buffer strip is added around the polygon, formed by joining the outer edges of the traps (Otis et al. 1978). The sampled area is now known as the effective trapping area (ETA) and is assumed to include the marginal animals (O'Connell et al. 2010). Various methods have been used to calculate this buffer strip width namely one-half of mean maximum distance moved (Dice 1938), inter-trap distances (Burt 1943), mean movements among traps, maximum movements among traps (Hayne 1949), nested grids (Otis et al. 1978) and assessment lines (Smith et al.

1971). However, most of these *ad hoc* methods are difficult to validate biologically as they neither acknowledge the importance of space in ecological processes nor do they account for the spatial biases induced by the sampling effort. Intuitively, if we increase our sampling area the abundance or N should also increase. However, in these non-spatial methods N remains constant no matter how much we increase or decrease the area as N is not linked to the landscape in any explicit manner (Royle at al. 2013).

Subsequently, Efford (2004) developed spatially explicit capture-recapture models (SECR) that consider the spatial nature of capture-recapture data alongside the temporal capture history in a maximum likelihood framework, thereby avoiding the use of ad hoc estimation of ETA. Herein, we use the information on spatial captures as well as the spatial layout of the traps along with a mask or a state space which delimits the maximum area from which animals will have non-negligible probability of being captured in the traps. We assume the "activity centres" of animals (or the theoretical centroid of an animal's home range/space usage) are distributed in a spatial Poisson point process and are independent and identically distributed. The home range centre does not mean specifically the biological home range centre but rather the centroid of the area/space actively used by the animal during the study period. Hence, this technique applies for non-territorial species as well (Royle et al. 2013).

Assuming detection at the activity centre of an individual, s_i, to be 'p_0' (or g_0), we infer that as an animal moves away from the centre, the detection probability falls, hence one can define 'p_{ij}' as the detection probability of an individual *i* at trap *j*, as a function of distance of the trap from the activity centre, 'd', g_0 and the spatial scale of detection (or till the distance detection is non-zero) 'σ', related through different encounter models such as Gaussian, hazard, negative exponential etc. (Royle et al. 2013). The outcome that we see in the form of number of detections of an individual at a trap, y_{ij}, is a binomial or a Bernoulli function of K trapping occasions and p_{ij} detection probability at the trap. However, these activity centres are unobservable hence one has to treat them as latent variables and marginalise the conditional-on- s_i out of the overall y_{ij}-*s* of all individuals. We can do so by considering each and every point in the mask as a probable activity centre for each individual (we assume s_i to have a uniform prior distribution). We then calculate the likelihood of the encounter history of an individual given a particular probable activity centre and integrating over the entire collection of such probable activity centres (in effect the entire mask). We can simultaneously include the missed/uncaptured individuals in our likelihood estimation by considering their encounter history comprising of 0's only and thereafter maximising likelihood for n_0 (undetected individuals) and detection probability. Thus we can obtain a spatially explicit abundance estimate. We can marginalise the above likelihood further where we remove the N from our likelihood model. In this case we consider that the prior distribution of N is Poisson, dependent on the intensity (or density) of the activity centres in the state space and the area of the state space. Hence we can maximise this likelihood to arrive at the value of density directly (Borchers and Efford 2008). We must keep in mind that here, number of activity centre is synonymous with the number of individuals as each individual can have only one activity centre. So unlike the *ad hoc* methods for estimating density, we see that SECR ties the detection process to the space usage of an animal.

Similar to the models in mark-recapture, here too one can model both g_0 and σ having effects of behaviour (overall response or trap specific response), heterogeneity, time or a combination of either of the three, wherein, such effects are modelled as a linear regression on the baseline detection probability of p_{ij}. Lastly, by extension SECR models can be further used for studying spatial processes such as individual movement, resource selection, space usage, and population dynamics.

In my case, I used both the conventional ETA method for comparing with previous studies which had employed the same, conducted in Sunderbans and elsewhere, and the more robust SECR method to account for the inherent importance of space in movement of tigers as well as variability due to the observation process. To estimate the ETA, I added a buffer of 5.73 (SE 0.72) km (the average home range radius obtained from 95 % fixed kernel areas of four radiocollared tigers) around the minimum bounding polygon joining the outermost camera traps (Roy et al. 2015). Naha et al. (2016) demonstrated that channels wider than 1 km width were generally avoided by tigers, so I masked these channels out of the larger polygon. I estimated variability on ETA by buffering the minimal bounding polygon with buffers of standard errors added and subtracted to and from the home range radius, and subsequent removal of non-tiger habitat from the computation in Arc-GIS 9.3 (ESRI 2011).

I then estimated the conventional population density (D) as N/ETA. The variability in tiger density (Karanth and Nichols 1998) is typically computed by combining the variability in population estimates with the variability in ETA by using the delta method (Seber 1973). However, this approach assumes a uniform buffer around the ETA and does not account for the associated patchiness in tiger habitat and non-habitat. Therefore, I computed the potential variation in tiger density in a more geographically informed manner, wherein, the lower limit of tiger population was divided by the upper estimate of effective area (obtained from the GIS analysis) to estimate the lower limit of tiger density while the higher limit of tiger population was divided by the lower effective area to estimate the upper tiger density limit.

I implemented SECR analysis in the maximum likelihood framework using the secr package (Efford 2015) in program R v 3.1.3 (R Core Team 2015). I created two matrices that summarized the spatio-temporal detection history of individuals and the spatio-temporal layout of the traps. I used proximity detectors specifying a buffer of 18 km. I used a habitat mask wherein, I removed areas separated from the trapping area by water channels > 1 km width. Similar to the abundance estimation, I estimated tiger density of 2010 and 2012 separately, while borrowing the information on g_0 and σ from both years. I estimated tiger density of 2014 separately. I modelled g_0 as constant (null), influenced by behaviour (b, where capture and recapture probabilities for tigers differ), and with trap-specific behaviour (bk, where the capture and recapture at specific traps differ) and σ as constant (null) or with two group heterogeneity (h2, differing in their movement patterns as two groups). The detection probability at a trap was modelled using a halfnormal distribution function. I then selected the model with minimum Akaike Information Criterion as the best model.

3.3 RESULTS

My sampling efforts comprised of 37 occasions (in both 2010 and 2012) and 57 in 2014. Number of unique tigers captured (M_{t+1}) was 10 in 2010, 22 in 2012 and 14 in West Range and 14 in Sajnekhali Range in 2014. Using the full likelihood estimators the, models in increasing order of AICc for 2010 and 2012 for West Range in program MARK are shown in Table 3.2.

Model	AIC values
Mbh	772.80
Mh	773.79
Mb	807.04
Mo	820.05

Table 3.2: AICc values of models for population abundance through program MARK for the years 2010 and 2012 for West range.

while models in increasing order of AICc for 2014 for West Range in program MARK are shown in Table 3.3.

Model	AIC values
Mb	341.28
Mbh	389.47
Mh	396.66
Mo	398.33

Table 3.3 : AICc values of models for population abundance through program MARK for the year 2014 for West range.

and using the Huggins conditional likelihood estimators, the models in increasing order of AICc for 2014 for Sajnekhali Range in program MARK are shown in Table 3.4.

Model	AIC values
Mbh	272.05
Mo	273.19
Mb	274.68
Mh	274.68

Table 3.4 : AICc values of models for population abundance through program MARK for the year 2014 for Sajnekhali range.

The combined effect of individual heterogeneity and behavioural response to traps (Mbh) model was the best in 2010 and 2012 while for 2014 behavioural response to traps (Mb) model was the best for West Range. In case of Sajnekhali Range, even though the behavioural response to traps and 2 mixture heterogeneity (Mbh) model was selected as the best on the basis of AICc values, I chose the null (Mo) model as the preceding model could not converge. I feel that not only lack of convergence was the issue at hand but there were too many single captures for complex models like M_h or M_{bh} to work. Going by the principle of parsimony, M_o is perhaps the best model to fit the current data.

Estimates of abundance (N) were 11 (SE 2) in 2010, 24 (SE 3) in 2012, 16 (SE 3) in West Range and 14 (SE 1) in Sajnekhali Range in 2014 (Table 3.5).

Parameter	**2010**	**2012**	**2014 West Range**	**2014 Sajnekhali Range**
Mt+1	10	22	14	14
Recaptured individuals	6	18	14	12
Total number of camera stations	11	29	76	40
Best Model	M_{bh} and M_h		M_b	M_o
Population estimate N	11 (SE 2)	24 (SE 3)	16 (SE 3)	14 (SE 1)
Group probability (p_i)	0.38 (SE 0.11)			
Capture probability of group 1 (p_1)	0.05 (SE 0.02) 0.05 (SE 0.02)		0.05 (SE 0.03)	0.14 (SE 0.02)
Capture probability of group 2 (p_2)	0.26 (SE 0.03)			
Recapture probability of group 1 (c_1)			0.19 (SE 0.02)	
Recapture probability of group 2 (c_1)	0.06 (SE 0.02)			

Table 3.5 : Abundance estimates of tigers from capture-mark-recapture analysis in MARK.

The ETA was estimated at 270 (SE range 251–291) km^2 for 2010 and 518 (SE range 500–535) km^2 for 2012 that gave density estimates of 4.07 (SE range 3.09–5.17) and 4.63 (SE range 3.92–5.40) tigers/100 km^2 for the 2 years respectively. In 2014, the ETA was estimated at 518 (SE range 498-537) km^2 for West Range and 347 (SE range

328-366) km^2 for Sajnekhali Range, giving density estimates of 3.1 (SE range 2.6-6.2) and 4 (SE range 3.8-5.5) tigers/100 km^2 for the two ranges respectively.

In SECR, the model with g_0 having trap-specific behavioural response and σ best explained as 2-mixture heterogeneity was selected as the best model in 2010-2012 (Table 3.6). Tiger densities estimated by these models were 4.08 (SE 1.51) in 2010 and 5.81 (SE 1.24) tigers/100 km^2 in 2012. For 2014, where I combined and allowed borrowing of information on detection probability (Lebreton et al. 1992; Williams et al. 2002) from the two ranges, for greater robustness, the best model of g_0 having equal catchability and σ 2-mixture heterogeneity was selected. This gave tiger density at 3.15 (SE 0.88) in West range while in Sajnekhali the density was 4.79 (SE 1.31).

Year	**Non-spatial estimates**			**Spatially explicit estimates**			
	Minimum bounding polygon (km^2)	**Effective trapping area (km^2)**	**Density [tigers/ 100 km^2 (SE)]**	**Best model**	**Sigma (σ) in km (SE) and group 1 probability (p_1) (SE)**	**g_0 (SE)**	**Density [tigers/ 100 km^2 (SE)]**
2010	104	270 (SE range 251–291)	4.07 (SE range 3.09–5.17)	D (year), g_0 (bk), σ (h2)	$\sigma_1 = 2.56$ (0.26); $\sigma_2 = 6.74$ (1.20); $p_1 = 0.91$ (0.06)	0.026 (0.01)	4.08 (1.51)
2012	372	518 (SE range 500–535)	4.63 (SE range 3.92–5.40)				5.81 (1.24)
2014	420 (West Range)	518 (SE range 498-537)	3.1 (SE range 2.6-6.2)	g_0(.), σ(h2)	$\sigma_1 = 1.89$ (0.21) $\sigma_2 = 4.24$ (0.43) $p_1 = 0.71$ (0.10)	0.04 (0.007)	3.15 (0.88)

188 (Sajnekhali Range)	347 (SE range 328–366)	4 (SE range 3.8-5.5)		4.79 (1.31)

Table 3.6 : Density estimates of tigers from non-spatial traditional capture-mark-recapture using home-range radius for computing ETA and Spatially explicit capture-recapture models.

3.4 DISCUSSION

Karanth and Nichols (2000) carried out camera trapping based capture-recapture in a subset of this landscape, reporting average tiger density of 0.7 tigers/ 100 km^2 (SD 1.67). The major shortcoming of this study arose from large and varying distances between neighboring camera traps, creating sampling holes, wherein residing individuals would be completely missed. This violates a critical assumption of conventional capture-recapture models that every individual should have non-zero probability of detection, and leads to negatively biased abundance estimate. Accuracy and precision of the study was further affected due to very low captures and no recaptures.

My study generated the first-ever reliable estimate of tiger abundance for the obscure yet ecologically significant Sunderbans using the established robust technique of mark-recapture. Sunderbans has a medium tiger density with densities varying from 3 to 6 tigers per 100 sq. km. when compared to other tiger occupying forests (Jhala et al. 2014). In conjunction with the estimates of Indian Sunderbans tiger population of 76 (62 to 96) tigers and Bangladesh Sunderbans tiger population of 106 (83 to 130) (Jhala et al. 2016), the entire Sunderbans landscape harbours 182 (145 to 226) tigers making this landscape one of the top 5 largest global populations of the species making it evident that this population is extremely important for the global recovery of the species.

By repeating my camera trap exercise in the same area in subsequent years in a reasonably large and representative area of Sunderbans, I demonstrate that tiger density is much lower than that reported by Barlow (2009). With the use of (a) appropriate camera spacing which minimised the chances of missing resident tigers, (b) baits to lure and maximise tiger photo-captures, (c) selecting a suitable study area so as to ensure geographic closure and reduce the uncertainty associated with ETA, and (d) explicitly modelling for differential capture and recapture probabilities due to baits as well as accounting for spatial heterogeneity in my analysis, I was able to achieve and demonstrate the reliability of my estimates.

The rewards for camera visitation (food and water) were small compared to the tiger's requirements and were replenished only after 2–3 days. Therefore, I believe that tiger movement, if at all altered, would be only at local scales. By modelling σ, the movement parameter, and g_0, the detection probability in SECR, for spatial heterogeneity and behaviour effects, I effectively accounted for the use of attractants. Additionally, there may be reservations about whether individuals residing outside the study area may get attracted to the camera traps by the usage of baits, thereby temporarily inflating the density. In my study, chances of attracting individuals outside the survey area were minimised by overseeing that the buffer between the outermost traps and the effective trapping area was larger than the distance over which traps can be detected (du Preez et al. 2014). I also delimited the study area by hard boundaries on three sides and included the adjacent sanctuary area of 326 km^2 in the north as model inference space for SECR and ETA in non spatial models in 2010-12, and in 2014, the northern sanctuary was included in the trapping area and the entire trapping area was surrounded by wide (>1 km width) water channels on all sides. I am therefore quite certain that use of attractants did not inflate local tiger density. By considering a large habitat mask, I could also account for animals which might have had a small chance to move in from areas outside the trapping array. Gerber et al. (2012) and du Preez et al. (2014) have further shown that in territorial animals like the Malagasy civet (*Fossa fossana*) and the leopard (*Panthera pardus*), even if the baits were to work at great distances, the species' inherent territoriality would stop outsiders from frequenting the traps located in their territories. This same argument can be extended to the tigers as well, thereby forming a ''biological'' barrier (du Preez et al. 2014) against intruders from outside the trapped area.

SECR approach gave comparable results to the non-spatial estimate by traditional capture-mark-recapture analysis wherein GPS telemetry based home range radius of radiocollared tigers was used to buffer the camera bounding polygon. In fact, the paired two samples for mean t-test showed there was no significant difference ($t(3)= 0.012$, $p= 0.495$) between the two methods of estimating densities. This similarity was primarily due to the geographical closure by large water channels thus ensuring minimal movement of individuals in and out of the study area.

Along with the advantages of this study, I believe it is important to also enunciate the flaws so as to improve such a study in the future. Perhaps the biggest challenge to this type of study is amount of personnel, finances involved. Due to the omnipresent threat of the tigers, I was forced to select camera trap stations at visible yet random locations. Selection of such sites automatically meant I had to find a way to coax the tigers to my cameras which inherently lead to greater costs in terms of bait procurement and the logistics involved with frequent visitations. Further since the trap sites were not on trails, clearing of the vegetation in select patches took added time and effort. My study was also dictated by tidal conditions, where submergence by the incoming brackish water lead to irreparable damage to the cameras. Lastly as mentioned afore, mark-recapture method works best with abundant species. Mark recapture studies focused on tiger abundance estimation often suffer from sparse data which is due to a. low detection b. small number of individuals detected c. long survey duration and d. heterogeneous detection amongst individuals (Gerber et al. 2014). The likelihood based estimators are said to be good estimators having properties of consistency, normality, and efficiency. This however is applicable when the sample size is large (Otis et al. 1978). In fact, White et al. (1982) mentioned that with small sampling occasions, if N is less than 100 and p is less than 0.3, a good capture–recapture study probably cannot be done and precision become especially problematic. Complex model fitting becomes statistically redundant with such poor information. Gerber et al. 2014 suggests that for such type of capture-recapture studies of low density population, one must strive to maximise the probability of detecting animals at least once and to redesign the study by trying to detect all or almost all of the population. Nevertheless, given the current available techniques available, mark-recapture is the 'best of the worst' in terms of generating reliable estimates for ecologically sensitive areas such as Sunderbans.

The outcome of this study has broader implication for similar population estimation exercises for landscapes occupied by low to medium density carnivores. In most animals, movement and space use is usually density dependent. Low density areas report larger movement parameters which can then conversely affect detection of individuals at traps (Van Moorter et al. 2016). In low density areas mark recapture techniques can suffer due to the inherent low capture probability of such populations. In such a scenario increasing capture efforts in terms of increased number of traps (both intensively and extensively) and sampling period can boost the capture probability. Baits and lures should also be used to increase detection. Selection of trapping area must be such that atleast geographic closure can be ensured for most parts of the area; the choice should be driven by prior knowledge on animal movement and habitat usage patterns from auxillary radiotelemetry data, if available. In general, spatial estimators of population size must be favoured over conventional mark-recapture estimators as the former takes into account the spatial process of animal distribution and sampling. A key point is to tailor standard techniques according to the local conditions without violating the core assumptions of the estimators.

CHAPTER IV - APPLICATION OF SIGN DECAY AND DEPOSITION RATES FOR ABUNDANCE ESTIMATION OF TIGERS

4.1 INTRODUCTION

Caughley (1977) stated that an index of abundance is "any measurable correlative of density". Indices carry information about the relative size of any population. In general, population indices, be it direct (capture or harvest indices) or indirect (singing count or dung piles), have a monotonic relationship with abundance and under the assumption of homogenous detectability, can provide information in change in size (Williams et al. 2001). To convert index or sign - abundance or density directly to population abundance or density, one needs to have information on – a. deposition rate i.e. the rate at which the selected index is produced and b. decay rate i.e. the rate at which the index decays (Laing et al. 2003).

This method of estimating animal abundance through sign density-deposition-decay is widely used for mammals such as forest elephant (*Loxodonta cyclotis*; Barnes and Jensen 1987), sika deer (*Cervus nippon*; Marques et al. 2001), roe deer (*Capreolus capreolus*; Tsaparis et al. 2009), orangutan (*Pongo pygmaeus*; Mathewson et al. 2008), chimpanzee (*Pan troglodytes*; Plumtre and Reynold 1996), gorilla (*Gorilla beringei beringei*; Guschanski et al. 2009), duiker (*Cephalophus* spp.; Van Vliet et al. 2009), kudu (*Tragelaphus strepsiceros*; Ellis and Bernard 2005) etc. which are rare, elusive or difficult to detect in closed habitats but leave signs such as dung or nest which are easier to survey (Laing et al. 2003).

Taking the example of estimating forest elephants (Barnes and Jensen 1987) - let us imagine a defined homogenous forest patch where there are no elephants and no elephant dung piles. Now a herd of 'E' elephants move in this patch and from day one, start eating and defecating. Let us say, 'D' dung pile is produced per elephant per day (hence the defecation rate or the deposition rate in this example), so after day one there should be 'Y' dung piles in the forest, which then goes on increasing linearly everyday. However, environmental factors (both biotic and abiotic) along with the gut microbiota will lead to decay of these dung piles. Let us consider that in a day, 'r' percentage of dung piles decay (i.e. the decay rate). Assuming the decay rate is constant, the same percentage of dung will decay everyday. Further assuming a steady state in fecal dropping (i.e. same number of D dung piles are being added to the system everyday), after some days the number of dung piles decaying will rise to equal the number of dung piles being deposited daily. At this stage there is equilibrium, and there is a steady state where the number of dung remains constant everyday. Now we can simply convert the dung density to elephant density by E x D = Y x r. Therefore,

E = (Y x r) / D (Barnes and Jensen 1987)..................... (equation 1)

In most cases, when using this method for surveying animal abundance, distance sampling is used to estimate the density of dung/nests/pellets (i.e. signs) to account for imperfect detection of signs (Laing et al. 2003). The depositon rate is either obtained from observing wild animals (eg. Wing and Buss 1970, Kouakou et al. 2009, Rivero et al. 2004) or from the zoo (Marques et al. 2010). The decay rate is estimated from observation in field and its variability can be accounted by including information on differing seasons, terrain and other relevant environmental factors.

The sign decay deposition ever since its conception has evolved over time. Kuehl et al. 2007 outlines three approaches that can be used to estimate animal densities using sign densities. The first approach, known as the retrospective decay rate entails that one locate freshly deposited signs during several regular spaced sampling periods preceding the "sign transect" survey; these signs are then revisited at the beginning of the transect survey to establish if they have decayed. As it addresses the inherent decay rate heterogeneity it bypasses the steady state assumption. But this in turn ultimately leads to poor precision. It is also plagued by poor precision as it does not take into account the spatial variation in decay rates. The second approach, i.e. the marked sign count, removes the decay parameter altogether. There are only two visits required- one in which one has to locate and mark all existing signs in a given transect detection zone and in the second visit, count all the new signs that have been deposited in the inter-visit interval. This method also allows for relaxation of the steady state assumption and estimates animal density as number of new signs/(detection zone area x length of inter-visit interval x daily sign deposition rate). However this method is also fraught with poor precision as the recent signs (deposited between inter-visit interval) forms only a fraction of the standing stock of signs. The last approach, called the prospective decay rate, requires a second visit after the transect survey to estimate decay rate. This method has higher precision compared to the other two approaches but requires a steady state assumption.

I decided to test if sign decay-depostion method could be used to estimate tiger density in Sunderbans. Sunderbans, lying at the interphase of land and sea, comprises of many islands crisscrossed by channels. A tiger's home range covers multiple islands (Naha et al. 2016). In order to move from one island to another, it has to swim across channels and in the process 'deposit' signs on the mud banks of the channels. Since each tiger uses multiple islands, the signs on the mud banks must also be indicative of the relative abundance of tigers. As Sunderbans is subjected to semidiurnal tides daily, I expected these signs to 'decay' due by the tidal action on the mud banks. I defined signs as the crossings (set of the pugmarks) deposited on the muddy banks of islands, when they cross channels as represented in Figure 4.1.

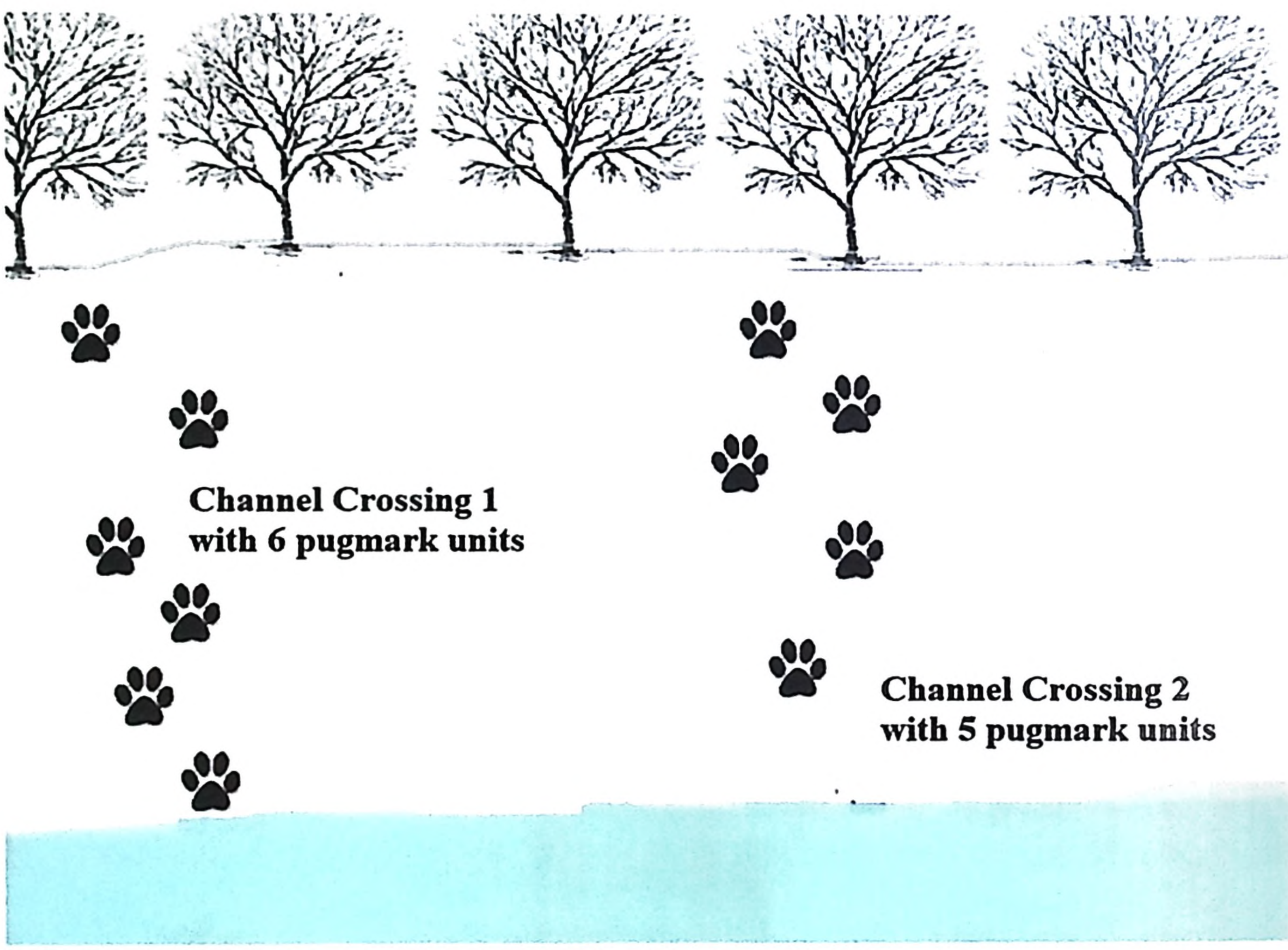


Figure 4.1 : A representational diagram to illustrate the sign (channel crossing) defined for this study

I used the retrospective decay rate as it relaxes the steady state assumption and I felt that the assumption of constant decay of signs was unrealistic. I sought to overcome the poor precision levels associated with retrospective decay rate by selecting multiple channels having varied natural characteristics to account for the spatial heterogeneity in decay rates. I considered the camera trap density to be the 'control' and compared with the same the density generated through signs. Camera trapping in Sundarban is a costly and dangerous (due to high chances of encountering the tiger inside the island) exercise. I wanted to test if this method, could work as a cheaper, less dangerous yet precise alternative as the fieldwork can be done in the safety of the boats.

4.2 METHODS

4.2.1 Field Methods

As I considered the 'signs' for this method to be pugmark sets deposited during channel crossing by tigers, I had to estimate both decay rates and deposition rates from my field data. The channel crossings are primarily decayed by the action of water, brought in by the tidal fluctuation. For estimating decay rates, I selected channels of varying widths in the same area where I conducted the camera trapping exercise (Table 4.1).

Transect ID	Channel length in kms	Number of crossings monitored till decay
Bhagoban Bharani	11.17	25
Storekhali	6.38	12
Moraboni	6.8	4
Lakhikhali	8.58	15
Khal opp Choramayadip	1.4	4
Nikarikhali	4.9	3
Choramayadip	8	1
Gubdi Khal	1	1
Khalsibani Khal	3.6	1

Table 4.1 Sampling details of the decay exercise

The channels selected had varying vegetation type, mudbank slope and varying softeness/hardness of the bank, so that the decay rate could be estimated against all possible sources of decay of pugmarks. These channels were visited during low tide when the mudbank would be exposed thus allowing me to detect the signs. On the first day, selecting only one side (so as to reduce confusion of missing signs) I marked all the channel crossings across the entire length of the channel. I revisited the same channel on the second day, to ensure that I had not missed any signs. On marking all the 'old signs' (the 'oldness' does not typify the age of the pugmark rather it stands for all the pugmarks visible before the start of the decay survey), I had effectively "cleared the slate" to allow for new channels crossing signs to be deposited and monitored. Once the decay survey started, I would visit the channels every alternate day and mark any new signs which had been deposited. Hence, this way I could be sure that the channel crossing signs being used for decay estimation had a known deposition time period (maximum two days) from the beginning. Once a new channel crossing sign was found, I would record the number of pugmark units (individual pumark) it had and then revisit the sign every alternate day to record its stage of decay. Pugmark units were classified as '1' if the it was decipherable as a tiger sign, while they were noted as '0' once they had decayed where they would lose their distinct shape and could be easily confused for a crab hole. I monitored the entire set of units (hence one channel crossing) till all the units had decayed. The number of days to decay for each channel crossing varied from a minimum of two to maximum of 20 days.

In 2010, since I was still trying to understand the system, I had collected data in a qualitative manner which could not be used for any analytical purpose but helped me to standardize the method. In 2011 and 2012, I used the above described method to record signs in a systematic, objective framework in the West Range.

For estimating the sign deposition rate I used the collared individuals' movement data. Only three collared individuals were used as they were territorial individuals and I felt that their movement would be representative of other resident tigers.

In 2014, I conducted my sign survey designed specifically to record channel crossings on banks irrespective of their age, which would give me the information of number of 'standing signs'. The survey was conducted both in the West and Sajnekhali Ranges. For this entire data collection, I tried to ensure that no signs were missed by being constantly vigilant as the boat moved at a speed of 4-5 km per hour.

4.2.2 Analytical Methods

I counted the number of days each of channel crossings survived and averaged them to estimate the survival rate. The reciprocal of this mean survival time gives the instantaneous decay rate (Barnes and Barnes 1992).

For estimating the deposition rate, as mentioned before, I used the movements of collared individuals. The collars were programmed to take fixes (GPS locations) variably, at every half an hour, or one/two/three hour periods. I selected only continuous fixes where two subsequent fixes made one time period. I would then check on GoogleEarth if the subsequent fixes were on the opposite side of a channel (only channels where our boat could pass through during low tide were considered) and record it as a crossing. One must mention here that the lines joining the fixes represent displacement rather than actual movement. Since the collars didn't provide minute by minute movement, I decided to test if the proportion of total no of crossings across all subsequent periods remained the same when the half an hour fix data was merged to make one hour data or the one hour data merged to two or more hours data. This way I could test if the proportion remained the same irrespective of the time period between the fixes, thus allowing me to use the same proportion of crossing at an instantaneous time frame too. I then took a mean of the crossings across the three individuals.

Since the channel crossings are counted in a linear scale (along the length of the channel), I took the encounter rate of signs at every channel (obtained from the 2014 data). I then averaged the encounter rates over all the channels to estimate the overall encounter rate of channel crossing in Sunderbans. I used this overall encounter rate as the "Y" of equation 1 (number of standing signs) to obtain the number of tigers per kilometer ("E" in equation 1). To convert this estimate of "E" to number of tigers, I then multiplied the number of tigers per kilometer with the total length of channels available for crossing by tigers and which can also be surveyed by boat during low tide in the study area. Lastly I calculated the area of the study site where the survey was conducted to convert the tiger abundance to tiger density. The standard error of the density was calculated using the delta variance method over the coefficients of variation of the sign encounter rate, decay rate and deposition rate.

4.3 RESULTS

The result of the testing of proportion of channel crossings across variable fix time periods is depicted in Figure 4.2.

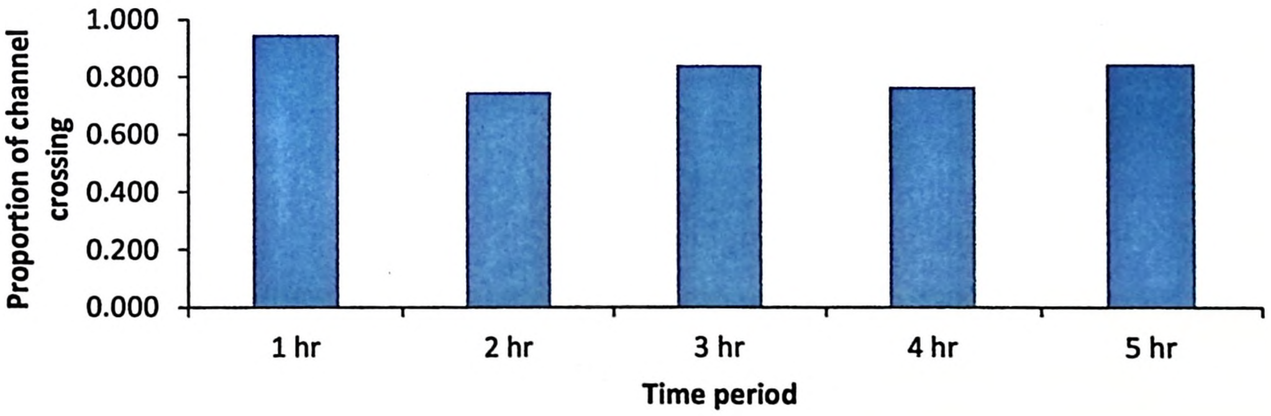


Figure 4.2 : Proportion of channel crossings over time-periods measured through fixes of GPS locations of collared tigers.

The deposition rate i.e. mean number of channel crossing per animal per day was estimated as 0.8 channels (SE 0.41). The decay rate of channel crossings was estimated as 0.2 signs per day. The average encounter rate was estimated as 0.343 (SE 0.089)/km. The total number of tiger per kilometre was estimated as 0.086 (SE 0.04) tigers/km. The tiger abundance in the study area was estimated as 25.88 (SE 11.2) tigers. Dividing the abundance with the area of the study site gave a tiger density of 3.34 (1.44) tigers per 100 sq. km.

4.4 DISCUSSION

This method has never been applied for any carnivore abundance estimation. Sunderbans with its ample mudbanks provided good opportunity to test if it could be applied for tigers. When comparing with the average camera trap density of the two ranges 3.9 (SE 1.5), the sign generated tiger density of 3.34 (SE 1.44) doesn't seem too far off.

Since collecting information for sign generated density is much less labour intensive and involves minimal risk from tigers compared to camera trapping, we could use this as a replacement for estimating tiger density in Sunderbans. Also the cost involved in such as exercise reduces drastically as the costs involve only expenditure associated with operation of the boat as opposed to the costs of camera trapping namely, baiting, extra labour and their associated expenditure. However, one must address the various issues that I feel could plague this method before it can be recommended as an alternative. First, there is the issue of detectability. Since this was the first time such a method was being used for tiger density estimation and I was testing if this method could work, I paid utmost care in detecting all the channel crossings in field. However, in reality, the precision and repeatability of this exercise cannot be guaranteed in all field conditions. And if this were to be standardised, one must take into consideration that detectability will vary across observers. Hence we must be able to tackle missing signs in our method. One can develop the observer based differences in detecting signs by carrying out a multi-observer experiment for known signs. Infact, the comparable densities could just be coincidental as I could not conduct the number of channel crossings survey more than once. Secondly, the decay rate needs to be modelled over the various environmental factors which could influence it. The effect of the water 'decaying' pugmarks will vary across channel widths, vegetation type, steepness of the bank and the mud quality over which the pugmarks have been deposited. Banks which have mostly Avicennia forests are usually gentle in slope and have relatively soft mud. Hence pugmarks deposited on such mudbanks may have deeper impression, taking longer to decay with time. On the otherhand, banks with Phoenix forests are mostly steep and have hard soil, where the pugmarks can erode easily. The speed of the water flowing in is influenced often by the width of the channel combined with its position with respect to larger channels; this conversely can also influence the micro wave action of the water over the pugmarks. Lastly, the deposition rate was based on a very small sample size, though we expect the number of crossings to be independent of an individual tiger's choice of whether to swim across or not (barring water channels wider than 1 km). The deposition rate should logically be dependent on the number of channels a tiger encounters and the area over which it resides. However, it would greatly increase the accuracy if collars could be programmed at minute level fixes; but such a tactic could be cost prohibitive in terms of logistics of collaring a tiger versus battery drainage.

In the end I would like to conclude that this method surely shows promise in terms of cost and accuracy, however the precision leaves much to be desired for and needs further testing before it can be used formally for density estimation of tigers in the Sunderbans. The sign decay-deposition method though used worldwide for many elusive species population enumeration has been found to be often plagued with low precision

(Barnes 2001). Elephant dung decay may vary due to seasonal variation (Nchanji and Plumtre 2001), activity of dung beetles (Neff 1968) and heterogeneous environment of a habitat (Putman 1984) and can thus bias the estimates of decay rates. The precision of decay rates of chimpanzee nests are influenced by tree species, rainfall, nest height and age (Kouakou et al. 2009). Deposition rates of dung may vary due to irregular dunging attributable to different age and sex classes or preferential dunging areas/vegetation types (Putman 1984) while the nesting behavior of chimpanzee influences the nest deposition rates (Plumtre and Reynolds 1997). The number of standing signs may also be further biased due to differential observer bias (Olivier et al. 2009) or differences in environmental variables such as rainfall (Walsh and White 2005). Thus bias in any of these three variables can significantly bias the estimation of animal abundance. However, Barnes (2001) concluded that the sign count method is as accurate or inaccurate as other abundance estimation techniques and that it is 'a valid and respectable means of estimating vertebrate populations'. Accounting for different sources of variation on the three variables can give comparable population size estimates with those from modern animal sampling approaches.

CHAPTER V – APPLICATION OF BOAT TRANSECT BASED DISTANCE SAMPLING FOR ABUNDANCE ESTIMATION OF PREY

5.1 INTRODUCTION

Many population enumeration studies rely on quadrat sampling or strip transect, wherein, plots of known areas are laid randomly, representative of the target area, and a complete census then being carried out in such plots (Williams et al. 2001). However in reality, such a method often fails to give unbiased estimates (Buckland et al. 2015). Firstly, there is no way of knowing if we have counted all the individuals in the plot, secondly since most animals are naturally unmarked we cannot guarantee if we have double counted individuals, thirdly, since animals are mobile, they might move in and out of the plot during the sampling period, and lastly, it is often difficult to determine if animals are standing inside or outside of the strip/quadrat edge when viewed from far (Buckland et al. 2001). Hence, various methods have been developed to overcome such uncertainties. One such technique, Distance Sampling (DS) which includes a suite of methods including line transect and point transect sampling, seeks to remove some of the biases by incorporating detection probability inside the plots, setting a pre-requisite of researcher speed being greater than animal movement, such that animals are detected at their initial locations, and modeling the width of the plot based on detectability rather than having a fixed predetermined width (Buckland et al. 2015).

In line transect based DS, series of lines of known lengths are placed at random to the distribution of the animals over a study area. This design thus ensures that the distribution of animals around each individual line is uniform. The observer then counts animals/clusters of group living animals and records their perpendicular distances from the line accurately while moving along the line. Conceptually, we can expect to encounter the same frequencies of animals at various distance intervals as we count away from the line. However, in reality due to various factors, such as habitat, terrain, inherent animal heterogeneity, the number of animals detected at each increasing distance interval falls, or inversely, chances of missing individuals increase as detectability declines with distance from the line. If we can then calculate the proportion of animals P_a, which were detected, we can correct the observed counts of animals to get the actual abundance.

The sample of perpendicular distances are used to estimate P_a, by modeling the detection probability g(x), as a function of distance x, of an animal from the line (Buckland et al. 2001). We can then simply estimate the density of animals by dividing the corrected abundance by the area denoted by the line transect length L, and the detection width w, the perpendicular distance from the line at which the farthest animal was observed or truncation width w, the perpendicular distance from the line beyond which observations where truncated (Buckland et al. 2001).

One of the critical assumption of conventional DS states that g(0) i.e. detection function at zero distance must be 1, hence all animals on the line must be detected. As g(x) can decline as we count away from the line to w, we can assume the detection function to follow any of the key functions (models) of a uniform or a half-normal or a hazard rate curve. A uniform model is defined as having detection function similar across all the distances from the line. The half-normal curve plots the decrease in detectability with increase in distance to the line and is defined by having a shape parameter or σ which determines the rate of fall or the point of inflexion of the curve. Hazard rate curve also charts similar decline in detectability and along with σ, has an additional shape criterion β, which determines how broad or narrow the shoulder of the curve (i.e. detectability at distance classes near the line) will be. We can 'bend' the curve further to make the curve/model fit the occasional spikes or bumps in our data (due to sudden increase in detectability in mid distance intervals brought about by local conditions in field, eg. heterogeneous vegetation patches) by the use of adjustment terms viz. cosine, simple polynomial and hermite polynomial series. Ultimately, since we know that the curve starts at zero ($g(0)=1$) and extends till w, we can then use maximum likelihood approach to estimate the points of inflexion and the shoulder of the detection curve by using the observed perpendicular distances.

A good detection function model in DS is characterized by having a shoulder (hence the detection function at nearby or close to the line is 1), being non-increasing function of distance and having pooling robustness property, wherein, abundance estimates remains largely unaffected inspite of having unmodelled heterogeneity that might affect detection probability (Buckland et al. 2015).

Studies focusing on estimation of tiger prey abundances/density in the Indian sub-continent use mostly line transect based DS approach (Khan et al. 1996, Karanth and Sunquist 1995, Karanth and Nichols 2000, Biswas and Sankar 2002, Bagchi et al. 2003, Andheria et al. 2007, Gopal et al. 2010, Jhala et al. 2011a) since it does not entail individual recognition or extensive prior knowledge, and it takes into account the spatial sampling and observability (Karanth & Nichols 1998), therefore making it more reliable and practical.

In Sunderbans, I used boat transect based DS as walking line transects inside the forest was impractical. The channels/khals were the transects and I assumed the channels were random with respect to the animal distribution. The largest natural prey available for Sunderbans tiger, is chital (Reza et al. 2001). A study of tiger predation in the Sunderbans by Khan (2004) indicated that the chital was the principal prey of the tiger accounting for 67% of the prey remains in the tiger scats, while wild pig made up 12%, followed by Rhesus macaque at 6%. According to the forest department and the locals in Sunderbans (pers. comm.) the tigers' main diet comprises of chital, wild pig and Rhesus macaque and probably supplemented by monitor lizard (*Varanus* spp.), fish, crab, birds, and in a few cases, even man. However, since I could not get a sizable amount of scats to verify such claims, for my study, I primarily focused on chital and wild pig as the principal prey species.

The boat transects were conducted in the same area in West Range and Sajnekhali Range, where I had carried out my camera trapping and sign decay exercises from 2011 to 2014 (Figure 3.1).

5.2 METHODS

5.2.1 Field Methods

Animal movement in Sunderbans is often dictated by the prevalent tidal condition. During high tide, as the tide reaches its peak, the mudflats on the edges of the islands get covered and channel water move inland, wherein the animals move away from the bank and seek higher grounds. As the low tide starts and the water recedes from the bank, animals move to the edge of the water channels to access the vegetation on the now exposed mud flat. In such a backdrop, using channel banks could possibly, positively bias the ungulate estimation. However, I assumed, that even though animals do access the mudflat feeding on the plants found at the treeline, these edible plants are found everywhere, both at the 'heart' of the islands and at the outer edges. The animals are thus in effect randomly distributed with respect to river banks during certain sections of the tidal cycle, thus justifying the selection of the channels as transects for distance sampling.

I conducted spatial and temporal boat transects in channels having at least a minimum width of 100 meters ensuring that I had enough space between the boat and the bank so that my boat didn't run aground. The transect lengths ranged from a minimum 5 kilometers to maximum 15 kilometers depending on the channel length. The temporal replicates of a single transect were added to represent the total length and number of detections for that transect and to account for the non-independence of these temporal replicates. Direct sighting of animals is low and a rare event in Sunderbans, primarily due to the thick vegetation and also due to the low abundance of animals. So during the exercise, only one side of the channel was surveyed so as to reduce confusion and chances of not detecting individuals on the bank being surveyed. The exercise was conducted when the tidal conditions were ideal. Three hours after the beginning of low tide and 3 hours from the beginning of high tide provided a window of 6 hours when mudflats would remain exposed during which sampling was done under appropriate light conditions. The boat would move at 5 km/hour so as to reduce the chances of missing any individual as well as minimizing noise which might scare the animals away. I maintained the distance between the boat and the sampled bank at a constant of 20 to 40 meters so as to measure the linear distance as accurately as possible and also not so far out that animals wouldn't be visible. There were two observers for each of the transects, one sweeping the far distances with binoculars, another concentrating on the closer immediate section of the bank. If the animal was spotted from afar, then I kept a mental note where it was first spotted by observing any nearby tree, log, creek etc. As the boat came parallel to the "landmark", I used range finder Scout DX 1000 Arc (Bushnell, Missouri, USA) to record the perpendicular distances of the observer to water, upper bank (the upper bank is defined as the point from where the land flattens out into the forest), grass patch (whenever present), vegetation (the point where the mangrove forest starts) and the animal. When a group of animals was spotted, measurements would be taken for the centre of the group. An animal was considered to be a part of a group if its distance from its nearest neighbor was less than 30 meters. The activity of the animals was also noted along with the nearby dominant plant species. As the distance sampling exercise was conducted in the summer in all the four years, I believe there would be no seasonal variation in the density across the years.

5.2.2 Analytical Methods

Density can be estimated through DS using three ways- 1. modelling g(x) the detection function and using it to correct P_a, and then using the detection width to convert the abundance to density 2. μ or effective strip width which can be defined as that width/perpendicular distance from the line beyond which the number of animals detected are equal to the number of animals missed within it. Conversely, since μ is also the integral i.e. summation over all the detection probabilities of different distance classes, it shares a relationship with P_a, where $P_a = \mu/w$, and 3. by using the probability density function f(x) of detected distances which is simply the g(x) rescaled so that it integrates to 1. In this case f(0) is used in the computation of the density since f(0) = g(0) or 1/ μ. The software DISTANCE typically uses the third method for its computation. It computes the maximum likelihood on the f(x)s. Since detected distances (or animals) are considered independent of each other the f(x)s have a joint distribution. The usage of f(x) becomes handy as it represents the relative likelihood of different detected distances, and there are general methods to fit such functions.

Before arranging my data in the format required by the software, I deducted the perpendicular distance of observer to water from perpendicular distance of observer to animal/animal cluster/animal group. This left truncation was carried out to deliberately remove the non-habitat, water belt. Further, my maximum detection width was at 97 meters. However, I truncated the width post-hoc at 83 meters to fit the detection curve better, since the g(>83) was less than 0.15 (Buckland et al. 2015) and this truncation led to minimal loss of data (n=1). DISTANCE software runs best when there are a minimum of 50-60 detections (Buckland et al. 2001). However, as one can see from Table 5.1, inspite of increasing effort, none of the years had even 40 sightings singly. Hence, I fitted a common detection function to all the years which is justifiable given that the same method was used by the same observer in the same area.

Year	Location	Number of independent transects	Total effort (in km)	Number of detections
2011	West Range	9	64	4
2012	West Range	20	177	13
2013	West Range	37	360	32
2014	West Range & Sajnekhali Range	53	554	19

Table 5.1 : Sampling details of boat transect based distance sampling exercise 2011-2014

I then used key functions uniform, half-normal and hazard rate with their adjustment terms (if needed) to model the detection probability and selected the relatively best model on the basis of minimum Akaike Information Criteria corrected for sample size (AICc, Akaike 1974) for inference. I then decided how best the model fit my data on the basis of the Q-Q plot and related tests. Traditionally, chi-square goodness of fit is used to assess model fitness. However, since this test is better suited for grouped data and is somewhat subjective (since the choice of cut-points on the distance intervals to examine observed versus expected count of animals in each distance class can differ from researcher to researcher), I have also reported the results of Kolmogorov-Smirnov (KS) test and Cramér–von Mises (C-vM) test which are better suited for testing on exact distances.

I post-stratified by year to estimate densities for each year. I believe that in this type of post-stratification, the pooling robustness property still holds unlike cases where one stratifies according to habitat, sex etc and then tries to fit a common detection function across all strata. For computing the cluster size or group size of chital, I used size biased regression method to correct for the increased detectability of larger groups in greater distances from the transect line due to their group size.

Lastly, I multiplied the estimated density by 2 since the software computes effectively sampled area by using the w or μ on both sides of the transect line, while I had in reality observed only one side at a time.

5.3 RESULTS

I was able to analyse only my chital data as I had very low (n=2) detections of wild pig over 4 years. Since wild pigs were rarely visible on the banks unlike chital, and they did not exhibit similar behaviour like chital (chital in Sunderbans are known to browse on tree leaves by standing on their hind limbs), and hence dissimilar micro-habitat usage, I felt it was not justified to use the chital detection function on wild pigs. Hence, I could only estimate chital densities from my study.

Hazard rate model with cosine adjustment (order of 2) was selected as the best model for the detection function. The selected model was a good fit to the observed data as determined by KS test ($p = 0.6278$) and C-vM test ($0.500 < p \leq 0.600$). The Q-Q plot at Figure 5.1 shows how the observed distribution function is spread around the expected distribution function.

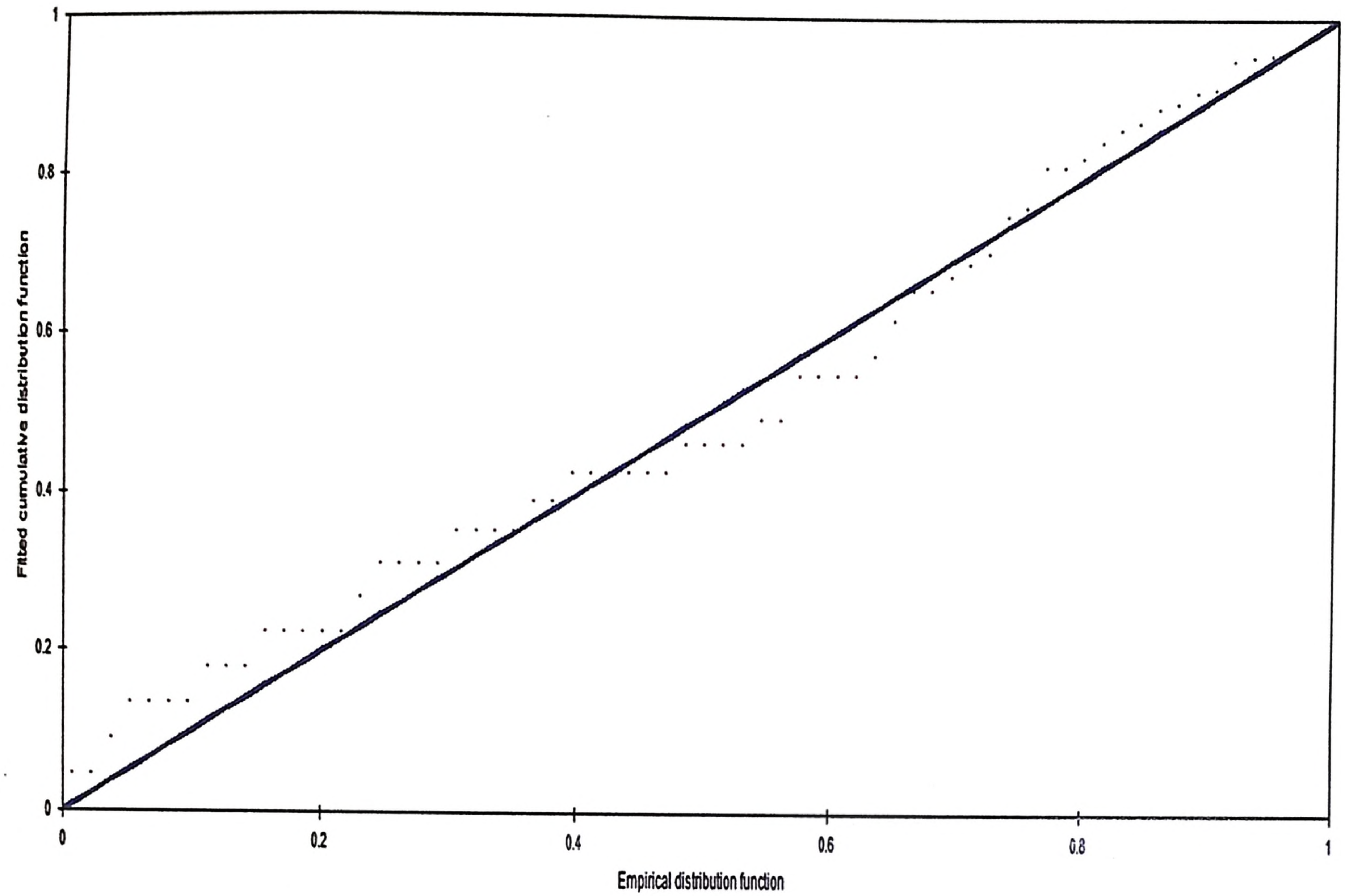


Figure 5.1 : Q-Q plot of observerd distribution versus expected distribution

The chi-square p value (0.55) also demonstrated the model fit to the data. P_a was estimated as 0.26 (SE 0.05), f(0) was estimated as 0.045 (SE 0.009), while μ was estimated as 21.95 (SE 4.40) meters. The Figure 5.2 shows how the detection function falls with the observed data grouped in interval classes at the backdrop for comparison.

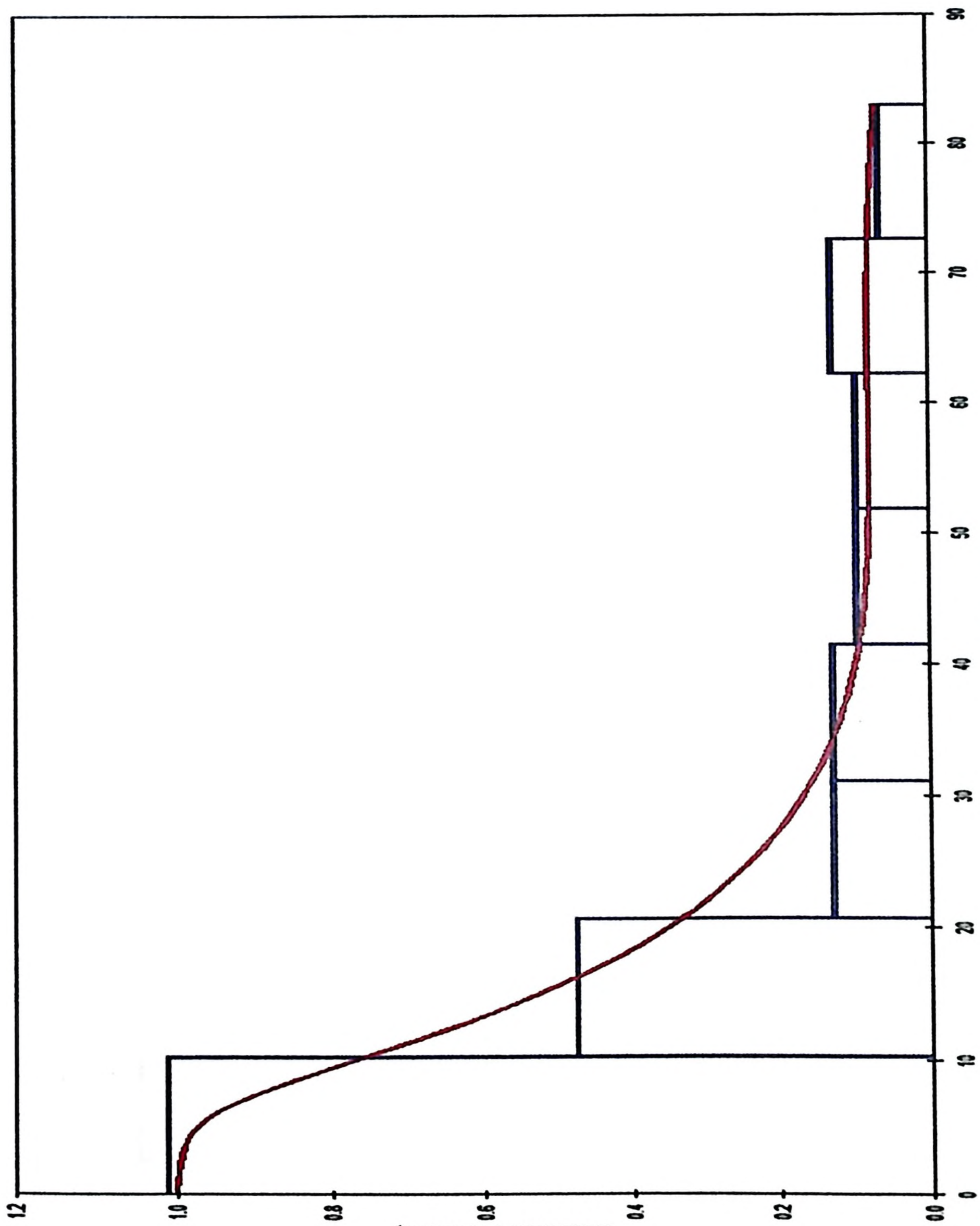


Figure 5.2 : Detection function g(x) curve of the best model

The individual density and group density estimates of the four years are given in Table 5.2.

Year	Encounter Rate (animal/km)	SE	Mean Cluster size	SE	Group Density (groups/sq km)	SE	Individual Density (animals/sq km)	SE
2011	0.06	0.03	1.75	0.75	2.82	1.52	4.94	2.68
2012	0.07	0.02	2.00	0.19	3.34	0.88	6.68	1.81
2013	0.08	0.02	1.39	0.14	4.04	1.03	5.6	1.48
2014	0.03	0.007	2.22	0.53	1.48	0.38	3.2	0.84

Table 5.2 Encounter Rate, Individual Density, Group Density across 2011-2014

The primary contributor to the variance in density was encounter rate (43.2 %), followed by detection probability (38.4%), and followed by group size (18.4%).

5.4 DISCUSSION

The selection of hazard rate model as the best curve seems appropriate and concordant with the field reality. The detection of animals at and near the 'line' was similar and would then sharply fall as visibility inside the forest was severely restricted- a characteristic of mangrove forests. As we can see in the Table 5.2, the mean densities differ between each other. However, on close inspection of the standard errors we see that they overlap over the years; hence density estimates are not significantly different between the years. The large variance on density can be mostly explained by the variability in encounter rate. A reason for such variable encounter rate could be due to skewed detections on transects; more than half of the transects (67%) had no sightings leading to most transects having zero encounter rates. The proportion of sightings/detections however did not differ amongst channel with varying lengths. The assumption that channels were random with respect to distribution of the animals itself could be incorrect; however, the transects were long and passed through different habitat types for the same transect, hence bias due to differential habitat on encounter rates would be minimised. A similar explanation would perhaps hold for the detection function variability. Higher visibility and higher usage by chital in certain vegetation patches like *Avicennia* and *Sonneratia* patches can induce higher variability in the detection process.

During the camera trap exercises there were almost no photo captures of prey species as I believe they deliberately avoided the baited camera stations. However, during the All India Tiger Estimation Project (2018), I had access to the camera trap datasets of Sunderbans Forest Department where lures instead of baits were used. There were quite a number of photo captures of spotted deer and wild pig in most of these cameras. As the cameras were set up at a grid scale of 1 sq km across the landscape, I believe they are representative of the actual species distribution. Hence the assumption of these natural channels being random with respect to the animal distribution may be valid.

The only other study to have used DS to estimate chital density in Sunderbans was carried out by Khan (2004). His study recorded the individual density of chital to be 20.9/km^2 in Bangladesh Sunderbans. Unlike boat transects, he walked line transect inside the forests. However, it must be mentioned that the area where that study was conducted (Sunderbans East Wildlife Sanctuary, Bangladesh) does not surprisingly, have incidents of conflict with humans, and the tigers in that area are said to be shy of humans. This area is also considered to have one of highest prey densities in entire

Sunderbans, which is supported by Khan's reported estimate. The substantial difference between Bangladesh and Indian Sunderbans spotted deer densities can likely be attributed to two factors- a. there are large tracts of grassland in Bangladesh Sunderbans as opposed to small patches on the bank in the Indian side; this not only increases visibility of the prey species but also facilitates occupancy by higher number of chital as the species is a generalist forager, and b. the Indian Sunderbans has higher saline concentration in its waters and the salinity decreases on a west to east (towards Bangladesh Sunderbans) gradient (Khan 2004). The availability of water with lower salinity levels could perhaps be the reason for the higher densities of spotted deer.

One of the key issues with DS technique is that it was developed on sessile objects like duck nests in open areas and then extended to mobile objects. Using such a technique on moving animals in woodland areas inherently violate many of the assumptions associated with it and hence bias density estimates. There are other sampling techniques available for example a. indirect sampling methods like faecal deposition and decay rates (Marques et al. 2001, Camargo-Sanabria & Salvador Mandujano 2011), or sampling for DNA from hair traps or pellets to estimate densities through a mark recapture framework (Bhagavatula & Singh 2006, Fickel & Hohmann 2006) or b. through direct sighting techniques such as random encounter models (REM) (Rowcliffe et al. 2008). However, all these techniques come with their own set of limitations especially in a scenario like Sunderbans. Sign decay-deposition rates often fail to account for the substantial spatial heterogeneity in decay rates which occurs due to the fluctuating environmental conditions and differential micro-climates (Walsh &

White 2005, Kuehl et al. 2007) and requires an estimate on the defecation rate which is further confounded by age, gender, food source, gut content, and other factors (Horino & Nomiya 2008). Pellet sampling for DNA extraction can not only be resource consuming as it requires data from multiple hypervariable loci for unequivocal identification of individual animals (Lukacs & Burnham 2005) but also impractical for forest ungulates (Spitzer et al. 2019). Usage of Random Encounter Model in Sunderbans also becomes impractical given the required extensive calibration of known distances from cameras.

The primary concern for usage of DS in Sunderbans is that in reality we do not know how animals are distributed at the channels and islands. Unless individual spotted deer are radio-tagged, it is impossible to get information on their movement pattern and space usage. However, even with such large CVs and the existing sampling techniques, currently DS probably provides the least biased density estimates for spotted deer in Sunderbans.

This is the first study to use boat transects to estimate ungulate population size. The conditions in Sunderbans make line (foot) transects infeasible. Thus it is difficult to compare this study's result with other studies where primarily line transects are used (Focardi et al. 2002, Jathanna et al. 2003, Seddon et al. 2003, Kruger et al. 2008, Wegge and Storaas 2009, Zero et al. 2013). Comparing prey estimates of other low-medium tiger density forests (Jhala et al. 2015), Sunderbans has low spotted deer density. Despite this low density as the tiger densities remain comparable; one could assume that other prey species constitute a significant portion of the Sunderbans tiger's diet.

CHAPTER VI – EVALUATING METHODS TO MONITOR TIGER ABUNDANCE AND ITS PREY

6.1 INTRODUCTION

Abundance is often used as a key parameter for monitoring populations (Maxwell and Jennings 2005). A trend in abundance determines conservation priorities, management direction and ultimately management effectiveness (Maxwell and Jennings 2005). With increasing anthropogenic pressure and limited conservation resources, it becomes essential to be able to glean such trends from reliable and robust data (Steidl et al. 1997).

The capacity of a survey technique to successfully capture if a population is changing depends on the statistical power of that technique (Gerrodette 1987). There are two types of statistical errors that could occur when we want to study trends in a population (Gerrodette 1987). In the first scenario, let us say the population in reality has not changed and our null hypothesis states that the population is stable, however we reject this hypothesis falsely, thereby leading to type 1 error or α (Zar 1974). This then leads to directed management effort towards a population that is not under stress and ultimately wastage of scarce resources (Maxwell and Jennings 2005). The other type of error is more severe and occurs when the population in reality has changed, our null hypothesis is that it is stable and we accept the null hypothesis, and hence commit a type 2 error or β (Zar 1974). This type of error could have adverse consequences especially if the population is decreasing and might go extinct before the management can act (Taylor and Gerrodette 1993). The probability to reject the null hypothesis when it is false is statistical power and is defined as 1-β (Gerrodette 1987).

Statistical power depends on the size/scale of the "effect" we wish to detect (Cohen 1988) and the variability in the data defined by the standard error or the coefficient of variation (CV) (Gerrodette 1987). As the effect size increases, power increases while as CV increases power decreases (Gerrodette 1987). Particularly, when we wish to understand negative trends (which is usually the focus of management practices), the probability of detecting that trend depends on the precision (hence CV), the rate of decline (hence effect size) as well as the α levels (Gerrodette 1987). When the population size is small or decreasing, and the rate of decline is low, the power to detect such a trend is poor (Gerrodette 1987). Conversely, if we keep our chance of committing a type 1 error high, the ability to detect a negative trend becomes higher.

Tiger conservation goals dictate monitoring population trends, especially at the backdrop of high poaching pressure and comparatively shorter life span of tigers. Thus it is essential to test and use multiple methods that can aid in detecting change and can help the management to act in time. Hence, usage of power analysis becomes central in evaluating any monitoring technique. However, as noted, power depends on precision. If a technique, inspite of best effort, provides abundance with wide confidence intervals, the question then rises- should we abandon that method, even if it is an otherwise standardized tool recognized as the most reliable, robust technique? This concluding chapter seeks to address that dilemma- should camera trapping based SECR, sign decay-deposition and boat transect based distance sampling be used to monitor tiger and its prey in Sunderbans? Hence, I tested the techniques' statistical power against the null hypothesis - 'the population has not changed/remain stable'.

6.2 METHODS

I used multiple field methods for abundance estimation of tigers *viz.* SECR, conventional capture-recapture and sign based abundance estimation. For density estimation, SECR is the most robust method while conventional capture-mark-recapture (CMR) and sign based methods give post hoc densities which do not take into account the spatial process of sampling and animal distribution. Hence I used the tiger density generated through SECR for my power analysis. However, since SECR has multiple parameters associated with space and the detection process, it inherently has higher CV in comparison to CMR when used for generating abundance. As my focus was on the ability to detect loss of adult individuals, I also selected the CMR abundance estimate for my power analysis as it presents a more parsimonious model. Alongside, I estimated the power on the sign decay-deposition method for density generation as I wanted to test the applicability of this experimental design. I tested for power on the boat transect based distance sampling used for estimating spotted deer density. I used the 2014 datasets generated for West range as the samples for power analyses through the fishmethods package in R 3.6.0.

Following (Gerrodette 1987), I expected the rate of change in abundance/density to be linear in both the tiger and spotted deer populations while the relationship between abundance and CV was kept as 1/√abundance or density for tiger (following the theoretical dependence observed in mark-recapture studies Seber (1982)) and as CV being constant to abundance or density (following the theoretical dependence observed in distance sampling (Moore 1954)) for spotted deer. The maximum number of years over which to project the start population parameter was kept at 10 years since both tiger and spotted deer are K-selected species. I investigated the difference in power as I varied the α levels from 0.1 to 0.4 (with a successive increment of 0.1) as I believe that it is better to err on the type 1 error than on β as rejecting a true trend is more harmful than rejecting a stable population hypothesis. Lastly, the type of tailed test was set as one-tailed.

Additionally using the overall abundance of tigers in Indian Sunderbans, I investigated that at which year could a decline be detected using the current techniques. I assumed a linear decrease of 10%, 20% and 30% annually on the initial abundance of 76 tigers (Jhala et al. 2015- generated partly from this thesis dataset). I used the CV on abundance of 2014 to generate confidence intervals on the hypothetical declining annual populations; I then sought to understand at which year the confidence intervals stop overlapping thus enabling us to predict the year at which we can see the reduced population due to a steady decline caused by stochastic events. This analysis can help us give an idea of whether the current technique can inform us of a decrease in the population before the limit of the theoretical minimum viable population as expounded in Chapron et al. 2008, is reached.

6.3 RESULTS

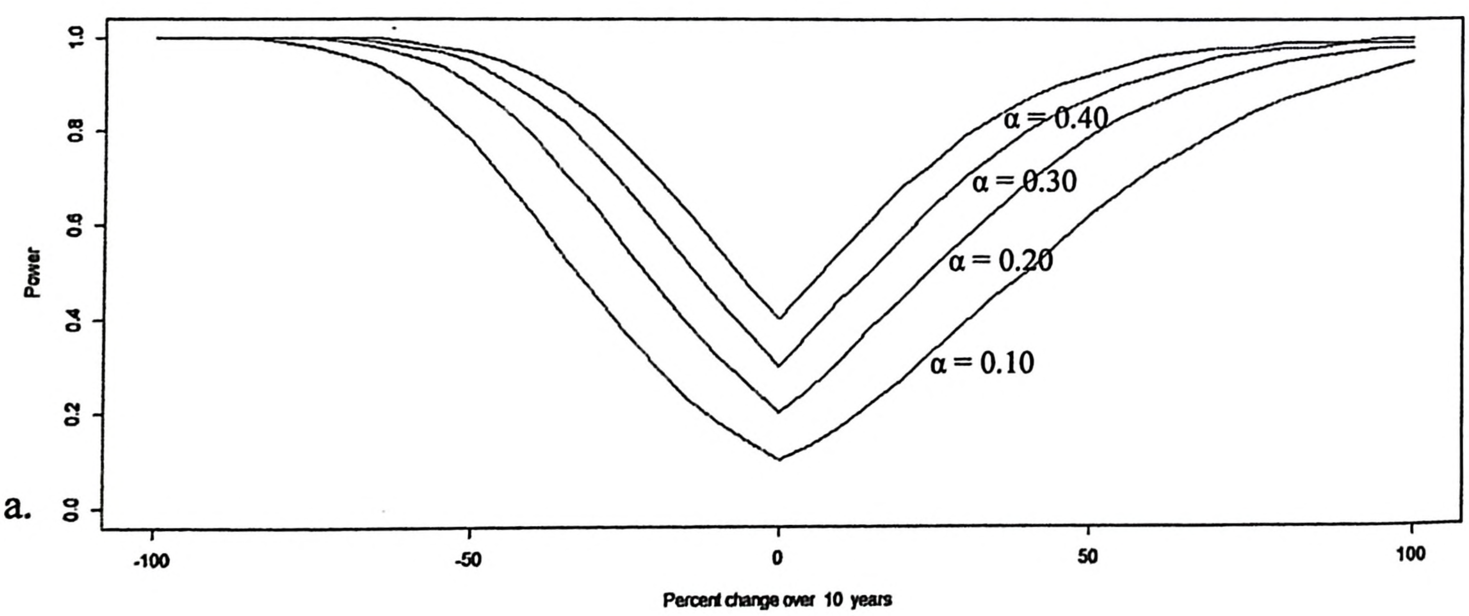
The results of power analysis on the densities and abundance of tigers are shown in the Table 6.1.

Year	Mean	SE	CV	α = 0.10		α = 0.20		α = 0.30		α = 0.40	
				1-β	%change	1-β	%change	1-β	%change	1-β	%change
SECR D2014	3.15	0.88	0.27	0.84	-55	0.85	-45	0.82	-35	0.83	-30
Sign based D2014	3.34	1.44	0.43	0.8	-75	0.79	-60	0.79	-50	0.79	-40
CMR N2014	16	3	0.18	0.78	-35	0.83	-30	0.83	-25	0.82	-20

Table 6.1 : Power (1-β) through different levels of α on tiger abundance and density. SECR- spatially explicit capture-recapture, CMR- conventional capture-mark-recapture, D- Density, N- Abundance

The change in power with changing α in both density and abundance of tigers obtained from camera trap based SECR and conventional CMR, respectively is depicted in the Figure 6.1.

a.



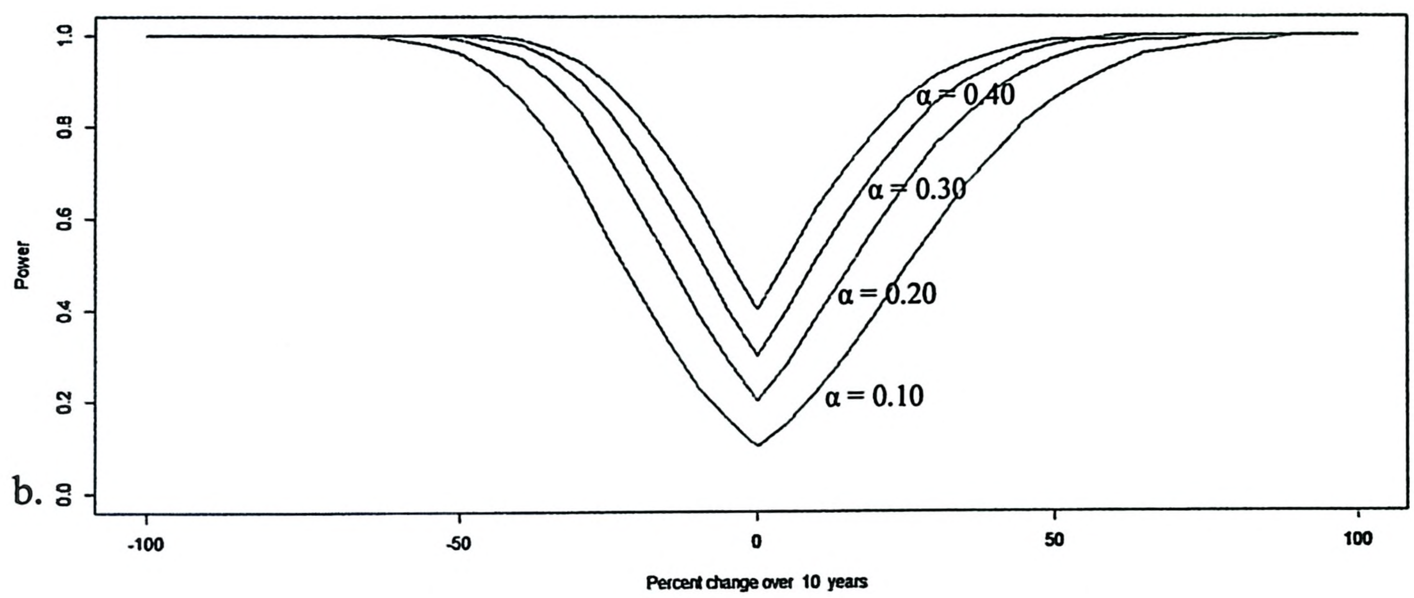


Figure 6.1 : Graphs depicting changing power with changing α levels for a) tiger density in 2014 and b) tiger abundance in 2014

The change in power with changing α in density of tigers obtained from sign decay-deposition method is depicted in the Figure 6.2.

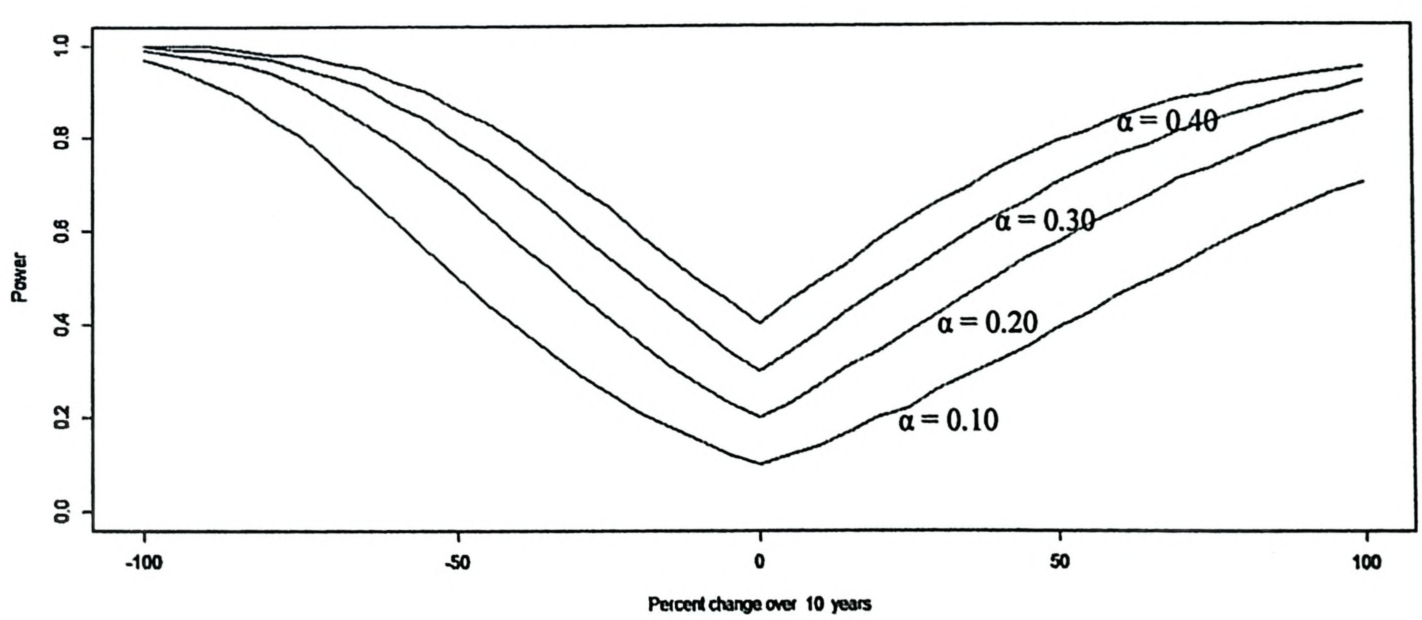


Figure 6.2 : Graph depicting changing power with changing α levels for tiger density obtained through sign based method

The decline in tiger abundance over the years, using the linear 10%, 20% and 30% decline on a starting population of 76 with a CV of 18% is shown in Figure 6.3.

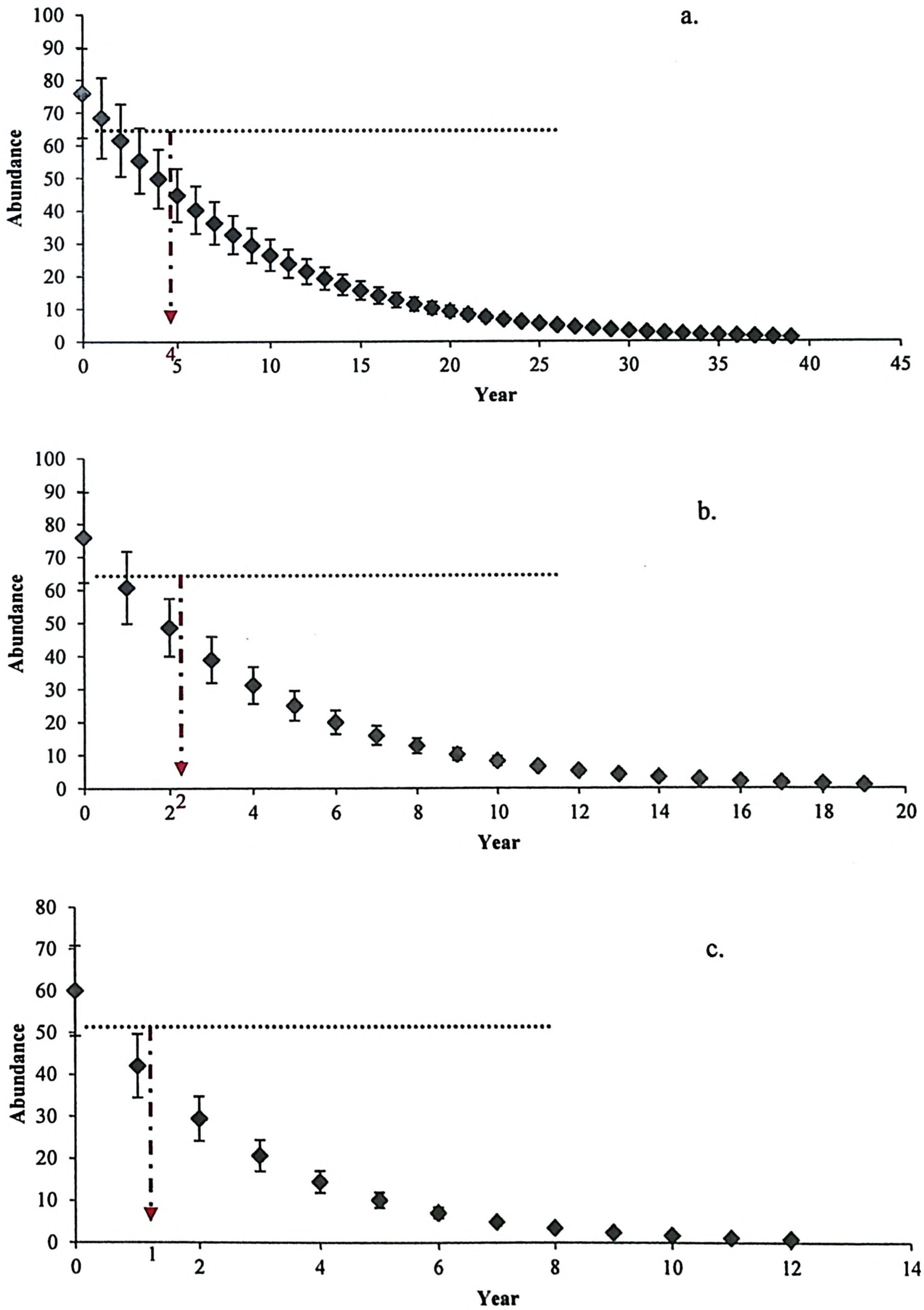


Figure 6.3 : Graphs showing decline in tiger abundance with an annual decrease of a. 10%, b. 20% and c. 30%

Hence, we can see that with the current CV, we can detect the negative trend in the fourth, second and first years respectively if there is a steady decline of 10%, 20% and 30%.

The result of power analysis on the density of spotted deer is shown in the Table 6.2.

Year	Mean	SE	CV	α = 0.10		α = 0.20		α = 0.30		α = 0.40	
				1-β	%change	1-β	%change	1-β	%change	1-β	%change
2014	3.2	0.84	0.26	0.79	-45	0.77	-35	0.8	-30	-25	0.8

Table 6.2 : Power (1-β) through different levels of α on spotted deer density derived through distance sampling based boat transect

The change in power with changing α in density of spotted deer is depicted in the Figure 6.4.

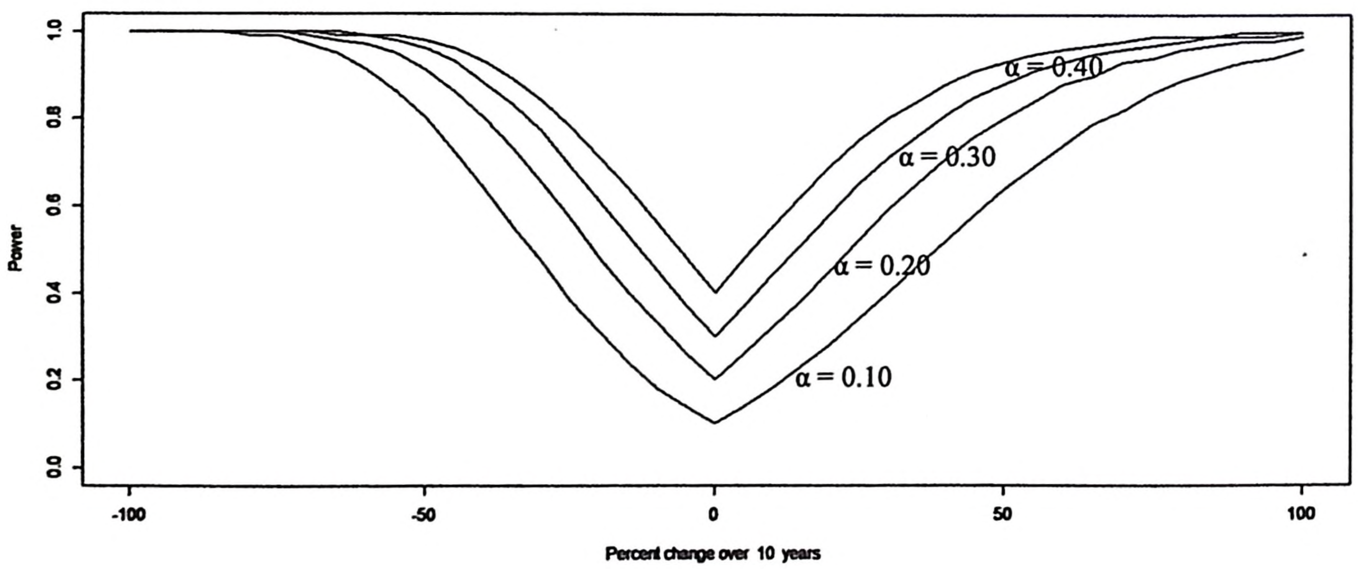


Figure 6.4 : Graph depicting changing power with changing α levels for prey density

6.4 DISCUSSION

The results of power analysis seem to indicate that camera trapping based SECR for estimating tiger density and distance sampling based boat transects for estimating spotted deer density are not the most adequate tools for monitoring in Sunderbans. The power associated with the sign based method was quite low due to the extremely high CV.

However, such inferences would be hasty. Retrospective power analysis is highly suspect to bias and can be unreliable to gauge the effectiveness of techniques after the survey has been conducted (Gerard et al. 1998). When we increase the α levels, the power for detecting negative trends using density (25% drop from initial abundance) increases and when we use abundance instead of density as our parameter, the power remains high at even low α levels. Similarly levels of increase in power is observed for spotted deer density when the α levels are increased. Hence, the power to detect changes using the current methods increase as we allow ourselves to err more on rejecting the null hypothesis (population has not changed) when it is true.

Our theoretical model of linear decline further showed that even with the high CV, one can still use the techniques to monitor the tiger population in Sunderbans as camera trapping based SECR is able to alert us of the declining trend before it reaches the minimum viable population levels (Chapron et al. 2008) to survive the onslaught of poaching and prey loss. This analysis was done on the Indian Sunderbans population. Considering that the technique can at best capture the real trend after the decline of 25% to 35% in the population, Sunderbans tiger population can still recover due to Sunderbans being a contiguous forest lying between India and Bangladesh, covering an area of approximately 10,000 sq km, and thus ensuring the long term persistence of tigers in Indian Sunderbans. A 35% decline in spotted deer translates to the density reducing to 1.12 spotted deer per sq km. Even at this level of decrease, distance sampling still remains a viable technique to monitor the prey as spotted deer is prolific breeder and timely intervention can stall its decline.

Both camera trap based SECR and distance sampling are the current standardised techniques used to estimate carnivores and their prey populations worldwide. Sunderbans with its many logistic and natural constraints force us to tailor these methods according to the prevailing local conditions. The error rates associated with these methods were higher when compared to the application of the same elsewhere. In the case of camera trapping, I was restricted to luring the tigers to my trapping stations rather than being able to place the cameras at optimal locations on tiger trails. The detection process thus with its inherent dependence on animal distribution and sampling process became further variable on the ability of the bait to lure tigers. The tidal cycle further added to the heterogeneity of the system as during high tide many of the traps were not accessible to the tigers. I was further limited by both logistics as well as number of teams who could manage camera trapping at an even finer scale. Boat transects were also plagued by the error rates associated with general distance sampling and non-availability of prey during moderate to high tide timings. These variations are part of the dynamic unique ecosystem of Sunderbans and inspite of my best efforts and increasing intensity, I could not overcome these sources of error. Further, these methods remains apt

Camera traps especially can give a whole range of information on population parameters besides abundance which can be used for monitoring. Information on turnover rates, number of breeding females, changing territories of residential tigers can help understand the dynamics of the population. Boat transects can also give us crude information on fawn/adult ratio, prey dispersion dependent on different environmental correlates can be further used as indices for monitoring.

This study could prove that inspite of the distinctive scenario in Sunderbans, the usage of camera trap based SECR and boat transect based distance sampling as effective monitoring tools for Sunderbans tiger and its prey is justified. The Sunderbans forest department has adopted the protocols for camera trapping and distance sampling, developed in this thesis for its quadrennial survey. During the All India Tiger Monitoring project (conducted by Government of India), the forest department could deploy traps at a scale of 2 sq. km. grid. Their effort gave an estimate of 3.6 (SE 0.4) tigers/ 100 sq. km. The CV of 11% confirms that camera trapping can indeed be used for monitoring tiger population in Sunderbans. Future studies can perhaps focus on boat transects and other alternatives of estimating spotted deer densities for example- spatially explicit capture-recapture, random emcounter model, etc.

REFERENCES

Adler P Raff R Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465-479

Akaike H (1974) A new look at the statistical model identification. Automatic Control IEEE Transactions 19:716-723

Alonso RS McClintock BT Lyren LM Boydston EE Crooks KR (2015) Mark-recapture and mark-resight methods for estimating abundance with remote cameras: a carnivore case study. PloS one 10(3) e0123032

Andheria AP Karanth KU Kumar NS (2007) Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. Journal of Zoology 273:169–175

Bagchi S Goyal SP and Sankar K (2003) Prey abundance and prey selection by tigers (Panthera tigris) in a semi-arid dry deciduous forest in western India. Journal of Zoology 260:285 – 290

Barlow AC (2009) The Sundarbans tiger adaptation population status and conflict management. PhD Thesis, University of Minnesota, Minneapolis

Barlow AC Ahmad IU Smith JL (2013) Profiling tigers (Panthera tigris) to formulate management responses to human-killing in the Bangladesh Sundarbans. Wildlife Biology in Practice 9:30–39

Barnes RF (2001) How reliable are dung counts for estimating elephant numbers? African Journal of Ecology 39(1) 1-9

Barnes RFW Barnes KL (1992) Estimating decay rates of elephant dung piles in forest African. Journal of Ecology 30(4):316-321

Barnes RFW Jensen KL (1987) How to count elephants in forests. IUCN African elephant and rhino specialist group Technical Bulletin 1(1):1-6

Barnes-Svarney P Svarney TE (1999) The Oryx Guide to Natural History: The Earth and All Its Inhabitants. Greenwood Press, USA

Bhagavatula J Singh L (2006) Genotyping faecal samples of Bengal tiger Panthera tigris tigris for population estimation: a pilot study. BMC genetics 7(1):48

Bisht S Banerjee S Qureshi Q Jhala YV (2019) Demography of a high-density tiger population and its implications for tiger recovery. Journal of Applied Ecology 56(7):1725-1740

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

Blair HW (1990) Local government and rural development in the Bengal Sundarbans: an inquiry in managing common property resources. Agric Hum Values 7:40–51

Blasco F Saenger P Janodet E (1996) Mangroves as indicators of coastal change. Catena 27:167–178

Borchers DL Efford M (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. Biometrics 64: 377-385

Brij G Chauhan M (2006) Biodiversity and its conservation in the Sundarban Mangrove Ecosystem. Aquatic Sciences 68(3):338-354

Broadley K Burton AC Avgar T Boutin S (2019) Density-dependent space use affects interpretation of camera trap detection rates. Ecology and evolution 9(24) 14031-14041

Buckland ST Anderson DR Burnham KP Laake JL Borchers DL Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, USA

Buckland ST Rexstad EA Marques TA Oedekoven CS (2015) Distance sampling: methods and applications. Springer, USA

Burt WH (1943) Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352

Camargo-Sanabria AA Mandujano S (2011) Comparison of pellet-group counting methods to estimate population density of white-tailed deer in a Mexican tropical dry forest. Tropical Conservation Science 4(2):230-243

Carbone C Christie S Conforti K Coulson T Franklin N Ginsberg JR Griffiths M Holden J Kawanishi K Kinnaird M Laidlaw R Lynam A Macdonald DW Martyr D McDougal C Nath L O'Brien T Seidensticker J Smith DJL Sunquist M Tilson R Wan Shahruddin WN (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. Animal Conservation 4(1): 75-79 doi:10.1017/S1367943001001081

Cardillo M Purvis A Sechrest W Gittleman JL Bielby J Mace GM (2004) Human population density and extinction risk in the world's carnivores. PLoS biology 2(7):197

Caughley G (1977) Analysis of vertebrate populations Analysis of vertebrate populations. The Blackburn Press, USA

Chakrabarti K (1980) Ecology of the Sunderbans tiger with a particular reference to range of habitats and adaptability to changes. Cheetal 20:2-3

Chakrabarti K (1992) Man-eating tigers. Darbari Prokashan, India

Champion HG Seth SK (1968) A revised survey of the forest types of India.

Chapman S Balme G (2010) An estimate of leopard population density in a private reserve in KwaZulu-Natal South Africa using camera—traps and capture-recapture models. African Journal of Wildlife Research 40(2) 114-120

Chapron G Miquelle DG Lambert A Goodrich JM Legendre S Clobert J (2008) The impact on tigers of poaching versus prey depletion. Journal of Applied Ecology 45(6):1667-1674

Chaudhuri AB Choudhury A (1994) Mangroves of the Sundarbans. 1 India International Union for Conservation of Nature and Natural Resources, Switzerland

Christopher J Michael S Runge C MacKenzie DI (2002) The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. Animal Conservation 5(2):119-120

Cooch E White G (2006) Program MARK: a gentle introduction. Colorado State University, USA

Cusack JJ Dickman AJ Rowcliffe JM Carbone C Macdonald DW Coulson T (2015) Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. PloS ONE 10(5):0126373 doi.org/10.1371/journal.pone.0126373

Datta A Anand MO Naniwadekar R (2008) Empty forests: Large carnivore and prey abundance in Namdapha National Park north-east India. Biological Conservation 141(5):1429-1435

Dawson DK Efford MG (2009) Bird population density estimated from acoustic signals. Journal of Applied Ecology 46(6) 1201-1209

Depraetere M Pavoine S Jiguet F Gasc A Duvail S Sueur J (2012) Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. Ecological Indicators 13(1):46-54

Dice LR (1938) Some census methods for mammals. Journal of Wildlife Management 2:119–130

Dinerstein E Loucks C Wikramanayake E Ginsberg J Sanderson E Seidensticker J Forrest J Bryja G Heydlauff A Klenzendorf S Leimgruber P (2007) The fate of wild tigers. BioScience 57(6):508-514

Dinerstein E Wikramanayake E Robinson J Karanth U Rabinowitz A Olson DM Mathew T Hedao P Connor M Hemley G Bolze D (1997) A framework for identifying high priority areas and actions for the conservation on tigers in the wild. World Wildlife Fund and Wildlife Conservation Society, USA

du Preez BD Loveridge AJ Macdonald DW (2014) To bait or not to bait: a comparison of camera-trapping methods for estimating leopard (Panthera pardus) density. Biological Conservation 176:153–161

Efford MG (2004) Density estimation in live-trapping studies. Oikos 106:598-610

Efford MG (2015) secr: Spatially explicit capture-recapture models. R package version, 2(3)

Ellis AM Bernard RT (2005) Estimating the density of kudu (Tragelaphus strepsiceros) in subtropical thicket using line transect surveys of dung and DISTANCE software. African Journal of Ecology 43(4) 362-368

Feller W (1950) An introduction to probability theory and its applications. 1 John Wiley & Sons Inc, USA

Fickel J Hohmann U (2006) A methodological approach for non-invasive sampling for population size estimates in wild boars (Sus scrofa). European Journal of Wildlife Research 52(1):28-33

Focardi S Isotti R Pelliccioni ER Iannuzzo D (2002) The use of distance sampling and mark-resight to estimate the local density of wildlife populations. Environmetrics: The official journal of the International Environmetrics Society 13(2) 177-186

Gardner B Royle JA Wegan MT Rainbolt RE Curtis PD (2010) Estimating black bear density using DNA data from hair snares. The Journal of Wildlife Management 74(2) 318-325

Gerber BD Ivan JS Burnham KP (2014) Estimating the abundance of rare and elusive carnivores from photographic-sampling data when the population size is very small. Population ecology 56(3): 463-470

Gerber BD Karpanty SM Kelly MJ (2012) Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. Population ecology 54:43-54

Gerrodette T (1987) A power analysis for detecting trend. Ecology 68(5):1364-1372

Gopal R Qureshi Q Bhardwaj M Singh RJ Jhala YV (2010) Evaluating the status of the endangered tiger Panthera tigris and its prey in Panna Tiger Reserve, Madhya Pradesh, India. Oryx 44(03): 383-389

Guschanski K Vigilant L McNeilage A Gray M Kagoda E Robbins MM (2009) Counting elusive animals: comparing field and genetic census of the entire mountain gorilla population of Bwindi Impenetrable National Park, Uganda. Biological Conservation 142(2):290-300

Harihar A Pandav B Goyal SP (2009) Responses of tiger (Panthera tigris) and their prey to removal of anthropogenic influences in Rajaji National Park, India. European Journal of Wildlife Research 55(2): 97-105

Harris RB Winnie Jr J Amish SJ BEJA-PEREIRA ALBANO Godinho R COSTA V Luikart G (2010) Argali abundance in the Afghan Pamir using capture–recapture modeling from fecal DNA. The Journal of Wildlife Management 74(4) pp668-677

Hayne DW (1949) Calculations of home range size. Journal of Mammalogy 30:1–18

Hendrichs H (1975) The status of the tiger Panthera tigris (Linne 1758) in the Sundarbans mangrove forest (Bay of Bengal). Saugertierkundliche Mitteilungen 23(3): 161–199

Horino SI Nomiya H (2008) Defecation of sika deer Cervus Nippon. Mammal study 33(4):143-150

Huggins RM (1989) On the statistical analysis of capture experiments. Biometrika 76: 133-140

Islam MS Wahab MA (2005) A review on the present status and management of mangrove wetland habitat resources in Bangladesh with emphasis on mangrove fisheries and aquaculture In: Segers H Martens K (eds) Aquatic biodiversity II Springer, Netherlands

Jackson RM Roe JD Wangchuk R Hunter DO (2006) Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildlife Society Bulletin 34(3) 772-781

Jathanna D Karanth KU Johnsingh AJT (2003) Estimation of large herbivore densities in the tropical forests of southern India using distance sampling. Journal of Zoology 261(3) 285-290

Jenks KE Chanteap P Kanda D Peter C Cutter P Redford T Antony JL Howard J Leimgruber P (2011) Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses–an example from Khao Yai National Park, Thailand. Tropical Conservation Science 4(2):113-131

Jhala YV Dey TK Qureshi Q Kabir J Md Bora J Roy M (2016) Status of tigers in the Sundarban landscape Bangladesh and India Bangladesh Forest Department. National Tiger Conservation Authority New Delhi Wildlife Institute of India Dehradun TRNO - 2016/002

Jhala YV Qureshi Q Gopal R (2014) The status of tigers in India 2014 National Tiger Conservation Authority New Delhi and the Wildlife Institute of India, India

Jhala YV Qureshi Q Gopal R Sinha PR (eds) (2011) Status of tigers co-predators and prey in India 2010. TR 2011(003):1–302 National tiger conservation authority and Wildlife Institute of India, India

Johnson A Vongkhamheng C Hedemark M Saithongdam T (2006) Effects of human–carnivore conflict on tiger (Panthera tigris) and prey populations in Lao PDR. Animal Conservation 9(4): 421-430

Joshi AR Dinerstein E Wikramanayake E Anderson ML Olson D Jones BS Seidensticker J Lumpkin S Hansen MC Sizer NC Davis CL (2016) Tracking changes and preventing loss in critical tiger habitat. Science advances 2(4):1501675

Kalle R Ramesh T Qureshi Q Sankar K (2011) Density of tiger and leopard in a tropical deciduous forest of Mudumalai Tiger Reserve, southern India as estimated using photographic capture–recapture sampling. Acta Theriologica 56(4): 335-342

Kanjilal B Mazumdar PG Mukherjee M Mondal S Barman D Singh S Mandal A (2010) Health care in the Sundarbans (India): challenges and plan for a better future. Institute of Health Management Research, India

Karanth K Chundawat RS Nichols JD Samba Kumar N (2004) Estimation of tiger densities in the tropical dry forests of Panna, Central India using photographic capture–recapture sampling. Animal Conservation 7(3): 285-290

Karanth KU (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. Biological conservation 71(3) 333-338

Karanth KU (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. Biological conservation 71(3):333-338

Karanth KU Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79: 2852-2862

Karanth KU Nichols JD (2000) Ecological Status and Conservation of Tigers in India. Final Technical Report

Karanth KU Nichols JD Kumar N Hines JE (2006) Assessing tiger population dynamics using photographic capture–recapture sampling. Ecology 87(11): 2925-2937

Karanth KU Sunquist ME (1995) Prey selection by tiger leopard and dhole in tropical forests. Journal of Animal Ecology 64:439-450

Karki JB Pandav B Jnawali SR Shrestha R Pradhan NMB Lamichane BR Jhala YV (2015) Estimating the abundance of Nepal's largest population of tigers Panthera tigris. Oryx 49(01):150-156

Kawanishi K Sunquist ME (2004) Conservation status of tigers in a primary rainforest of Peninsular Malaysia. Biological Conservation 120(3): 329-344

Kays R Parsons AW Baker MC Kalies EL Forrester T Costello R McShea WJ (2017) Does hunting or hiking affect wildlife communities in protected areas? Journal of Applied Ecology 54(1) 242-252

Kelly MJ Holub EL (2008) Camera trapping of carnivores: trap success among camera types and across species and habitat selection by species on Salt Pond Mountain Giles County Virginia. Northeastern naturalist 15(2) 249-262

Khan JA Chellam R Rodgers WA Johnsingh AJT (1996) Ungulate densities and biomass in tropical dry deciduous forests of Gir, Gujarat. India Journal of Tropical Ecology 12:149-162

Khan MMH (2004) Ecology and conservation of the Bengal tiger in the Sunderbans Mangrove forest of Bangladesh. Phd thesis, University of Cambridge, Cambridge

Kouakou CY Boesch C Kuehl H (2009) Estimating chimpanzee population size with nest counts: validating methods in Taï National Park. American Journal of Primatology: Official Journal of the American Society of Primatologists 71(6) 447-457

Kouakou CY Boesch C Kuehl H (2009) Estimating chimpanzee population size with nest counts: validating methods in Taï National Park. American Journal of Primatology 71(6):447-457

Kruger JM Reilly BK Whyte IJ (2008) Application of distance sampling to estimate population densities of large herbivores in Kruger National Park. Wildlife Research 35(4) 371-376

Kuehl HS Todd A Boesch C Walsh PD (2007) Manipulating decay time for efficient large-mammal density estimation: gorillas and dung height. Ecological Applications 17(8):2403-2414

Kvale EP (2006) Comment on "The origin of neap–spring tidal cycles". Marine Geology 235:5–18

Laing SE Buckland ST Burn RW Lambie D Amphlett A (2003) Dung and nest surveys: estimating decay rates. Journal of Applied Ecology 40(6):1102-1111

Lebreton JD Burnham KP Clobert J Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118

Lettink M Armstrong DP (2003) An introduction to using mark-recapture analysis for monitoring threatened species. Department of Conservation Technical Series A 28: 5-32

Loucks C Barber-Meyer S Hossain MAA Barlow A Chowdhury RM (2010) Sea level rise and tigers: predicted impacts to Bangladesh's Sundarbans mangroves. Climate Change 98:291–298

Lukacs PM Burnham KP (2005) Review of capture–recapture methods applicable to noninvasive genetic sampling. Molecular ecology 14(13):3909-3919

Lynam AJ Rabinowitz A Myint T Maung M Latt KT Po SHT (2009) Estimating abundance with sparse data: tigers in northern Myanmar. Population Ecology 51(1): 115-121

Marques FF Buckland ST Goffin D Dixon CE Borchers DL Mayle BA Peace AJ (2001) Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. Journal of Applied Ecology 349-363

Marques FF Buckland ST Goffin D Dixon CE Borchers DL Mayle BA Peace AJ (2001) Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. Journal of Applied Ecology 38(2):349-363

Marques Tiago A Len Thomas Jessica Ward Nancy DiMarzio and Peter L Tyack Estimating cetacean population density using fixed passive acoustic sensors: An example with Blainville's beaked whales. The Journal of the Acoustical Society of America 125 no 4 (2009): 1982-1994

Marsh DM Trenham PC (2008) Current trends in plant and animal population monitoring. Conservation Biology 22:647-655

Mathewson PD Spehar SN Meijaard E Sasmirul A Marshall AJ (2008) Evaluating orangutan census techniques using nest decay rates: implications for population estimates. Ecological Applications 18(1):208-221

Maxwell D Jennings S (2005) Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. Journal of Applied Ecology 42(1):25-37

Milliman JD Rutkowski C Meybeck M (1995) River Discharge in the Sea: A Global River Index (GLORI). LOICZ Reports and Studies. Netherlands Institute for Sea Research, The Netherlands

Moore PG (1954) Spacing in plant populations. Ecology 35:222-227

Morgan JP McIntyre WG (1959) Quaternary Geology of the Bengal Basin East Pakistan and India. Bulletin of Geological Society 70:319-342

Mowat G Strobeck C (2000) Estimating population size of grizzly bears using hair capture DNA profiling and mark-recapture analysis. The Journal of wildlife management 183-193

Mukherjee S (2005) Ecological investigations on mangroves of the Sundarbans Tiger Reserve in West Bengal (India) with special reference to effective conservation through management practice. PhD Thesis, University of Kalyani, Kalyani

Nagelkerken I (ed) 2009 Ecological Connectivity Among Tropical Coastal Ecosystems. Springer, USA

Naha D Jhala YV Qureshi Q Roy M Sankar K Gopal R (2016) Ranging Activity and Habitat Use by Tigers in the Mangrove Forests of the Sundarban. PLoS ONE 11(4):e0152119 doi:101371/journalpone0152119

Naskar K Guha Bakshi DN (1987) Mangrove swamps of the Sunderbans: an ecological perspective. Naya Prakash, India

Naskar K Mandal R (1999) Ecology and biodiversity of Indian mangroves. 1 Daya Books, India

Nchanji AC Plumptre AJ (2001) Seasonality in elephant dung decay and implications for censusing and population monitoring in south-western Cameroon. African Journal of Ecology 39(1) 24-32

Neff DJ (1968) The pellet-group count technique for big game trend census and distribution: a review. The Journal of Wildlife Management 597-614

Neumann-Denzau G Denzau H (2010) Examining certain aspects of human-tiger conflict in the Sundarbans forest Bangladesh. Tigerpapers 37:1–11

Nichols JD (2010) The wildlife picture index monitoring and conservation. Animal Conservation 134:344-346

Nichols JD Conroy MJ (1996) Estimation of species richness. Pages 227–234 in D Wilson et al editors Measuring and monitoring biological diversity: standard methods for mammals. Smithsonian Institution Press, USA

Norris JL Pollock KH (1996) Nonparametric MLE under two closed capture-recapture models with heterogeneity. Biometrics 639-649

O'Brien TG Kinnaird MF Wibisono HT (2003) Crouching tigers hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation 6(02): 131-139

O'Connell AF Nichols JD Karanth KU (Eds) (2010) Camera traps in animal ecology: methods and analyses. Springer Science & Business Media, USA

O'Kelly HJ Evans TD Stokes EJ Clements TJ Dara A Gately M Menghor N Pollard EHB Soriyun M Walston J (2012) Identifying conservation successes failures and future opportunities; assessing recovery potential of wild ungulates and tigers in eastern Cambodia. PloS ONE 7(10): e40482

Otis DL Burnham KP White GC Anderson DR (1978) Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:3-135

Packer C Holt RD Hudson PJ Lafferty KD Dobson AP (2003) Keeping the herds healthy and alert: implications of predator control for infectious disease. Ecology Letters 6(9):797-802

Palmer MS Swanson A Kosmala M Arnold T Packer C (2018) Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. African Journal of Ecology 56(4):791-803

Plumptre AJ Reynolds V (1996) Censusing chimpanzees in the Budongo forest Uganda. International Journal of Primatology 17(1):85-99

Pollock KH Solomon DL Robson DS (1974) Tests for mortality and recruitment in a K-sample tag-recapture experiment. Biometries 30(1):77-87

Prasad S Krishnaswamy J Chellam R Goyal SP (2006) Ruminant-mediated Seed Dispersal of an Economically Valuable Tree in Indian Dry Forests. Biotropica 38(5):679-682

Prugh LR Ritland CE Arthur SM Crebs CJ (2005) Monitoring coyote population dynamics by genotyping faeces. Molecular Ecology 14:1585–1596

Putman RJ (1984) Facts from faeces. Mammal review 14(2) 79-97

Qureshi Q Gopal R Shirish K Basu S Mitra A Jhala YV (2006) Evaluating tiger habitat at the Tehsil level. Project tiger directorate and Wildlife Institute of India, India

Rahman AF Dragoni D El-Masri B (2011) Response of the Sundarbans coastline to sea level rise and decreased sediment flow: A remote sensing assessment. Remote Sensing of Environment 115:3121–3128

Rahman LM (2000) The Sundarbans: a unique wilderness of the world. Proceedings - Rocky Mountain Research Station USDA Forest Service 2000 No RMRS-P-15 2:143-148

Reza A Feeroz MM Islam MA (2001) Food habits of the Bengal tiger (Panthera tigris tigris) in the Sunderbans. Bangladesh Journal of Zoology 29:173-180

Ripple WJ Beschta RL (2012) Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biological Conservation 145(1):205-213

Ripple WJ Estes JA Beschta RL Wilmers CC Ritchie EG Hebblewhite M Berger J Elmhagen B Letnic M Nelson MP Schmitz OJ (2014) Status and ecological effects of the world's largest carnivores. Science 343(6167) 1241484

Ripple WJ Wirsing AJ Wilmers CC Letnic M (2013) Widespread mesopredator effects after wolf extirpation. Biological Conservation 160:70-79

Rivero K Rumiz DI Taber AB (2004) Estimating brocket deer (Mazama gouazoubira and M americana) abundance by dung pellet counts and other indices in seasonal Chiquitano forest habitats of Santa Cruz Bolivia. European Journal of Wildlife Research 50(4):161-167

Robsons DS Regeir HA (1964) Sample size in Petersen mark-recapture experiments. Transactions of the American Fisheries Society 93(3):215-226

Rowcliffe JM Field J Turvey ST Carbone C (2008) Estimating animal density using camera traps without the need for individual recognition. Journal of Applied Ecology 45(4):1228-1236

Roy M Qureshi Q Naha D Sankar K Gopal R Jhala YV (2016) Demystifying the Sundarban tiger: novel application of conventional population estimation methods in a unique ecosystem. Population ecology 58(1): 81-89

Royle JA Chandler RB Sollmann R Gardner B (2013) Spatial capture-recapture. Academic Press, USA

Royle JA Magoun AJ Gardner B Valkenburg P Lowell RE (2011) Density estimation in a wolverine population using spatial capture–recapture models. The Journal of wildlife management 75(3) 604-611

Royle JA Nichols JD Karanth KU Gopalaswamy AM (2009) A hierarchical model for estimating density in camera-trap studies. Journal of Applied Ecology 46(1):118-127

Sanderson EW Forrest J Loucks C Ginsberg J Dinerstein E Seidensticker J Leimgruber P Songer M Heydlauff A O'Brien T Bryja G (2010) Setting priorities for tiger conservation: 2005–2015. In Tigers of the world (143-161) William Andrew Publishing, USA

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

Sarmento PB Cruz JP Eira CI Fonseca C (2010) Habitat selection and abundance of common genets Genetta genetta using camera capture-mark-recapture data. European Journal of Wildlife Research 56(1) 59-66

Schwarz CJ Seber GAF (1999) Estimating animal abundance: review III. Statistical Science 427-456

Seber GAF (1973) The Estimation of Animal Abundance and Related Parameters. Charles Griffin & Company Limited, London

Seddon PJ Ismail K Shobrak M Ostrowski S Magin C (2003) A comparison of derived population estimate mark-resighting and distance sampling methods to determine the population size of a desert ungulate the Arabian oryx. Oryx 37(3) 286-294

Seidensticker J Hai MA (1983) The Sundarbans wildlife management plan: conservation in the Bangladesh coastal zone.

Silver SC Ostro LE Marsh LK Maffei L Noss AJ Kelly MJ Wallace RB Gomez H Ayala G (2004) The use of camera traps for estimating jaguar Panthera onca abundance and density using capture/recapture analysis. Oryx 38(2) pp148-154

Simcharoen S Pattanavibool A Karanth KU Nichols JD Kumar NS (2007) How many tigers Panthera tigris are there in Huai Kha Khaeng Wildlife Sanctuary Thailand? An estimate using photographic capture-recapture sampling. Oryx 41(04):447-453

Singh R Qureshi Q Sankar K Krausman PR Goyal SP (2013) Use of camera traps to determine dispersal of tigers in semi-arid landscape western India. Journal of arid environments 98:105-108

Singh SK Mishra S Aspi J Kvist L Nigam P Pandey P Sharma R Goyal SP (2015) Tigers of Sundarbans in India: is the population a separate conservation unit? PloS ONE 10(4):pe0118846

Smith JLD (1993) The role of dispersal in structuring the Chitwan tiger population. Behaviour 124:169–195

Smith MH Blessing R Chelton JG Gentry JB Golley FB McGinnis JT (1971) Determining density for small mammal populations using a grid and assessment lines. Acta Theriologica 16:105–125

Snedaker C (1991) Notes on the Sundarbans with emphasis on geology hydrology and forestry. In: J Seidensticker R Kurin and A K Townsend (eds) The Commons in South Asia: Societal Pressures and Environmental Integrity in the Sundarbans, The International Center Smithsonian Institution, USA

Solberg KH Bellemain E Drageset OM Taberlet P Swenson JE (2006) An evaluation of field and non-invasive genetic methods to estimate brown bear (Ursus arctos) population size. Biological Conservation 128:158–168

Sollmann R Gardner B Chandler RB Shindle DB Onorato DP Royle JA O'Connell A F (2013) Using multiple data sources provides density estimates for endangered Florida panther. Journal of Applied Ecology 50(4) 961-968

Speakman TR Lane SM Schwacke LH Fair PA Zolman ES (2010) Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (Tursiops truncatus) near Charleston South Carolina USA. Journal of Cetacean Research and Management 11(2) 153-162

Spitzer R Churski M. Felton A Heurich M Kuijper DP Landman M Rodriguez E Singh NJ Taberlet P van Beeck Calkoen ST Widemo F (2019) Doubting dung: eDNA reveals high rates of misidentification in diverse European ungulate communities. European Journal of Wildlife Research 65(2) p.28.

Steidl RJ Hayes JP Schauber E (1997) Statistical power analysis in wildlife research. Journal of Wildlife Management 61:270–279

Steinmetz R Chutipong W Seuaturien N Chirngsaard E Khaengkhetkarn M (2010) Population recovery patterns of Southeast Asian ungulates after poaching. Biological Conservation 143(1):42-51

Stevens TH Echeverria J Glass RJ Hager T More TA (1991) Measuring the existence value of wildlife: what do CVM estimates really show? Land Economics 67(4):390-400

Sunquist ME (1981) The social organization of tigers (Panthera tigris) in Royal Chitawan National Park, Nepal. Smithsonian Contributions to Zoology 336:1–98

Sutherland WJ (Ed) (2006) Ecological census techniques: a handbook. Cambridge University Press, Cambridge

Taylor BL Gerrodette T (1993) The uses of statistical power in conservation biology: the vaquita and northern spotted owl. Conservation biology 7(3):489-500

Terborgh J Lopez L Nuñez P Rao M Shahabuddin G Orihuela G Riveros M Ascanio R Adler GH Lambert TD Balbas L (2001) Ecological meltdown in predator-free forest fragments. Science 294(5548):1923-1926

Thom BG (1967) Mangrove ecology and deltaic geomorphology: Tabasco. Mexico Journal of Ecology 55:301-343

Tilson R Defu H Muntifering J Nyhus PJ (2004) Dramatic decline of wild South China tigers Panthera tigris amoyensis: field survey of priority tiger reserves. Oryx 38 40–47

Townsend SE Galtbalt B Myagmar M Baillie J O'Brien TG (2014) The Wildlife Picture Index: monitoring Mongolian biodiversity with camera trapping. Camera trapping: Wildlife management and research. CSIRO Publishing, Australia

Trolle M Kéry M (2003) Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. Journal of mammalogy 84(2) 607-614

Tsaparis D Katsanevakis S Ntolka E Legakis A (2009) Estimating dung decay rates of roe deer (Capreolus capreolus) in different habitat types of a Mediterranean ecosystem: an information theory approach. European Journal of Wildlife Research 55(2) 167-172

Van Vliet N Nasi R Lumaret JP (2009) Factors influencing duiker dung decay in north-east Gabon: are dung beetles hiding duikers? African Journal of ecology 47(1) 40-47

Walpole MJ Leader-Williams N (2002) Tourism and flagship species in conservation. Biodiversity and conservation 11(3):543-547

Walsh PD White LJ (2005) Evaluating the steady state assumption: simulations of gorilla nest decay. Ecological Applications 15(4):1342-1350

Wang SW Macdonald DW (2009) The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. Biological Conservation 142(3):606-613

Wegge P Storaas T (2009) Sampling tiger ungulate prey by the distance method: lessons learned in Bardia National Park Nepal. Animal Conservation 12(1) 78-84

White GC Anderson DR Burnham KP Otis DL (1982) Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, USA

White GC Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird study 46(1):S120-S139

Wikramanayake E McKnight M Dinerstein E Joshi A Gurung B Smith D (2004) Designing a conservation landscape for tigers in human-dominated environments. Conservation Biology 18:839–844

Williams BK Nichols JD Conroy MJ (2002) Analysis and management of animal populations. Academic Press, USA

Wing LD Buss IO (1970) Elephants and forests. Wildlife monographs 19:3-92

Wingard GJ Harris RB Amgalanbaatar S Reading RP (2011) Estimating abundance of mountain ungulates incorporating imperfect detection: argali Ovis ammon in the Gobi Desert Mongolia. Wildlife Biology 17(1) 93-101

Yoccoz NG Nichols JD Boulinier T (2001) Monitoring of biological diversity in space and time. Trends in ecology & evolution 16(8):446-453

Zar JH (1974) Biostatistical analysis. Prentice H

Zero VH Sundaresan SR O'Brien TG Kinnaird MF (2013) Monitoring an endangered savannah ungulate Grevy's zebra Equus grevyi: choosing a method for estimating population densities. Oryx 47(3) 410-419