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**Evaluating the Effect of Design and Sampling  
intensity on Estimating Tiger Population and  
Density**

*Dissertation Submitted to*  
Saurashtra University, Rajkot.  
in Partial Fulfillment of the Master's Degree in Wildlife Science

*By*  
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## Certificate

This is to certify that **Ms. Deep Contractor** student of the Wildlife Institute of India has carried out original research titled "*Evaluating Effect of Design and Sampling Intensity on Estimating Tiger Population and Density*" for the partial fulfillment of the Master of (Wildlife) Science Degree from the Saurashtra University, Rajkot, India. These investigations were carried out under our supervision from November 2006 to June 2007. We also certify that this research has not been submitted for any other degree to any University

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For Maa..

*For Maa..*

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## SUMMARY

Population estimation is one of the most important aspects of ecological studies as it plays a pivotal role in establishing priorities for species specific conservation and for delineating management practices. The tiger serves as a flagship and umbrella species for conservation efforts in the Indian subcontinent but, unfortunately wild tiger populations are on a drastic decline owing to factors like poaching, habitat fragmentation and degradation. In such a scenario reliable population estimates prove to be of vital importance. Camera trapping technique has been widely used for population estimation of cryptic carnivores including tigers, but the issues regarding sampling design and effort required to effectively sample an area have been paid less attention. An attempt was made, through this study, to arrive at population and density estimates for Corbett NP through camera trapping technique following the mark recapture framework and answering some key questions regarding the importance of sampling effort required for arriving at such reliable estimates. A total of 7865 trap nights yielded 358 captures of 103 individual tigers within an intensively sampled area of (MCP) 420.86 km<sup>2</sup>. The estimated density of tiger was 16.01 ( $\pm 1.6$ ) per 100 km<sup>2</sup> for RPSV, a new approach to calculate effectively sampled area. These estimates coincided with the estimates using full MMDM method. Also, the conventional method of using half MMDM seems to overestimate the density. The estimated sampling effort required for arriving at accurate and precise estimates of the true population in terms of sampling occasions amounted to 35 – 40 days. Evaluation of the influence of trap density revealed that high trap density (25 traps/km<sup>2</sup> ca.) is required to get reliable estimates of population irrespective of the underlying population/density gradient.

## 1. INTRODUCTION

Population estimation is one of the most important aspects of ecological studies. Not only is it essential for establishing priorities for species specific conservation, but also for delineating management practices (Carbone *et al* 2001).

Most modern methods of animal population estimation come under a general statistical framework that deals with two central concepts viz. spatial sampling and observability (Lancia *et al* 1994, Thompson *et al* 1998). Out of the two, spatial sampling concerns frequent inability of animal survey methods to cover entire area of interest. In such cases, we representatively survey some subset of that area, and then use these results to draw inferences about the entire area (Smallwood and Schonewald 1998).

Greig - Smith (1983) stated that the best way study an animal population is with reference to its distribution and abundance. In other words, density is an ideal instrument for studying animal population. The density estimates can be an operational term in ecology but only if they are defined with reference to its spatial scale which is often not the case (Smallwood and Schonewald 1996).

The methods employed for the estimation of endangered large carnivores suffers from the limitation of low numbers and poor detection probability and this limitation makes it a difficult to arrive at reliable population estimates. Also reliable estimates of status and population trend of large carnivores are lacking due to high cost of sampling across large geographical areas (Smallwood & Fitzhugh, 1995)

Bertram (1979) rightly stated that felids are notoriously difficult to count. Sampling through methods like transects, waterhole counts etc is unimaginable for a species like tiger (*Panthera tigris*), owing to their territoriality, low density and nocturnal and cryptic habit (Bertram 1979; Karanth & Nichols, 1998, 2000). In such a scenario indirect methods of population estimation like camera trapping in the mark recapture

framework proves to be instrumental. Plus it has an added advantage of being non intrusive as unlike the traditional mark recapture techniques, camera trapping does not involve actual “trapping” of tigers and marking them.

Tigers (*Panthera tigris*) have always been enigmatic/mysterious creatures in the minds of one and all and its cryptic and shy nature adds to its mystery. Its majestic presence in the Indian landscape has given it a special place in the folklore, art and cultural history of the country and also has endowed it with the status of the national animal.

The tiger once had the widest geographical distribution among large felids, stretching originally from almost 10° latitude south of the equator to (Java and Bali) to more than 60° north (the Russian Far East) and through more than 100° longitude (Nowell & Jackson, 1996).

As a top predator in most Indian forest ecosystem, it plays a crucial role in the functioning and continuation of ecological processes. Tigers have also been the focus of conservation activities in the country because of its dual function as an umbrella species i.e. species requiring such large areas of continuous habitat that their protection might automatically protect other species, as well as a flagship species i.e. a charismatic public appeal which helps to acquire good amount of support from the general public. It has attracted a myriad of scientists from India and abroad to study the ever fascinating aspects of its ecology (see Schaller 1967, Sunquist et al 1999, Siedensticker and McDougal 1993etc).

Unfortunately, wild tiger population is on a rapid decline despite what seems like our best conservation efforts. Three of the eight putative subspecies are extinct and a fourth is close to extinction in the wild (Nowell & Jackson, 1996). Tiger populations are now being affected by adverse factors such as prey depletion due to over hunting

(Karanth and Stith 1999), tiger poaching/ hunting for their fur and for their use in traditional Chinese medicine (Kenny et al 1995, Kitchner 1999) and habitat shrinkage and fragmentation (Wikramanayake et al 1998).

It needs large undisturbed habitats with ample amount of prey to breed successfully and maintain a genetically viable population (Seidensticker and McDougal 1993) which are deteriorating at a rapid rate due to the pressures of the ever growing human population. Whatever protection is being provided is through the 28 tiger reserves in 17 states of the country extant today, but they have largely become analogous to small islands surrounded by a sea of land under heavy anthropogenic exploitation (Qureshi et al 2006).

In such a scenario, it is crucial to have reliable estimates of tiger densities to assess its status and viability in different landscapes across the country. We need these estimates to prioritize conservation areas as well as concentrate the resources available in terms of effort as well as skill.

Utility for assessing the status and viability of tiger populations is limited by the absence of reliable data on population densities. Lack of reliable data on tiger densities not only has constrained our ability to understand the ecological factors shaping communities of large, solitary felids, but also has undermined the effective conservation of these animals. Establishing theoretically sound and practically feasible population sampling methods to estimate densities of wild tiger populations is critically important for both scientific and management reasons (Karanth and Nichols 1998, Carbone 2001)

## **1.1 Literature review**

### ***1.1.1. Methods used for estimating tiger populations***

The most commonly used method in India (before the advent of mark recapture through camera trapping) was the pug mark census method (Choudhary 1970, 1972;

Panwar 1980; Singh 1999) In this method forest department personnel would fan out in their respective divisions and search for tiger tracks. The pugmarks are either collected through plaster casts or traced. These are then compared to identify individual tigers relying on perceived differences in shape, other measurements and ancillary local knowledge. For thirty years this method has been exclusively used on country wide basis and is claimed yield accurate results in a cost affective manner (Panwar 1980; Singh 1999). However, their method fails on two counts. The goal of absolute abundance proves to be unrealistic and the crude method of allocating pugmarks to individual tigers through perceived variations, which may vary themselves depending on the identifying officials, who are assumed to have a well versed knowledge and experience of such type of identification, often leads to false estimates. Because pugmark census fails to attain its unrealistic goal of absolute abundance, three decades of tiger monitoring has basically failed in India, despite being backed my massive investment and best of intentions (Karanth et al 2003).

Sharma et al (2005) provided a solution to this problem by describing an objective multivariate technique. They traced as well as photographed pugmark sets of tigers and after rigourous testing and validation selected 11 variables which do not differ between left and right pugmarks and help in correctly classifying pug – sets to individual tigers through the help of step wise discriminant function analysis. They also recommended the soil depth for collection of pugmark and strongly suggested the use of photographs instead of tracings of pugmarks. Their study suggested that tigers can be individually identified from their pugmarks with a high level of accuracy and pugmark-sets could be used for population estimation of tigers within a statistically designed mark–recapture framework.

One of the most recent developments in estimation of population is genotyping faeces. Four steps are involved in this process. First, collection of faeces from paths or trails, second, extraction of DNA from the faeces for species identification and determination of sex through mitochondrial DNA and Y – chromosome typing, third is typing of microsatellite loci from the faeces and the last is rarefaction analysis to estimate the population size from faecal genotype. Although this method is non invasive, it is very expensive, requires specialized skill personnel and sophisticated lab facilities (Kohn et al 1999)

Radio tagging/ telemetry has also been used to study tiger populations. But these studies are mostly pertaining to the behavioural and long term demographic aspects of the tiger's ecology (Sunquist 1981, Smith 1993). Tiger density estimation through this method is constrained by the high costs of radio collars, being able to tag a small number of animals simultaneously and uncertainty of untagged animals, and the high effort involved.

For tigers and other forest dwelling carnivores, mark – recapture using camera traps following Karanth(1995) and Karanth and Nichols (1998) provides a very useful technique for estimating population size and other population parameters (Carbone et al 2001). Camera trapping furnishes an important non invasive tool for assessing patterns of abundance throughout space and time. The advantages involve the possibility of evaluating sex, age and population structure and density in large tracts of land (Kelly et al 1998, Mace et al 1994) In naturally marked species like tigers, the method can raise relevant ecological information, as substitutes for other intrusive methods, such as capturing and radio – collaring of individuals.(L. Silveira et al 2003). The initial costs of camera trapping may be relatively high but, compared to methods such as pugmark censuses and line transects etc, it can be handled more easily and with relatively low

costs in a long term run. It also has the advantage of sampling a considerable extent of area simultaneously and also offers the possibility of being used in further population studies.

### ***1.1.2 Mark recapture:***

As already stated mark recapture approach has gained much momentum in recent tiger population studies, which brings about the following discussion which will set the foreground for the objectives in question.

It is often considered that this method was first used by C.G.J. Peterson (1889) but Bailey (1952) points out that it was Lincoln (1930) who used it first as Peterson never calculated the total population from the marked fish recaptures. Le Cren (1965) is of the opinion Dahl (1918-19) may have been the first person to use mark recapture for total population count.

The origin of mark recapture methodology is the two occasion case (Chao and Huggins 2005). The intuitive idea is to assume on first capture occasion a known number of individuals ( $n_1$ ) are captured, marked and released back to mix with the population ( $N$ ) and then taking a second sample ( $n_2$ ) of known size and finding the number of marked individuals it contains ( $m_2$ ). Based on the notion that the ratio of the marked individuals to the total animals in second sample should reflect the same ratio in population ( $N$ ), therefore

$$m_2 / n_2 = n_1 / N$$

therefore it yields the estimate of population size,

$$N = n_1 n_2 / m_2$$

This estimator can be used to determine the total population and is known as Peterson estimate or Lincoln Index (Seber 1982).

It was realized that two capture occasions may not result in reliable estimates and thus they were extended to multiple occasions by Schnabel (1938) and Darroch (1958). Their approaches formed the basis for classical models, and like the Peterson-Lincoln model, these early models assume the equal probability of capture of animal on each occasion, although it can be allowed to vary among sampling occasions.

### *1.1.3 Population estimation models:*

Population analysis very often requires modeling to bridge gaps in the knowledge which are usually created as an outcome of our inability to study the entire area and get absolute numbers (Johnson 1994). Such inability is only obvious and constrains our inference to 'estimates' and not actual numbers. Various models have been developed for arriving at these estimates within the mark recapture framework.

Every estimation method is based on a set of assumptions. . Otis et al (1978) listed the assumptions for capture recapture estimators. They are:

- (1) Population is geographically and demographically closed.
- (2) Animals do not lose their marks.
- (3) All the marks are recorded correctly at each trapping occasion.
- (4) The assumption of equal catchability of animals.

The fourth assumption for equal catchability is seldom met in naturally occurring animal populations. The common causes for the failure of the assumption of equal probability of capture are (1) the dependence of animal's capture probability on the previous capture history i.e. response to the treatment during the trapping occasion like

baiting or toe clipping. The former might make the animal 'trap happy' while the latter might make it 'trap shy' and (2) the capture probability being the property of the animal and thus capture probability being heterogeneous across individuals in the population. Capture probability may vary with a number of parameters e.g. age or sex of the animal or the location of the trap with relevance to the animal's home range etc. These two causes are usually mixed and cannot be easily distangled in statistical data analysis (Chao and Huggins 2005).

Otis et al (1978) considered the three main factors that can produce variations in capture probabilities viz. (i) time effect, where capture probabilities may vary due to factors such as temperature, time of the day, rainfall etc, (ii) behavioural response to capture i.e. trap shyness or trap happiness and (iii) individual heterogeneity due to factors like sex, age or bodyweight or unobservable inherent characteristics.

On identifying these sources of variations, Otis et al (1978) and White et al (1982) formulated seven models based on all possible combinations of these variables and a starting null model.

**Model  $M_0$**  is the simplest model where all individuals have equal probability of capture at all trapping occasions. Moreover, it assumes that the occasions themselves do not affect the capture probabilities. It involves only two parameters:  $N$ , population size and  $p$ , the capture probability that an animal is captured on any given trapping occasion (Otis et al 1978). Chao and Huggins (2005) have pointed out a number of problems associated with model  $M_0$ . They feel that the simple model does not fit the actual data properly and although this model is used as a starting model but often proves to have limited use in practice.

**Model  $M_t$**  is the modification of the classical model to allow capture probabilities to vary with time. Thus, all animals have the same probability of capture on any

particular trapping occasion, but that probability can change from one occasion to the next. Unlike model  $M_0$  which uses only one parameter to model capture probability,  $M_t$  uses  $k$  parameters to describe capture probabilities given there are  $k$  occasions. Since the assumption of equal catchability is unrealistic for natural population, the estimator may give biased results. According to Carothers (1973) the violation of this assumption can be assessed and the biases may not be too severe under some circumstances.

These two models still adhere to the classical framework. These estimators are likely to be biased if there is a behavioral response to trapping or inherent heterogeneity of capture in the population (Otis et al 1978). Although they may have good precision and produce narrow confidence limits, these intervals might be unrealistically optimistic and may not reveal their bias (Chao and Huggins 2005). However, in some cases biases resulting from assumption violation may be small and have little impact on study conclusions. Nonetheless, the need for more complex models that allow for unequal catchability was felt which led to the development of the subsequent models.

**Model  $M_b$**  allows the animal to exhibit a behavioural response to capture and become either "trap shy" or "trap happy". Thus, the model deals with the failure of the assumption that the initial capture does not affect subsequent capture probabilities. Weaknesses observed in this model are that it requires all the animals to have the same behavioural response to initial capture and only the first captures are used for estimation of population size (Seber 1982).

**Model  $M_h$**  has the assumption that each animal has its own probability of capture independent of all other members of the population. The capture probability remains constant over all trapping occasions. Burnham and Newton (1978) proposed the use of jackknife estimators for estimate population size in order to reduce bias of a biased estimator. Otis et al (1978) commented that jackknife estimator has a tolerable bias if the

number of trapping occasions is sufficiently large and if the number of untrappable animals is negligible. It should be noted that it usually underestimates the true population if the mean capture probabilities are very small. Alternatively, it tends to overestimate the population size if nearly all the animals present in the sampled area are captured (Chao and Huggins 2005). This model is useful for many species, as heterogeneity is expected in all natural populations (Edwards and Eberhardt 1967, Cooch and White 1995).

**Model  $M_{bh}$**  is in effect a generalization of the  $M_h$  model for allowance of capture probability to depend on the previous capture history. It has some of the disadvantages associated with models  $M_h$  and  $M_b$ . For example, it derives the information of the population size only from the first captures like model  $M_b$ , and the individual heterogeneity contributes to somewhat biased estimates like model  $M_h$ . Otis et al (1978) proposed a generalized removal method for this model. However simulation studies by Otis et al (1978) as well as Pollock and Otto (1983) have shown that this estimator generally has a negative bias, which can be large if the removal (capture) probabilities are very heterogeneous. An improved estimator was described by Pollock and Otto (1983).

**Model  $M_{th}$**  takes the combined effect of time as well as heterogeneity. Chao and Huggins (2005) state that since in some capture recapture studies of large animals actual recapture is not necessary and resighting records suffice to provide the required recapture information, there is no need to model any behaviour response to capture. It may also be considered when different trapping methods for the same population are feasible.

**Model  $M_{tb}$**  is an extension of model  $M_t$  to incorporate behaviour response. It accounts for the assumption of change in the capture probability after the first capture and temporal changes also influence the capture probability. The model might suffer from too many parameters for calculation of its likelihood function. This might

necessitate that certain assumptions and restrictions be made beforehand (Chao and Huggins 2005).

Model  $M_{tbh}$  considers all three sources of variation. Previously, it had been considered only conceptually useful and too complicated to be applied to practical situations if no restrictions are made, despite the assumptions for closure being the most realistic in this model. This model offers a unified approach for all eight models and can offer robust estimates if reasonable assumptions can be made (White et al 1982, Chao and Huggins 2005).

The models stated above are *discrete – time* models with unequal catchabilities. In a typical discrete – time model, trappings are conducted on a definite number of distinct occasions where each trapping day is treated as an occasion. A group of animals is caught on each occasion. However, the exact capture time of each animal in a group is unknown. Due to this the information about the order of captures is not available, and recaptures within the same capture occasion are not allowed. In other words time jumps in discrete – time models (Chao and Huggins 2005).

When trapping is conducted over a fixed period of time, and captures or sightings of individuals can occur at any time during the data collection, thus leaving space for only one capture on each occasion, it is known as a *continuous – time* experiment (formulated by Craig (1953)). In this type of a model time flows continuously instead of jumping like in discrete time model. In studies of large mammals like tigers, usually one individual is sighted at time. Since, tigers can be individually identified by their marking or stripe patterns (Schaller 1967), it is not necessary to actually capture them and photographs can provide enough information for identifying individuals.

As in discrete time models, a series of eight continuous time models can be derived depending on the sources of variability due to time, behavioural response and heterogeneity (Chao and Huggins 2005).

Continuous – time format has an advantage of providing more information than the discrete – time models because the latter ignores recapture of the same individuals in a fixed occasion. Chao and Higgins (2005) found continuous time experiments to be more precise than their discrete time counterparts.

According to Peters and Herrick (2004), there exists a difficulty in generating accurate predictions due to the dilemma that exists between simple and complex approaches. Simple models often exclude key processes resulting in unknown prediction biases while complex approaches reduce prediction bias at the expense of increased estimation and measurement error.

Most studies on large mammals are restricted to the discrete time framework. Whatever limited number of studies that have been done within the continuous time framework are restricted to small mammals e.g. rodents. A study within the continuous time framework for a cryptic large mammal like the tiger is likely to produce much more refined estimates.

#### ***1.1.4 Programs for computing population estimates:***

Since 1978, analytical tools have come a long way and so has the methodology for model selection. A very brief overview is presented over here.

After formulating the various models for population estimation with equal as well as unequal capture probability, software CAPTURE (Rexstad and Burnham 1991) was developed to calculate estimators for each of the models. It uses likelihood ratio test for model selection. Manly et al (2005) pointed out that the limitation of this approach is that it applies correctly only to nested models i.e. where one model is a special case or subset

of another model. Despite this limitation, CAPTURE is widely used for population estimation (Chao and Huggins 2005). The current version available is CAPTURE2 (Rexstad and Burnham 1991).

The above mentioned limitation of the model selection through likelihood ratio led to the adoption of alternative model selection approaches. One such extensively used approach is Akaike's information criterion (AIC) (Akaike 1973; Burnham and Anderson 2000). AIC is calculated for a set of models which are candidates for being chosen as the most suitable to the data. Each model is then fitted to the data and its corresponding AIC is calculated. The model with the lowest AIC is considered best. Many programs use AIC as a model selection tool. One such program is Program MARK (Cooch and White 1995). These programs would suffice for estimating population through the estimators established long ago. But, to accommodate the recently developed estimators and covariates (Huggins 1989, 1991), additional programs are necessary. A program CARE (CAPture-REcapture) containing three parts, has been developed. CARE-1 is an interactive S-PLUS program, CARE-2 is a windows based program written in C language. It calculates various estimates for models with or without covariates. CARE-3 is written in GAUSS language and is an integrated program for analyzing the class of continuous-time models already mentioned in previous section.

#### ***1.1.5 The problem with density estimates and effective sampled area:***

Brown (1984) suggested an abundance – distribution theory to explain this variation. According to this theory the abundance is greatest at the centre of the distribution and declines towards the boundaries. Secondly, there is a linear relationship (positive correlation) between the spatial distribution and average abundance. This pattern holds for local regions to entire geographical range. This underlying property is often ignored while extrapolating density estimates over an unsampled area.

Also, there is a tendency to sample preferably in the high density areas, especially if the study is short term (Smallwood and Schonewald 1996). The estimates obtained through such an assessment can only lead to erroneous estimates if the gradient of low or declining density is not accounted for while arriving at estimates. (Smallwood and Schonewald 1996, 1998)

In mark recapture studies, especially for large mammals, the trapping is done in a small area and a buffer strip is added to it to account for the space use by animals trapped at the periphery. The total area calculated thus, is known as the effective area sampled and is denoted by  $A(W)$  where  $W$  is the calculated strip width or buffer area. The strip width is calculated, most often through the half MMDM (mean maximum distance moved) between recaptures. When traps are randomly placed at high use locations to maximize capture, not in a specific designed frame, the effective trapping area is very likely to be an artifact of the placing of traps. Finally density will be calibrated based on this distance and when densities are averaged among sampling units, mean density is usually weighted by the proportion of total area in which individuals are living which may be just partly or fractionally sampled, leading to an overestimate and often high CVs (Soisalo and Cavalcanti 2006).

If the inter trap distance is predetermined and the traps are laid in a systematic fashion, it will constrain the simultaneous trapping of a large area (for e.g. due to lack of a very large number of traps available as the case in Wegge et al (2004). This may restrict the study to be carried out in small areas, or non – simultaneously in different blocks covering a larger area. The density estimates derived through such a method will be highly specific to the study site and not a part of the whole area which will restrict the estimates only to the area sampled and make the estimates not extrapolatable. When the density, estimated through sub sample units in this fashion, is extrapolated over the entire

area including unsampled blocks for population estimation it is bound to produce erroneous estimates (Smallwood and Schonewald 1996).

A linear process has the property that the expected value of a function,  $f(x)$ , is equivalent to the function evaluated when the independent values are set to their expected value,  $x$ . This is the literal case when it comes to plants and in case of animals, if sampling through indirect signs. Even when sampling through line transects or quadrat sampling method, the individual is spotted at one place at a particular time. Such a framework makes extrapolation straight forward and reliable.

Non-linear systems do not have the above mentioned property, thus they require the function to be integrated across the distributions of  $x$ 's. Although non-linearities are important in spatial systems, they are often ignored when making spatial extrapolations (Peters and Herrick 2004). If motile, large animals are being sampled through mark recapture framework their movements are not strictly delineated. An individual may get recaptured in many traps spaced at different distances. Animals at the periphery may be particularly problematic as they are much likely to use a considerable amount of area outside the trapping grid. As already mentioned, widths added to the trapping grid based on the average maximum distance moved by individuals may be an artifact of the way in which the cameras are placed and create discrepancies in density estimates.

A recent study on jaguars (*Panthera onca*) in Brazilian Pantanal using capture recapture sampling in combination with radio telemetry was carried out by Soisalo and Cavalcanti (2006) to compare the estimates of effectively sampled area based on camera traps with independent estimates of home range size and animal movement obtained from telemetry data. They found that the effectively sampled area derived through the MMDM method for camera trapping was smaller than the MMDM calculated by using the

telemetry locations thus suggesting that using the MMDM method for calculation of ESA and density based on this ESA is more than likely to produce overestimates.

It should be kept in mind that it is not always possible to use methods such as radio telemetry to derive the estimates of animal movement considering the constraints of resources associated with any study.

A feasible solution to the above mentioned problem might be to have a new approach towards the calculation of the effectively sampled area  $A(W)$

Burnham suggested use of asymptotic range length (ARL) for the estimation of effectively trapped area in an experiment carried out using trapping web (Anderson et al 1983) for meadow voles (*Microtus pennsylvanicus*) (Jett and Nichols 1987). In their experiment, they used a model based on the fact that mean maximum distance moved generally increases as the number of recaptures increases (Jett and Nichols 1987). The model is based on the calculation of the actual average distance moved by animals ( $W^*$ ) based on the expected value of maximum distance moved  $E(W_i)$  for animals captures  $i$  times and model parameter  $b$ .  $W_i$  is obtained from the field data and a nonlinear least squares is used to derive  $W^*$ . The boundary strip is obtained as  $W^{\wedge} = W^*/2$  (Jett and Nichols 1987).

Recently, Efford (2004) suggested the use of root pooled spatial variance (RPSV) to calculate the area of trapping thus not restricting the density estimates to the sampled area and makes it applicable across the given landscape.

The model for calculation of RPSV works on the conceptual model of trapping process and was explained by Efford (2004) as follows: Animal range centres are distributed across the study area as point processes in space with density ( $D$ ). During a closed population study each animal is assumed to occupy a home range centred at an unknown location and the traps are set at known locations and catch at the most one

animal. Considering only one animal per trap, the capture probability of the animal is a declining function of distance ( $d$ ) between the range centre and the trap, which is analogous to the detection function  $g(d)$  in distance analysis (Borchers et al 2002). This function requires parameters  $g_0$  for overall magnitude and  $\sigma$  for the spatial scale over which the density declines. These parameters along with  $D$  define the individual based model of the capture process.

Consider a distribution of point process with density  $D$ . The expected number of such processes in two-dimension by simple multiplying density  $D$  with the Area  $A$  ( $N = D.A$ ), but in reality the actual number varies depending on the spatial variance associated with each point process. Inverse prediction incorporates this variance into the uncertainty of the estimate of the number of such processes. This is appropriate for the generalization of entire spatial process rather than the conventional method of restricting to the measure of density of one realization obtained in the vicinity of the trap grid. It is also more appropriate to incorporate this spatial variance into the estimate as the animal distribution in nature is a Poisson process. For the calculation of the above mentioned spatial variance can be carried out using program DENSITY (Efford 2004). The software simulates the area of trapping into a tiled grid with square cells each containing an animal and then the location of each animal is randomized uniformly within each cell. Poisson distribution is assumed an animal density estimates are obtained through simulations.

This process results in the density estimates with superior confidence coverage and does not restrict the density to the being local (of the sampled area) but makes it global (Efford 2004).

It is crucial to get reliable estimates of population as well density of endangered carnivores not only for the formulation of conservation strategy but also for establishing sound management practices (Carbone 2001). Endangered carnivore estimates influence

allocation of resources for conservation efforts, and for evaluation of success of conservation programs (Nowell & Jackson, 1996; Karanth 2003).

**1.2 Objectives:**

1. To estimate population and density of tigers in Corbett National Park.
2. To estimate the sampling effort required to obtain precise and accurate population estimates of tigers.
3. To evaluate the effect of camera density on population and density estimate of tigers.

## **2. STUDY AREA**

### **2.1. Location:**

Popularly known as the land of trumpet roar and song, Corbett National Park is situated in the foothills of the Himalayas i.e. the Siwlaik range. CNP falls within Nainital and Pauri Garhwal districts of the state of Uttarakhand (Figure 2.1). The total area of the NP is 520.82 sq. km and is a part of Corbett Tiger Reserve which also includes 301.18 sq. km of adjoining Sonanadi Wildlife Sanctuary along with 466.32 sq.km of buffer zone together forming 1288.32 sq. km of the tiger reserve (Barthari 1999). Corbett NP lies between 29° 25' N to 29°40' N latitudes and 78°5'E to 79°5'E longitudes. The area is more or less trapezoidal in shape. After undergoing various name changes it came to be recognized as Corbett NP after the hunter turned conservationist Jim Corbett in the year 1957. It houses a variety of endemic as well as endangered species and is perhaps their last refuge providing hope for their continued survival.

### **2.2. History:**

Corbett NP was established on 8<sup>th</sup> August, 1936. Not only was it the first national park in the country, but in the whole of the Asian mainland (Bharthari 1999). Back in 1936 it was named Hailey NP after Sir Malcolm Hailey, the then governor of Uttar Pradesh, who was influential in creation of a 257 sq. km of protected forest in what used to be a common British hunting ground.

Post independence it was named Ramganga NP in 1954 and finally it was rechristened as Corbett NP in honour of Jim Corbett, the hunter-naturalist who later turned author and photographer and the man who facilitated the charting out of boundaries and set up of the NP.

In 1973, with the help of World Wildlife Fund, Project Tiger was launched in CNP and it was one of the first such tiger reserves in the country. The area has increased

from 257 sq. km to 323.75 sq. km to the present 520.82 sq. km in 1966 to compensate for the land submergence due to the creation of the dam at Kalagadh (Barthari 1999).

### **2.3. Geology/ Physical features:**

The area under study lies in the Siwalik range situated in the outer foothills of the Himalayas and is composed of alluvial detritus material derived mainly from sub aerial waste from the Himalayan system (Pant 1986). The Himalayan Rivers bring coarse material which deposits immediately along the foothills forming a layer of boulders known as Bhabar. CNP is confined to the Bhabar tract of Siwalik formation with an altitude range of 350 – 1050m (Pant 1986). It is characterized by hilly, undulating terrain with ridges and valleys and dry river beds with coarse boulders. The boulders being porous are responsible for low water levels. This also leads to the disappearance of streams from the surface during the hot season only to re emerge following the first rainfall of the season. The topography is considerably varied with hilly and riverine areas, temporary marshy depressions, plateaus and ravines (Johnsingh et al 2004). A series of more or less parallel ridges run from the North West to the South East decreasing in height on approaching the plains along the southern boundary. Conglomerates, sand rock, sand stone and bhabar deposits together contribute to the geological aspect of the park. The river Ramganga and its tributaries form the drainage pattern and are the primary source of water. The reservoir formed due to the construction of the dam is 80 sq.km, out of which 42 sq. km falls within the park. The reservoir also proves to be a perennial source of water to the park. Kosi River flows along the eastern boundary of the park which also acts as a water source to CNP.

### **2.4. Climate:**

The general climate is tropical with three main seasons viz. winter from November to February, summer from March to June and monsoon from mid June to

October (Bhartari 1999). The temperature ranges from 3°C in December – January to 42°C in May-June. The maximum winter temperature is rarely known to exceed 30°C while the maximum summer temperature is observed to stay below 44°C. Since the NP is situated in the densely forested Siwlaiks, it remains fairly humid throughout the year. The South West monsoons are the main source of rainfall with maximum rainfall occurring from June to September. The average rainfall recorded is 1646mm ca. Thunderstorms accompanied by hail are often observed in April and May and also occasional erratic rainfall is observed in the months of January and February (Bharthari 1999).

## 2.5. Vegetation:

The forests of Corbett NP are classified into three major forest types viz. Northern moist deciduous, Northern tropical dry deciduous and Himalayan sub tropical pine forest (Champion and Seth 1968). The classification is summarized table 2.1.

**Table 2.1:** Forest types of CNP following Champion and Seth (1968) classification.

Forest type	Nomenclature
Sub-group 3C: North Moist Deciduous	
3C/C2a	Moist Siwalik Sal
3C/C2b1	Moist Bhabar Dun Sal
3C/C3a	Western Gangetic Moist Mixed deciduous
Sub-group 5B: Northern Tropical Dry Deciduous	
5B/C1a	Dry Siwalik Sal
5B/C2	Northern Dry Mixed Deciduous
5/IS2	Khair - Sissoo Forest
Sub-group 9: Himalayan Sub- Tropical Pine	
9/C1a	Lower Siwalik Chir Pine Forest

Pant further grouped the mixed deciduous tropical and subtropical forests of CNP into nine forest types, they are:

- i) Moist Siwalik Sal forest
- ii) High alluvium Sal forest
- iii) Dry Siwalik Sal forest
- iv) Northern tropical mixed deciduous forest
- v) Moist Savanna forest
- vi) North Indian moist deciduous forest
- vii) Khair- Sissoo forest
- viii) Dry Bamboo brakes
- ix) Himalayan sub tropical forest

617 species of plants were reported by Pant (1986) out of which 594 were angiosperms, 1 species of gymnosperms and 22 species of ferns and fern allies. Upreti and Chatterjee (1999) recently added 69 species of lichens to the flora of CNP.

Sal *Shorea robusta* is the most dominant tree species gregariously growing in the park area. Evergreen species like *Mallotus philippinensis* and *Syzygium cuminii* are also commonly seen. Other medium sized evergreens include *Litsea monopetala*, *L. glutinosa*, and the fragrant *Murraya paniculata*. Among deciduous species *Terminalia alata*, *T. chebula*, *Semicarpus anacardium*, *Lannea coromandelica*, *Sapium insigne*, *Lagerstormia parviflora*, *Butea monspersma*, *Cassia fistula* and *Ehretia levis* can be seen throughout the park in good numbers. At several places *Bombax ceiba* and *Anogeissus latifolia* can be seen as Sal associates. *Phyllanthus emblica*, *Acacia catechu*, *Kydia calycina*, *Dalbergia sissoo* and *Holoptelia integrifolia* can be seen at open sunny faces near *sots* and lining grasslands. Plantations of *Tactona grandis* and *Eucalyptus spp* can be seen near the eastern and southern boundaries of the park. Commonly occurring shrubs are *Colebrookea oppositifolia*, *Glycosmis arborea*, *Murraya koenigii*, *Justicia adhatoda*

and *Woodfordia fruticosa*. *Lantana camara* and *Cannabis sativa* are the commonly occurring intruders. *Pinus roxburghii* is the only gymnosperm occurring in the park.

Vast sprawling grasslands are the characteristic of some areas of the park. The main grass species found in these grasslands are *Saccharum bengalenses*, *Themeda arundinacea*, *Arundo donax*, *Vetiveria ziznoides*, *Apluda mutica*, *Heteropogon contortus*, *Eragrostis spp.* and *Cynodon dactylon*. *Eulaliopsis binata* and *Thysanolenia maxima* can be seen growing on cliffs and moist shady places.

## 2.6. Fauna:

Corbett NP supports a sizeable variety of faunal diversity (Lamba 1980). Other than the tiger (*Panthera tigris*) the park supports felids like leopard (*Panthera pardus*), leopard cat (*Prionailurus bengalensis*) and jungle cat (*Felis chaus*). Other carnivores include the golden jackal (*Canis aureus*), sloth bear (*Melursus ursinus*) and Himalayan black bear (*Ursus thibetanus*). Herbivores include Elephants (*Elaphus maximus*), sambar (*Cervus unicolor*), cheetal (*Axis axis*), barking deer (*Muntiacus muntjak*) and Hog deer (*Axis porcinus*). Nilgai (*Boselaphus tragocamelus*) is seen only in the disturbed fringes. Small Indian civet (*Viverricula indica*), Himalayan palm civet (*Paguma larvata*) common palm civet (*Paradoxurus hermaphroditus*) are found along with mustelids like yellow throated marten (*Martes flavigula*) and mongoose (*Herpestes spp.*). Black napped hare (*Lepus nigricollis nigricollis*) and Indian porcupine (*Hystrix indica*) are of common occurrence. The Ramganga river system also supports a good population of otters (*Lutra lutra*, *Lutrogale perspicillata*).

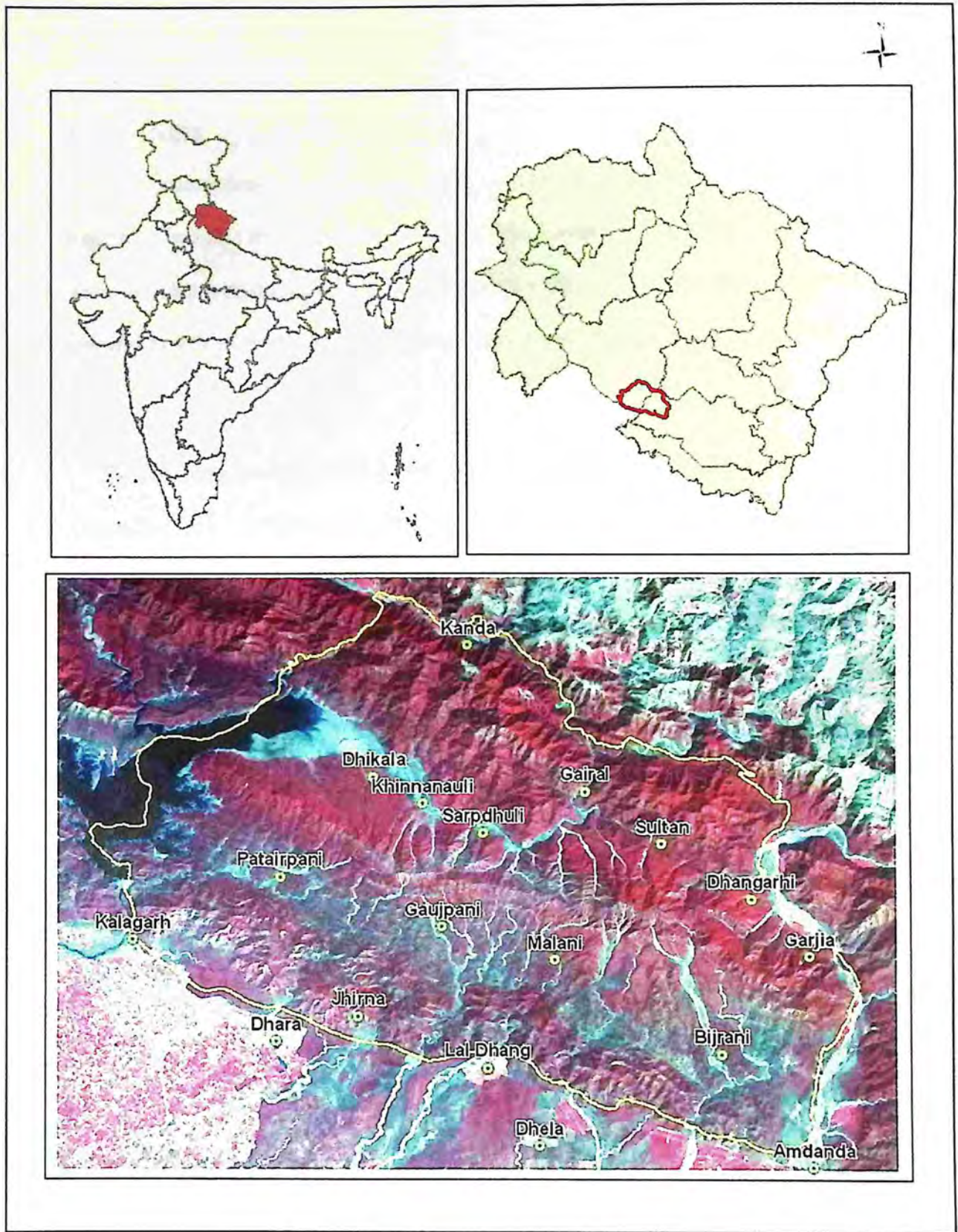
Among reptiles, a good population of Gharials (*Gavialis gangeticus*) and Mugger (*Crocodylus palustris*) can be seen in the river as well as the reservoir. Snakes like King cobra (*Naja bungarus*), cobra (*Naja naja*) and Python (*Python molurus*). Among other reptiles are the rock agama (*Agama spp.*), Monitor lizard (*Various spp.*) and various turtle

species like *Lessimys punctata*, Indian black turtle (*Melanocheilus trijuga*) and Tricarinate hill turtle (*M. tricarinata*) (Barthari 1999).

The avifauna of CNP is very rich. 549 species of resident and migratory birds have been reported from the park. Some of the noteworthy species occurring in the park are Great pied hornbill (*Buceros bicornis*), Great slaty woodpecker (*Mulleripicus pulverulentus*), Khaliy pheasant (*Lophura leucomelanos*), Himalayan griffon (*Gyps himalayensis*), Cinereous vulture (*Aegypius monachus*), collared falconet (*Microhierax caerulescens*), etc.

### **2.7. Human disturbance:**

There are no villages in the NP at the moment. Three villages were relocated in 1994 from the southern boundary of the park after which the park has been free from human settlements. However, the villages of Dhara, Laldhang, Dhela as well as small *gujjar* settlements like the one in Jhirna continue to enjoy rights within the forest blocks of the national park adjoining these settlements. Despite the clear demarcation of the core area boundaries through firelines, the villagers continue to move inside the core zone for collection of NTFP (Barthari 1999). Corbett NP is immensely popular as a tourist location and draws considerable number of visitors each year. There has been tremendous growth in the number of privately owned resorts and hotels along the eastern boundary of the park cutting off the access of animals from the park to Kosi river flowing along the eastern boundary.



**Figure 2.1** Map of Study Area : (a) Position of Uttarakhand in India, (b) Uttarakhand with the boundary of Corbett National Park, (c) False colour composite (FCC) of a LANDSAT image of Corbett National Park.

### 3. METHODS

For the estimation of tiger population, capture-recapture of tigers through camera trapping (Karanth 1995, Karanth and Nichols 1998, Karanth et al 2004) was selected. It was a two step procedure, first step involving field work and data collection and second, analytical methods employed to arrive at estimates.

#### 3.1. Reconnaissance survey:

The reconnaissance survey was conducted in the months of November and December. To determine suitable sites for deploying camera traps, sign surveys were carried out in every beat. Indirect signs of usage by tigers like scrapes, scat, scent marks, claw marks/ rakes and of course pugmarks were used as indicators of use of the particular path or trail of the surveyed beat. Secondary information on extensive usage of trails and paths was collected from the guards of respective beats. This was verified by walking 5 – 10 km on these trails and dry river beds locally known as *sots*. The ‘high use’ locations, i.e. where considerably more above mentioned indirect signs were observed, were marked using a handheld Global Positioning System (GPS) Garmin 72™. These locations were overlaid on a LISS III image of the study area to observe the spatial distribution of the trapping locations and rectify any large gaps left there within. During the survey itself it was kept in mind that the cameras have to be laid out in 4 sq. km grids (2km X 2 km). The locations thus finalized were such that no two cameras were closer than 1.7 km and not further than 2.3 km from each other.

#### 3.2 Camera trapping for estimation of tiger population

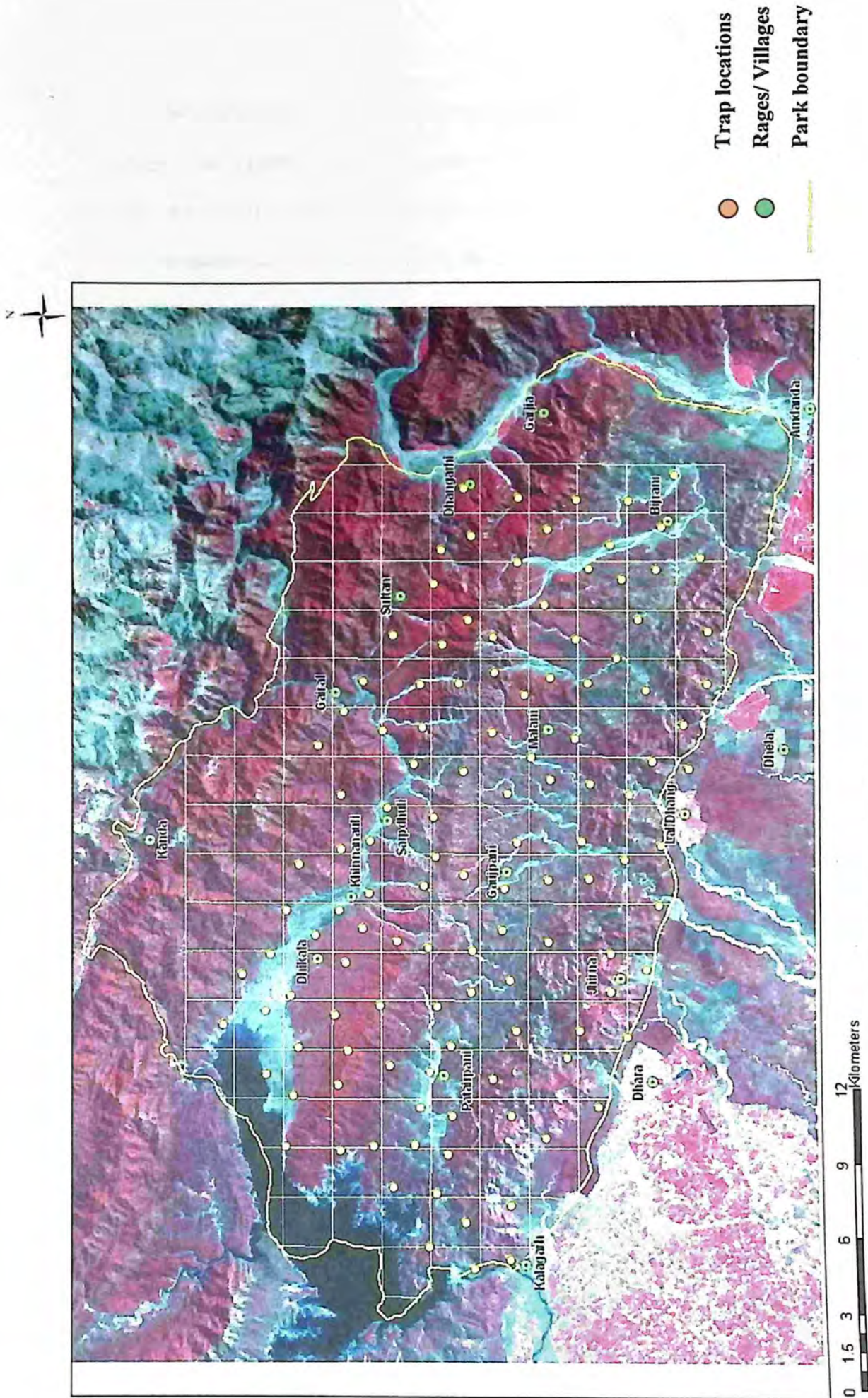
Karanth (1995) and Karanth & Nichols (1998) described in detail the procedure of camera trapping tigers for estimation of abundance. Essentially, the idea is to cover the area of interest with camera traps in such a way that the chances of photo trapping the resident tigers of that area are maximized. Nichols & Karanth (2002) further emphasized

the importance of adequate coverage of the area so that it is difficult for a tiger to move about in the sampled area without encountering at least one camera trap. Deviating from their method of placing traps in a non random fashion based purely on tiger movement, we placed the traps in a spatially explicit sampling design. A systematic grid of 2km x 2km as already mentioned was laid on the map of the study area and a trap was placed within each 4 sq. km grid cell. The idea behind using a 4 sq. km grid is to cover the study area fairly well and to assure systematic placing and spread of traps throughout the sampled area (Figure 3.1).

A total of 60 camera trap units out of which 15 were Trail Master units and 45 were Deer Cam units were available for the purpose of this study.

TrailMaster TM1550 (Goodson and Associates, Lenexa, Kansas, USA) active infrared trail monitor is a two-piece active infrared trail monitoring system which uses an invisible infrared beam across the trail between the transmitter and receiver with a range of 150 feet. The cameras accompanying the TM unit are Canon A1 mini DX. A multi trigger device was used to connect the two cameras so that they would fire simultaneously taking pictures of both the flanks of the animal. The camera units were placed 5 m away from the trail to maximize the chances of getting full body photographs of tigers. The camera delay was set at minimum (0.1 = 6 sec) to minimize chances of missing mating pairs or cubs with mother. The pulse was set at 4 keeping the gait and size of the animal.

Deer Cam DC 300 Scouting cameras work on passive infrared motion/ heat sensors which can sense up to 60 feet from the camera unit. It is equipped with a 35mm lens camera which can imprint date and time of the photograph. Two of such camera units were deployed at 5 m on either side of the road to capture both the flanks of the animal in photographs. The camera delay was kept at minimum/ default (15 sec). The sensitivity of the sensor was set at 'high'.



**Figure 3.1** Map of Corbett NP with the layout of camera trap locations

The cameras and Trailmasters as well as DeerCams were placed within wooden housings so as to protect the units as most of the cameras were present in elephant used habitat, some in tourist areas and some close to habitation.

To maximize the effort and given the resource constraint of 60 trapping units, the study area was divided into two blocks. The division was made purely based on the convenience of accessing the traps from available field stations in such a way that all traps within a range can be checked every alternate day. Dhela, Bijrani and half of Sapdhuli range (from Dhangadi to Sarpduli resthouse) were covered in the first block (Figure 3.2). The trapping was carried out for 35 days starting 30<sup>th</sup> Dec 2006 to 2<sup>nd</sup> Feb 2007. The second block consisted of Kalagadh, Jhirna, Dhikala and rest of Sarpduli range (Khinanauli) (Figure 3.3). The trapping was carried out for 35 days from 16<sup>th</sup> Feb 2007 to 22<sup>nd</sup> March 2007. Finally sampling was carried out for another 30 days by spreading the traps all over the park, covering trapping stations with high individual captures as well as ones having single flank photos in order to maximize the number of recaptures and get both flanks of individuals whose single flanks had been photographed in previous trapping occasions.

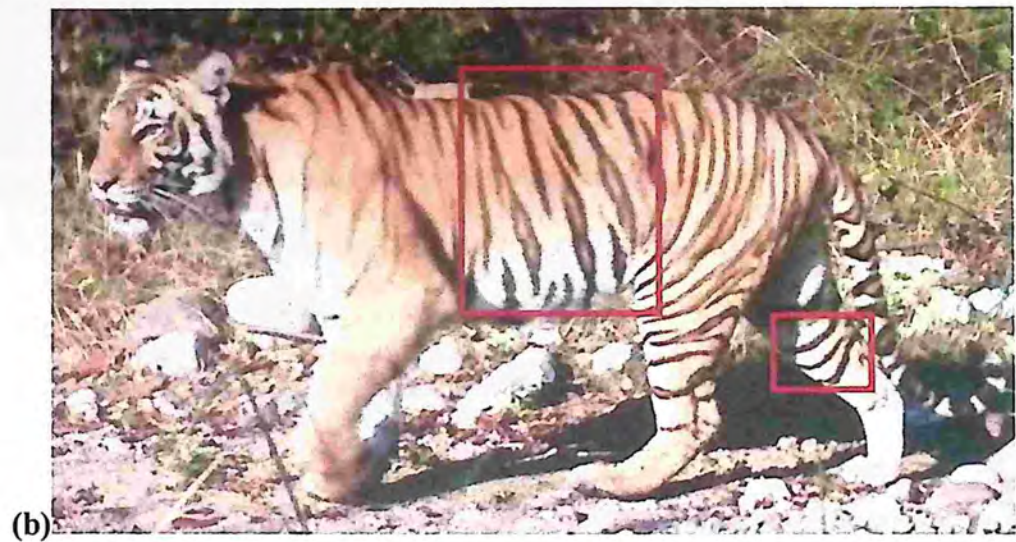
Each camera was given a unique identification based on the name of the location where it was placed (e.g. *Champion road* or *Bhimsot*). Each film roll carried a tag with the name of the location as well as date (Cam 7, *Bhimsot*, 15/3/07). Further a 'marker shot' was taken as the first frame of each role with the name of the location, roll serial number and date of change to remove any ambiguity. The cameras stamped each photograph with the date and time of capture which enabled the accurate allocation of tigers captured at various locations.

After repeated careful examination of the tiger photographs, every tiger captured through photographs was given a unique identification number (e.g. Indv 1, Indv 2etc)

Individual tiger

Identification was done based on thorough examination of the position and shape of stripes on the flanks, limbs, forequarters and even tail (Schaller, 1967; McDougal, 1977;

**PLATE 1: Identification of tigers based on unique stripe pattern**



**(a) A tigress (Indv 001) photographed by a camera trap (b) Another photograph of the same tigress(Indv 001)(c) Photograph of a different tigress(Indv 003)**

Karanth, 1995; Franklin *et al.*, 1999).

### 3.3 Estimating the population and density of tigers

After identification of individual tigers through stripe patterns, capture history for each individual was generated in an X matrix (Otis *et al.*, 1978; Nichols, 1992). The capture history of animal  $i$  consists of a row vector of  $t$  entries, where  $t$  denoted the number of sampling occasions for the study site.

Each entry denoted as  $X_{ij}$  for individual  $i$  on occasion  $j$  assumed a value of either '1' if the animal was captured on that occasion or '0', if the animal was not captured during that particular sampling occasion. For example a capture history of 0111001000 indicates that the particular individual tiger was captured only on second, third, fourth and seventh sampling occasion in a survey comprising of ten sampling occasions.

Here  $t = 65$  because the days from the first and second sampling sessions, of 35d days and 30 days each, were clubbed together. Moreover, the data was analysed by pooling the individuals from both blocks, so that it would appear as if recorded by 121 traps operating simultaneously.

Owing to the fact that tigers are long lived animals (Sunquist, 1981; Smith, 1993), the sampled population was assumed to be demographically closed for the 65 days of sampling (Otis *et al.*, 1978; Karanth, 1995; Karanth & Nichols, 1998, Karanth *et al.*, 2004).

The capture history data was analyzed using program CAPTURE 2 (Rexstad & Burnham, 1991) freeware from <http://www.mbr-pwrc.usgs.gov/software.html>. Program CAPTURE 2 facilitates the estimation of population size  $N$  under the objective comparison of several probabilistic models of the underlying capture-recapture process, which differ in their assumed sources of variation in capture probability ( $p$  - hat) and are likely have generated the observed capture histories (Otis *et al.*, 1978; Nichols, 1992). The program CAPTURE 2 provides a statistical test for the assumption of population closure.

The same data was also analysed using program CARE-2 Program CARE-2 calculates various estimates for models with or without covariates similar to the eight models in capture but with new approach to MLE and estimating equation (EE) approach.

The capture history was also recorded in a continuous-time format where the trapping occasions are considered as a continuous process instead sampling occasions being discrete where time 'jumps' from one sample to the next. The advantage of this format is that it provides more information than the regular discrete-time X matrix as it recognizes captures within the same trapping occasion. The population is sampled over a fixed time interval  $[0, \tau]$ . For each animal captured in the experiment, the exact capture times for each individual are recorded and the complete capture history consists of a series of capture times e.g. (1, 4, 6.5, 8.2, 9). The continuous-time capture history was analysed using program CARE-3. Program CARE-3 is written in GAUSS language and is an integrated program for analyzing the class of continuous-time models.

The population estimate ultimately leads to the derivation of estimate of density ( $D$ ) of tigers for the sampled area. For this purpose population size ( $N$ ) is divided by the effective sampled area ( $A(W)$ ). In trapping studies,  $A(W)$  is calculated by assuming that the perimeter traps represent the minimum sampling area  $A$ . The mean maximum distance  $d$  between recaptures of individual animals is calculated and the boundary strip width  $W$  is calculated as  $W = d/2$  (Dice 1938, Wilson and Anderson 1985). Karanth and Nichols (1998) suggested that the minimum sampling area  $A$  should be calculated directly from the study area maps by connecting the outermost trap points and (assuming the area  $A$  similar to a circle) and adding the boundary strip  $W$  around the 'perimeter' to obtain the effectively sampled areas. An alternative approach is to add the strip  $W$  to the minimum sampling area  $A$  on a GIS domain and thus calculate  $A(W)$ .

Both of these methods have been used to calculate the density of tigers in the study area. Density was also calculated using alternative approaches viz. RPSV and ARL/2

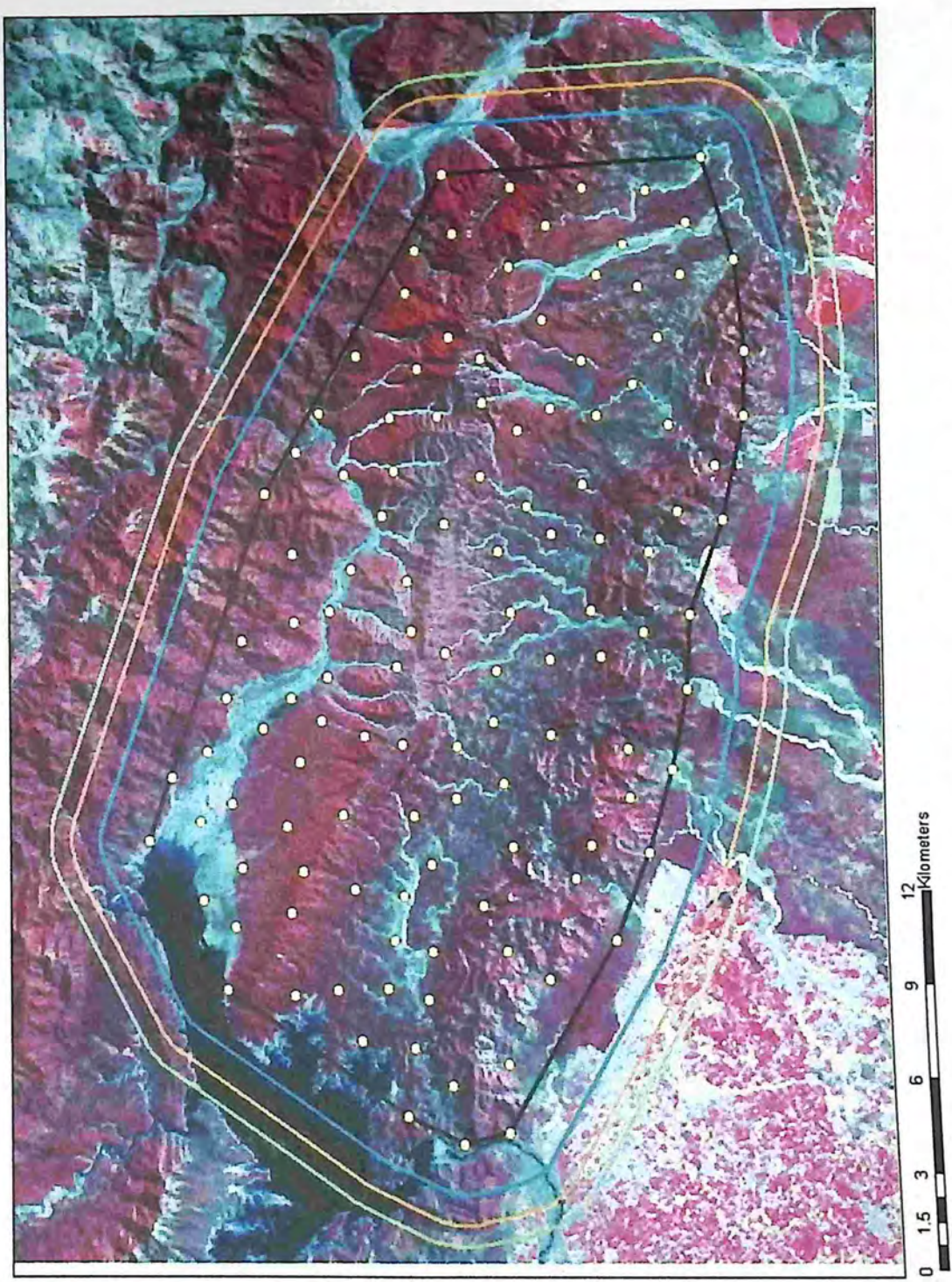
for calculating the effectively sampled area (ESA). The former deviates from the conventional method of calculation of  $A(W)$  as it calculates ESA through root pooled spatial variance (RPSV) instead of adding a buffer strip to the intensively sampled area  $A$  and the latter uses asymptotic trap-revealed range length for the calculation of ESA (Section 1.2). The necessary calculations for the above mentioned methods can be carried out using a new software DENSITY (Efford 2004). Program DENSITY 3.3 (Efford 2004) can be downloaded from [www.landcareresearch.co.nz/services/software/density/](http://www.landcareresearch.co.nz/services/software/density/).

### 3.4 Estimating required the sampling effort

To evaluate the effect of day pooling, the information on capture histories of individuals in 2,3,4,5,6,10,12 and 15 days each were pooled together to form an occasion and population estimates were calculated for each. A comparison of these estimates was made to see if there is an effect of pooling days together to form a session.

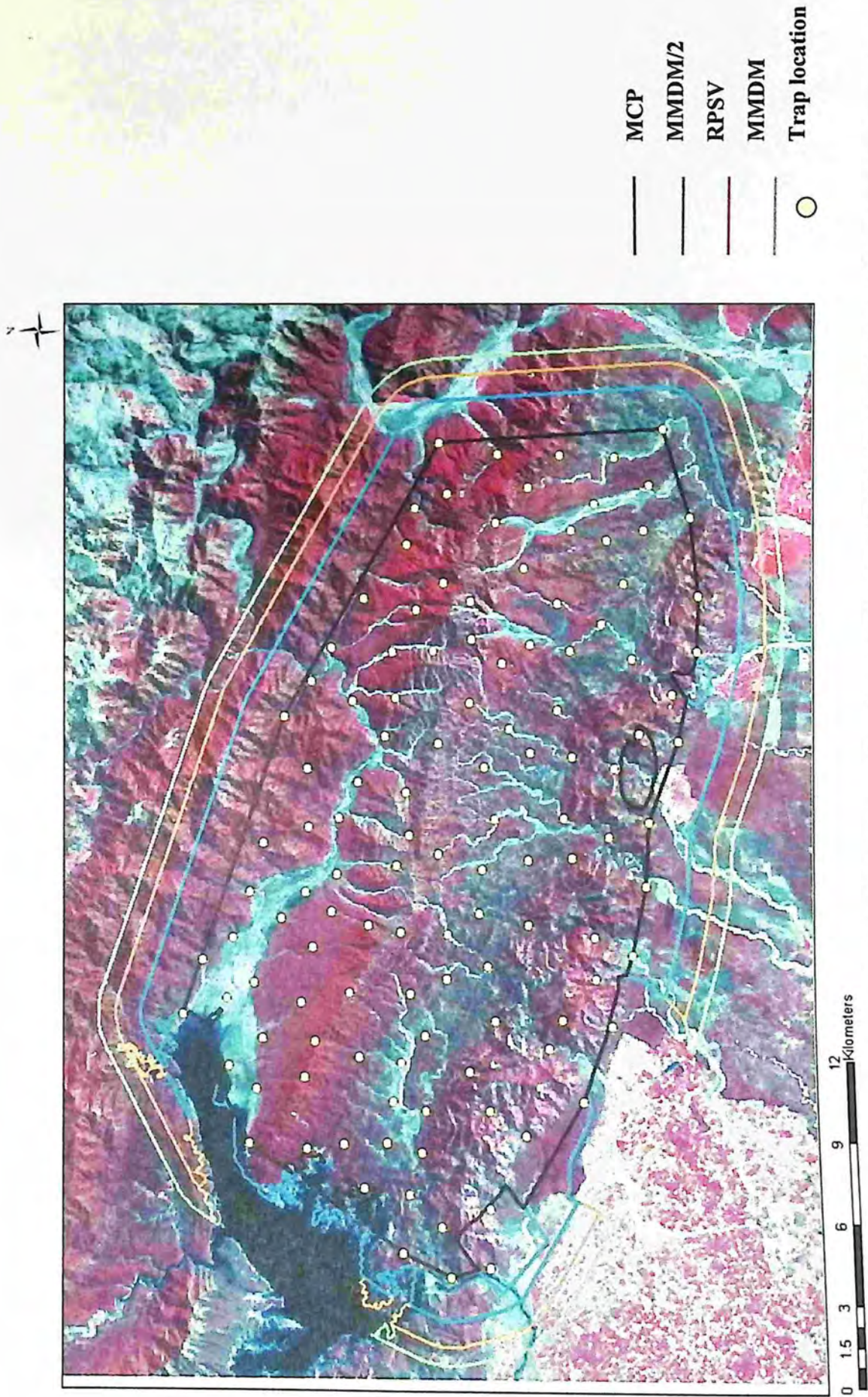
To estimate required sampling effort, population estimates were derived by considering 3 days and 5 days as the total no. of sampling occasions. 5 days were added to every subsequent class and estimates were derived for 10, 15, 25...65 (actual no. of occasions) days each and compared to see where the population estimate stabilized as that will be the minimum required effort to arrive at reliable estimates.

The population estimates were derived using program CAPTURE 2 and the estimates for Models  $M_0$  and  $M(h)$  were compared. The best model was not selected for comparison as it varied with different samples making comparisons within them futile. Estimates of Models  $M_0$  and  $M_h$  were selected for comparison as the former has the least number of parameters and meets all the assumptions of capture-recapture including the one of equal catchability, and the latter because as heterogeneity is expected in all natural populations (Edwards and Eberhardt 1967, Cooch and White 1995).



- MCP
- MMDM/2
- RPSV
- MMDM
- Trap location

Figure 3.2 Map of sampled area with the layout of camera trap locations and buffers.



**Figure 3.3** Map of sampled area with the layout of camera trap locations and buffers with habitat mask (excluding the reservoir and adjoining villages)

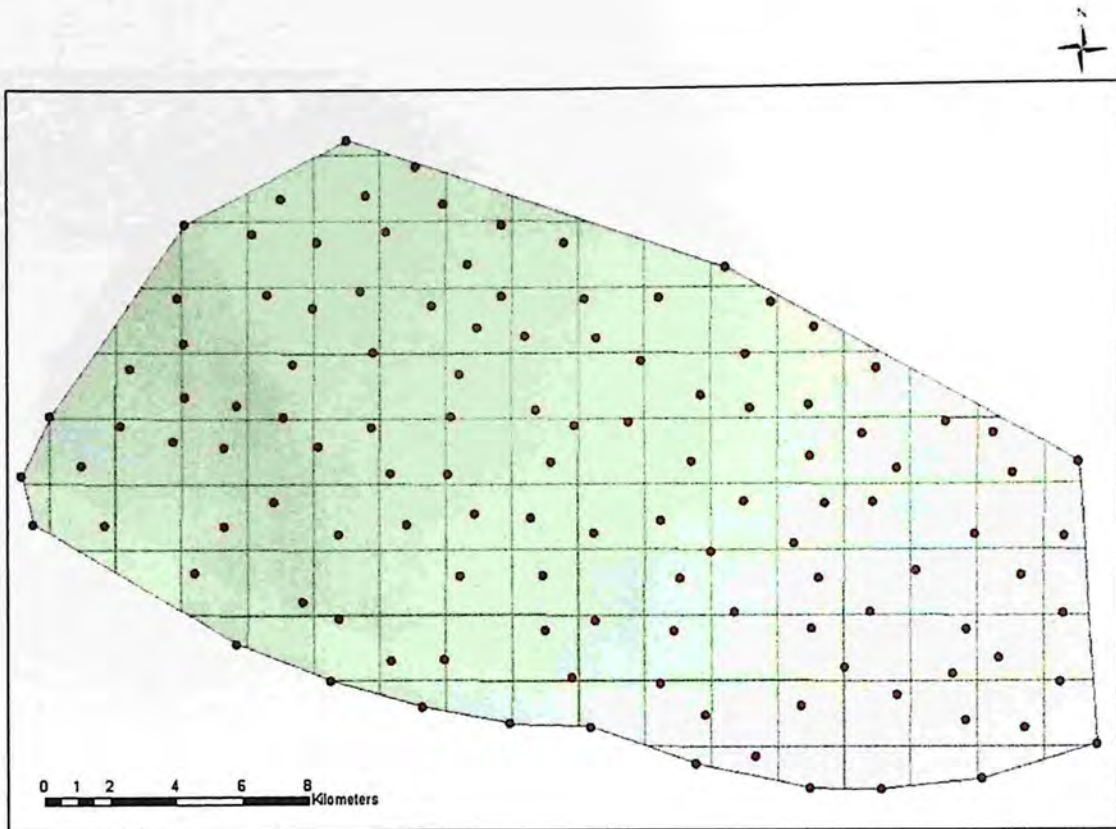
### **3.5. Evaluating the effect of camera density on population and density estimates.**

The actual camera density in the study area is an approximate 28 cameras/100 sq.km. To evaluate the effect of camera density on population estimates, the information from selective camera traps were dropped from analysis assuming lower than actual camera density (Figure 3.4). This was done in two ways. First, camera trap stations from every alternate grid were dropped along with the information on capture histories associated with them. This reduced the camera density to half of actual i.e. 14 cameras/100 sq.km. To smoothen out the effect of variability of no. of individuals per camera trap, five different combinations were used to remove camera locations and associated information.

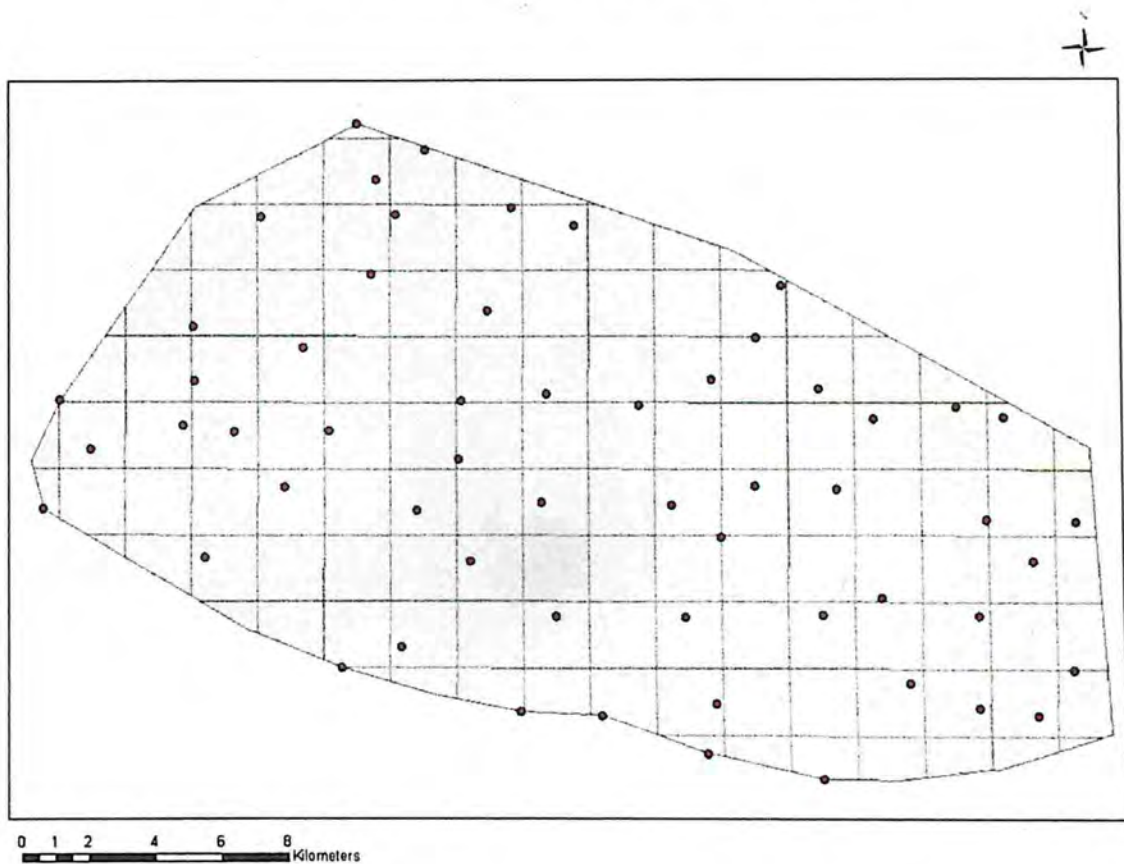
Second, camera locations were picked at random and all the camera traps from the surrounding grids were removed and the population estimates were derived using the individual capture histories from the remaining camera traps. Here to five different combinations were used to smoothen out the variability of captures per camera.

These population estimates were compared as well as densities were calculated using these estimates and those too were compared to evaluate effect of camera density in a high density tiger area.

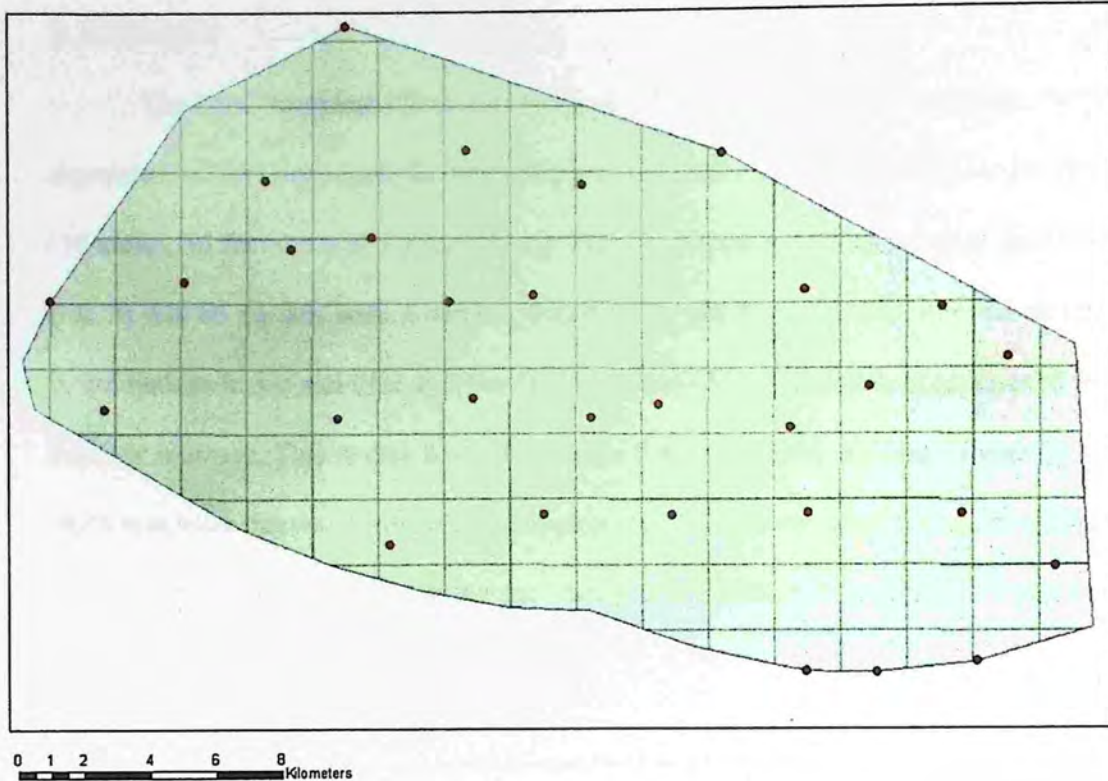
To test the effect of camera density in low density tiger area, the no. of individuals were dropped to 2, 5, 10 and 25 tigers. Population estimates were calculated for each of these by keeping the camera density at the actual 28/100, with a density of 14 cameras /100 and with 7 cameras /100. Five repeats were formulated for each camera density – tiger density combination and the associated bias and precision were plotted.



3.4. a Actual trap density 28 traps/100 sq.km.



3.4. b Simulated trap density 14 traps/100 sq.km.



3.4. c Simulated trap density 7 traps/100 sq.km.

**Figure 3.4 Varying densities of camera trap locations in the sampled area**

#### 4. RESULTS

The total trapping effort for 70 days of trapping over 121 trapping station amounted to 7865 trap nights documenting a total of 358 photographs of 103 individuals (38 males, 56 females and 9 unclassified). The 121 trapping stations covered an area of (MCP) 420.86 sq. km with a camera density of 1 per 3.45 km. The number of new individuals seems to stabilize after the 40<sup>th</sup> trap night while the number of captures shows a steady increase. This makes it safe to assume that most of the resident animals in the study area were trapped during the 65 trapping nights. However, considering the addition of a new individual on 54<sup>th</sup> day the possibility of individuals being missed cannot be completely ruled out.

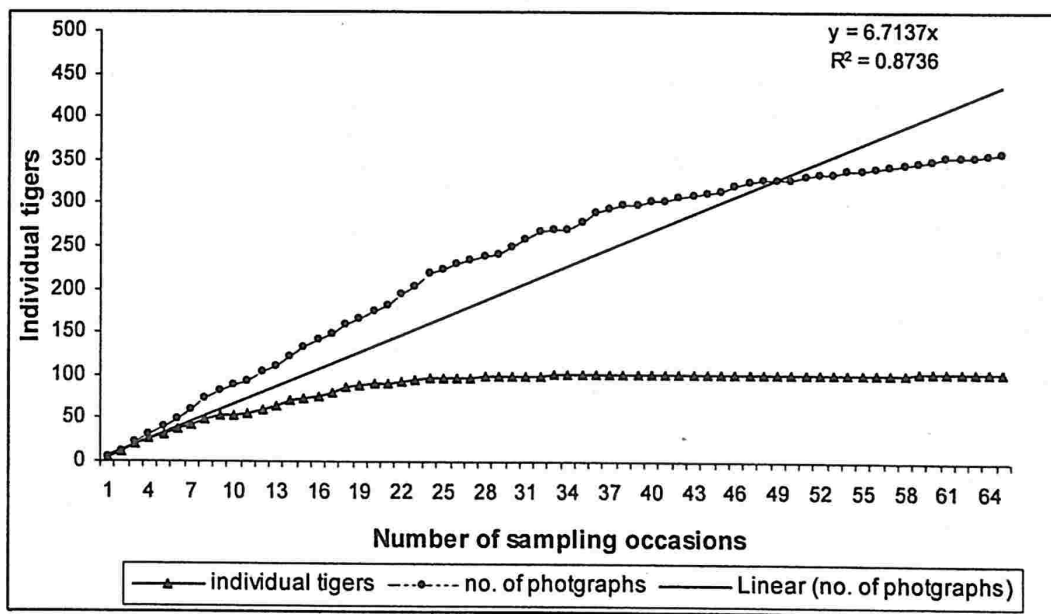


Figure 4.1: Cumulative number of tiger photographs, indicating the number of individual tigers captured with increasing sampling occasions.

##### 4.1. Population and density estimates:

The statistical test for population closure using program CAPTURE (Otis *et al.*, 1978; Rexstad & Burnham 1991) rejected the closure assumption for the sampled

population ( $z = -7.436$ ,  $P = 0.0000$ ). Model Mtb was selected as appropriate model by program capture which gave an estimate of 108 with a standard error of 4.5591.

Although, the appropriate model selected by the CAPTURE was Mtb, the estimates for Mo as well as Mh are reported here. Model Mo is selected as it is the starting model with minimum number of parameter restriction in the calculation of capture probability and meets the assumption of equal catchability thus giving high precision (Chao and Huggins 2005). Model Mh is selected because heterogeneity is expected in all natural populations (Edwards and Eberhardt 1967, Cooch and White 1995).

**Table 4.1** Population estimates calculated through different models within different programs.

Model/ Estimator	N	SE	CV in %	Program used
<b>Discreet-time models</b>				
Mo	106	1.9520	1.95	CAPTURE 2
Mh	131	8.3754	8.38	CAPTURE 2
Mtb	108	4.5591	4.56	CAPTURE 2
Mo CMLE	106	1.9800	1.98	CARE 2
Mo UMLE	106	1.9500	1.95	CARE 2
Mh(jk1)	134	7.7800	7.78	CARE 2
Mh(jk1)	138	13.3300	13.33	CARE 2
Mtb CMLE	109	4.2400	4.24	CARE 2
Mtb UMLE	107	3.6700	3.67	CARE 2
Mtb	108	3.2790	3.28	CARE 3
<b>Continuous-time models</b>				
Mt	106	1.9000	1.90	CARE 3
Mtb	109	3.6150	3.62	CARE 3

Program CARE-2 selected model Mtb and gave an estimate of 109 with standard error of 4.24. Model Mb did not converge for the continuous time-model in program CARE-3. The estimate given by model Mtb in the continuous-time framework gives a better estimate of the population in terms of precision as its CV is lower than that of its discrete-time model counterpart calculated through CARE-2 as well as CAPTURE 2. Different estimates of population given by different models are summarized in table 4.1

The minimum convex polygon ( $A$ ) formed using peripheral camera traps was found to be 420.86 sq. km. The boundary strip width  $W$  was estimated as 3.22 km using the mean maximum distance moved (MMDM) and was estimated 2.55 using the root pooled spatial variance (RPSV) as well as  $ARL/2$ . The effectively trapped area  $A(W)$  and the resulting density estimates using various methods are summarized in table 4.2.

The estimates obtained through RPSV seem to be ecologically more realistic (Section 1.2) than the ones obtained through MMDM/2. RPSV densities are not restricted to the sampled area and have a global applicability (Efford 2004). It makes sense to use the estimates calculated with the habitat mask i.e. by excluding the area of the Ramganga reservoir and the adjoining villages as these are likely to be hard boundaries restricting the movement of animals. The population estimates for model Mo and selected model Mtb do not vary greatly and therefore, neither does the resulting density estimate. Densities calculated by using MMDM and habitat mask coincide with the densities obtained through RPSV. The density of tigers in Corbett National Park is 16.04 tigers /100 sq. km.

**Table 4.2.** Density estimates calculated using different methods of calculating effectively trapped area (ETA).

Model	N <sup>^</sup>	SE N	Method for calculating ETA	W (km)	SE W	ETA (sq.km.)	D	SE D	CV (D) (%)
M(o)	106	3.3345	MMDM/2 (Circular (without habitat mask))	1.61	0.31	546.11	19.59	0.37	1.87
			MMDM/2 (actual shape without habitat mask)	1.61	0.31	562.4	18.85	1.55	8.22
			MMDM/2 (with habitat mask)	1.61	0.31	519.58	20.4	1.74	8.52
			MMDM (Circular (without habitat mask))	3.22	0.28	687.66	15.56	0.29	1.86
			MMDM (actual shape without habitat mask)	3.22	0.28	720.29	14.72	1.35	9.19
			MMDM ( with habitat mask)	3.22	0.28	651.05	16.28	1.57	9.63
			RPSV	2.55	na	652.56	16.04	1.6	9.98
			ARL/2	2.55	0.9	656.26	16.3	0.9	5.52
			M(tb)*	108	4.5591	MMDM/2 (Circular (without habitat mask))	1.61	0.31	546.11
MMDM/2 (actual shape without habitat mask)	1.61	0.31				562.4	19.2	1.6	8.33
MMDM/2 ( with habitat mask)	1.61	0.31				519.58	20.79	1.79	8.63
MMDM (Circular (without habitat mask))	3.22	0.28				687.66	15.71	0.66	4.23
MMDM (actual shape without habitat mask)	3.22	0.28				720.29	15	1.39	9.29
MMDM ( with habitat mask)	3.22	0.28				651.05	16.59	1.61	9.73

Where

N<sup>^</sup> = Population estimate

W = Buffer strip width

ETA = Effectively trapped area

D = Density estimate

MMDM = Mean maximum distance moved

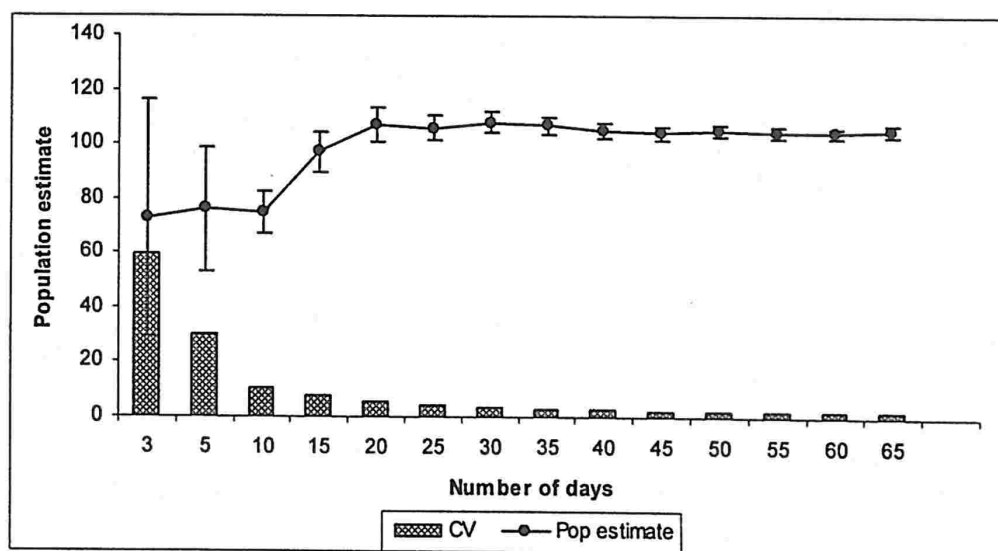
RPSV = Root pooled spatial variance

ARL/2 = Asymptotic trap-revealed range length

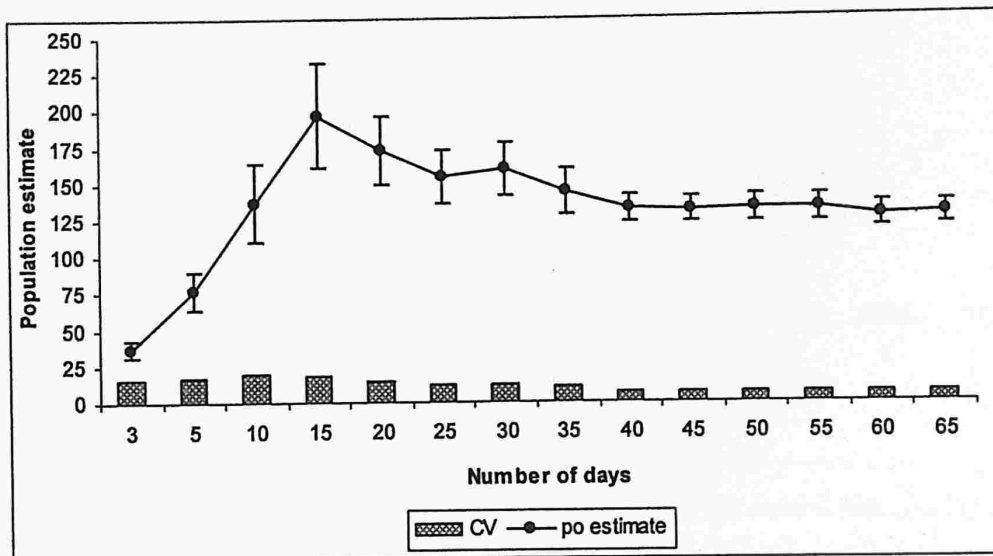
## 4.2. Required sampling effort

Population estimates were calculated using model Mo and Mh by considering a very small number of sampling occasions and systematically increasing it. The estimates from model Mo suggest that minimum 35 days of sampling is required to get reliable estimates of the population (Figure 4.2a). The precision too seems to improve beyond the 30<sup>th</sup> day of sampling. Use of model Mh suggests minimum 40 days of sampling for precise and reliable estimates.

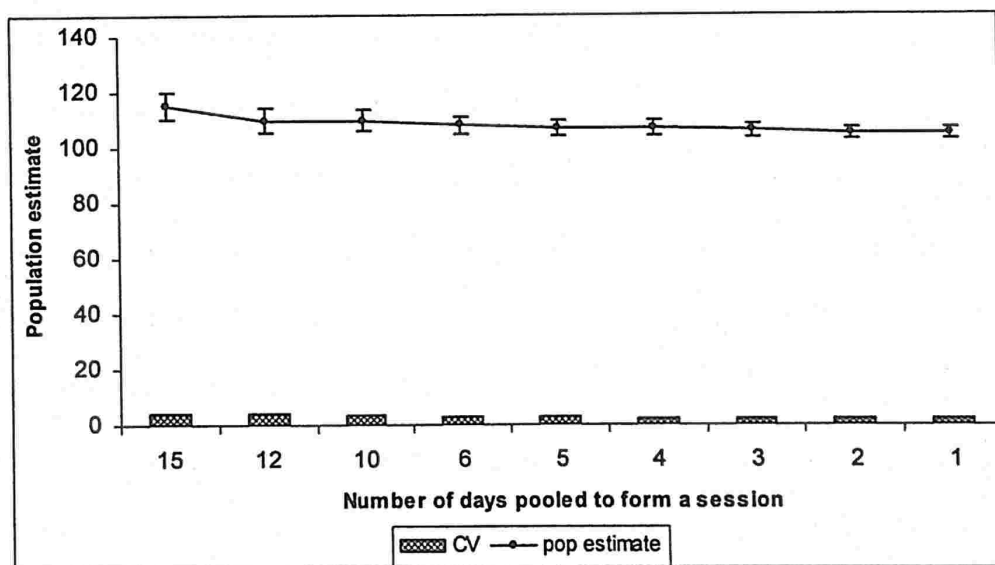
The individual capture histories were pooled over varying number of days to evaluate the effect of session length/session size on population estimates. It appears that there is negligible effect of session size on the estimates obtained through model Mo and there model Mh seems to perform consistently irrespective of the size of the session in terms of number of days combined (Figure 4.3a and 4.3b).



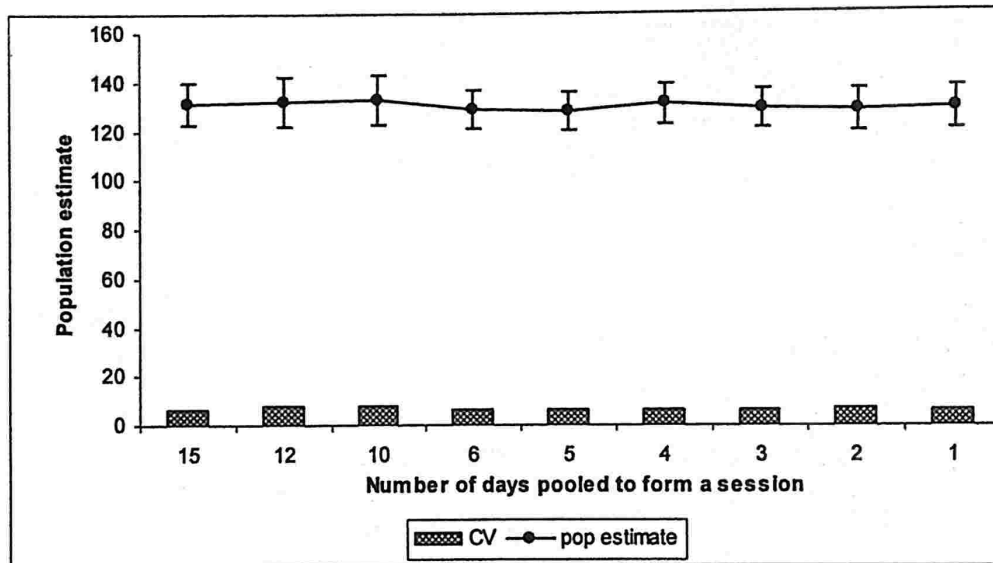
**Figure 4.2a** Population estimate (with standard error) for **model Mo** and associated CV plotted against number of sampling occasions/days.



**Figure 4.2b** Population estimate (with standard error) for **model Mh** and associated CV plotted against number of sampling occasions/days.



**Figure 4.3a** Population estimate (with standard error) for **model Mo** and associated CV plotted against sessions with varying number of days.

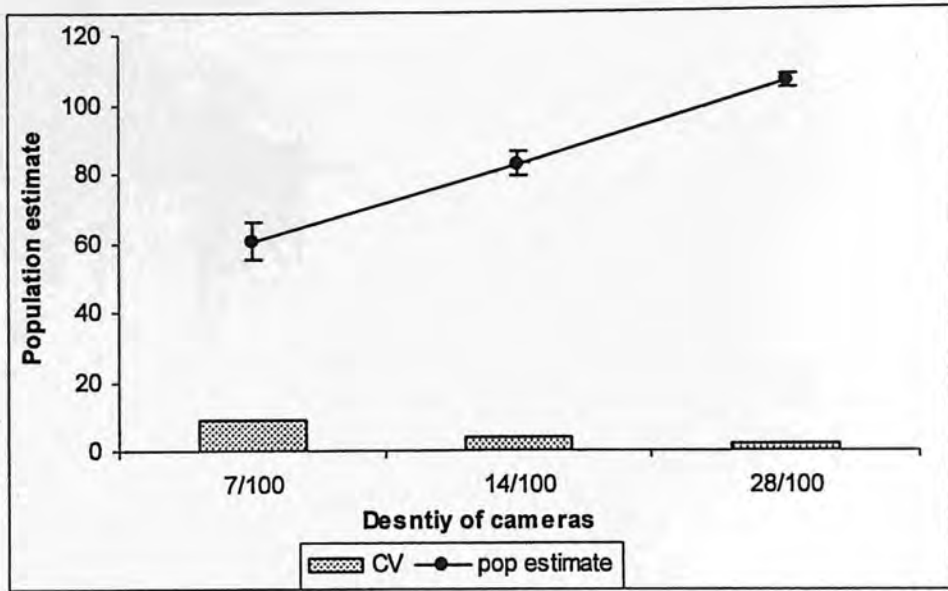


**Figure 4.3b** Population estimate (with standard error) for model Mh and associated CV plotted against sessions with varying number of days.

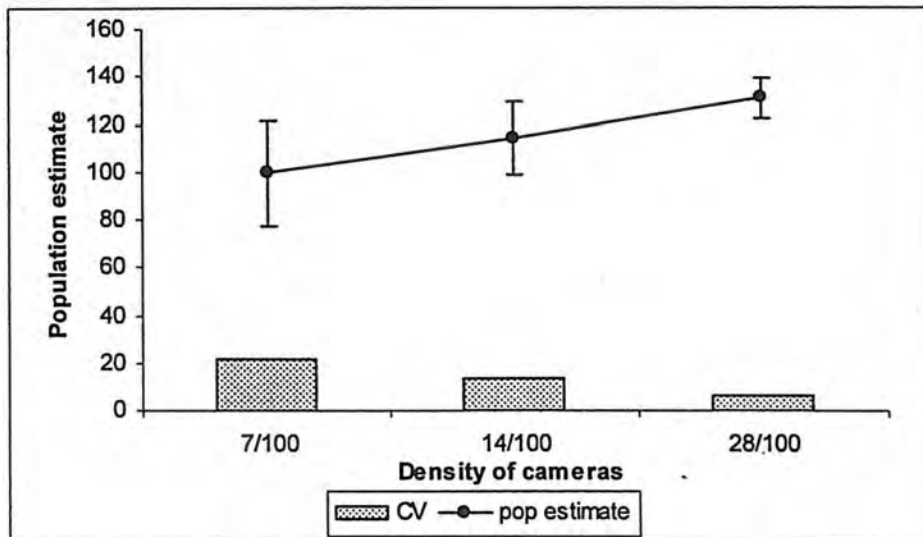
### 4.3 Effect of camera trap density on population and density estimates

#### 4.3.1 Effect of trap density on population estimates

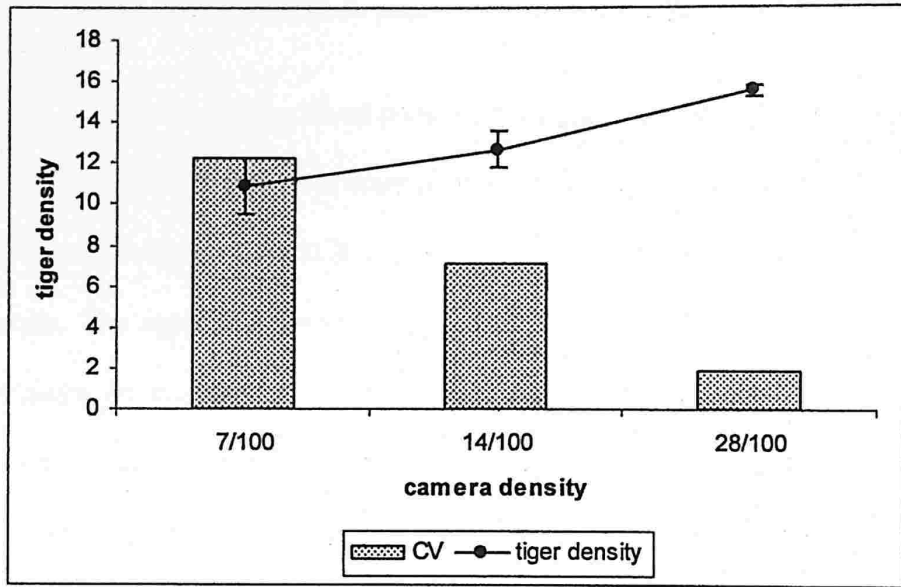
Camera trap density was reduced to half and then 1/4<sup>th</sup> of the actual density at which sampling was carried out in field by systematic removal of trap locations and associated capture histories from the analysis. There seems to be a linear relationship between trap density and population estimates. Population estimates show a drastic decline along with reduction in the number of camera traps per given area. The precision of the estimates also seems to get affected by trap density. At higher trap densities the population estimates have lower CV resulting in superior precision. This trend is reflected in estimates of both model Mo and model Mh (Figure 4.4a and 4.4b). Similarly, the effect of camera trap density was evaluated on the density estimates. Density estimates too respond to camera trap density and show a decrease with the decrease in trap density. This was observed not only for the density calculated by MMDM localised to the sampled area, but also for the density estimates calculated through RPSV (Figure 4.5a and 4.5b).



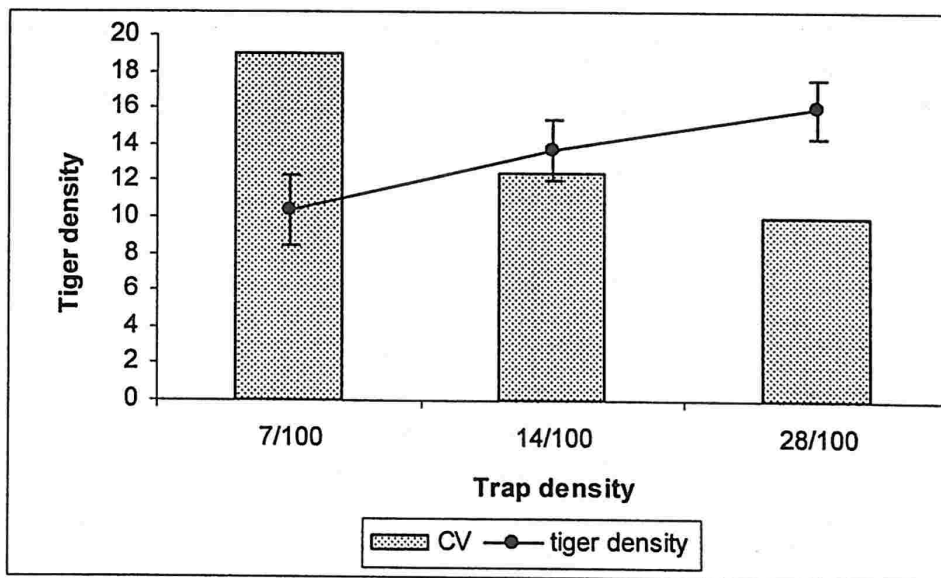
**Figure 4.4a** Population estimate using model Mo and associated CV plotted against trap camera trap density



**Figure 4.4b** Population estimate using model Mh and associated CV plotted against trap camera trap density



**Figure 4.5a** Density estimates calculated through MMDM plotted against camera density



**Figure 4.5b** Density estimates calculated through RPSV plotted against camera density

#### 4.3.2 Effect of trap density on population estimates assuming low and medium tiger density

Samples assuming a total population varying from low (2 and 5) to medium (10 and 25) number of tigers were drawn at random for each and population estimates were calculated. Program CAPTURE 2 was used for estimating the population for each sample. The appropriate model selected by the CAPTURE was either Mo or Mh. Estimates for model Mo is reported here. As already mentioned, model Mo has the minimum number of parameter restriction in the calculation of capture probability and meets the assumption of equal catchability thus giving high precision (Chao and Huggins 2005)

It seems that at very low population levels, the number of camera traps does not seem to bias the estimates but precision is clearly affected. At medium level of population, low camera density fairs poorly on both bias as well as precision. The CVs at low camera densities are much higher compared to the ones associated with population estimates derived from high density of cameras.

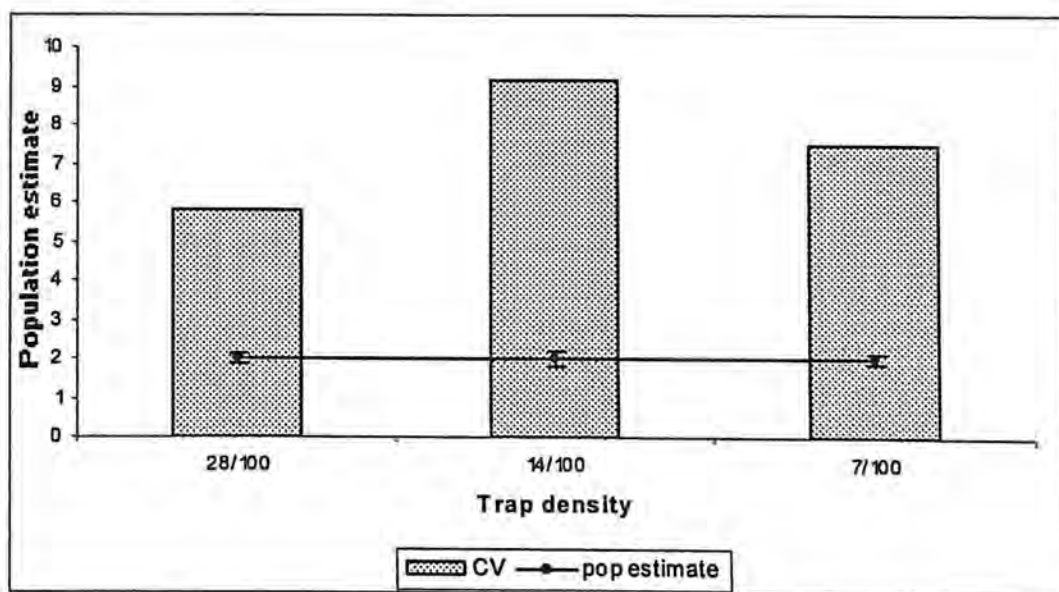
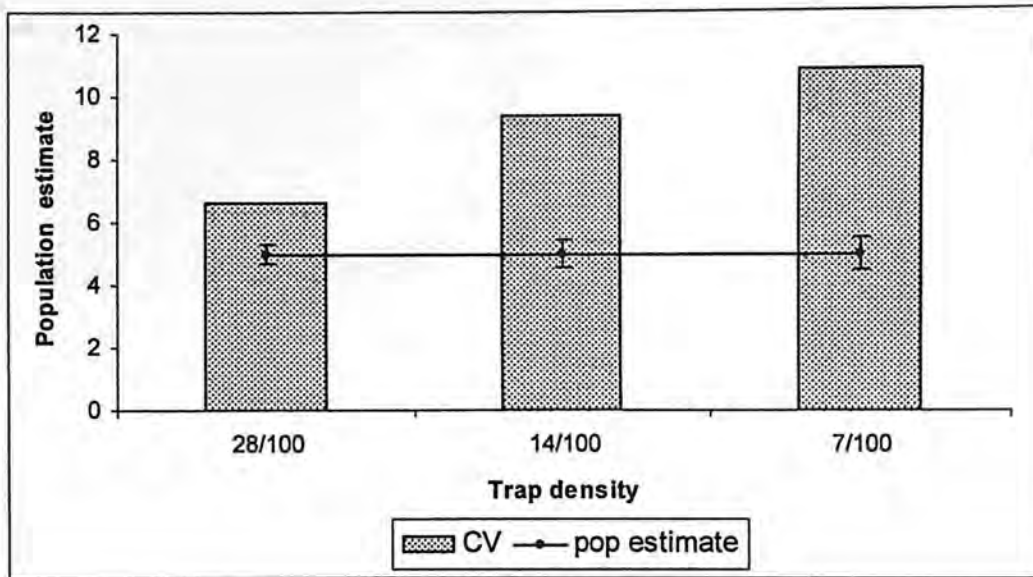
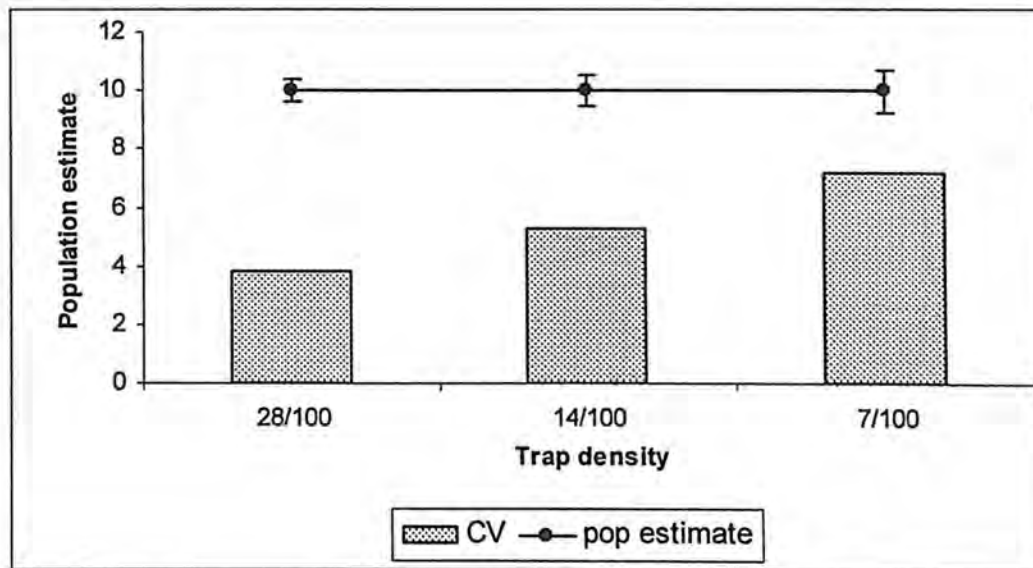


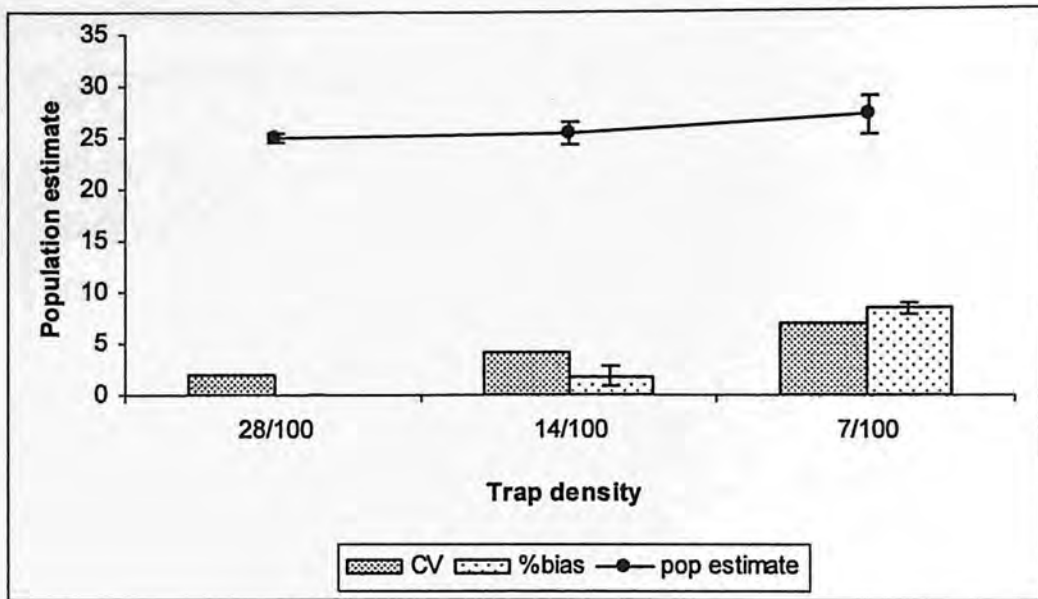
Figure 4.6a Population estimate of simulated / assumed population of 2 tigers plotted against trap density.



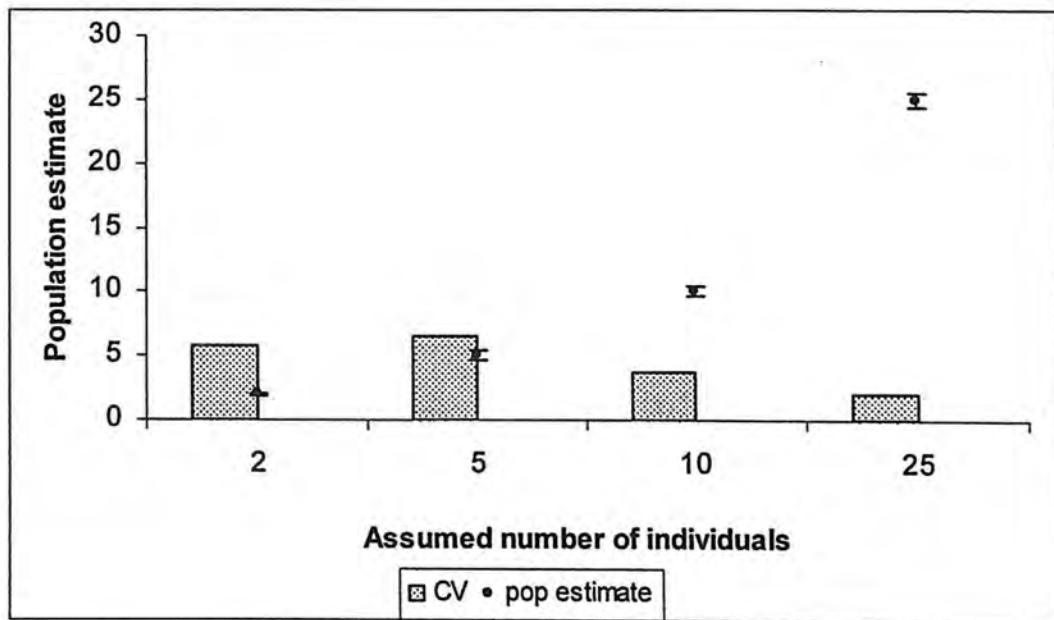
**Figure 4.6b** Population estimate of simulated / assumed population of 5 tigers plotted against trap density.



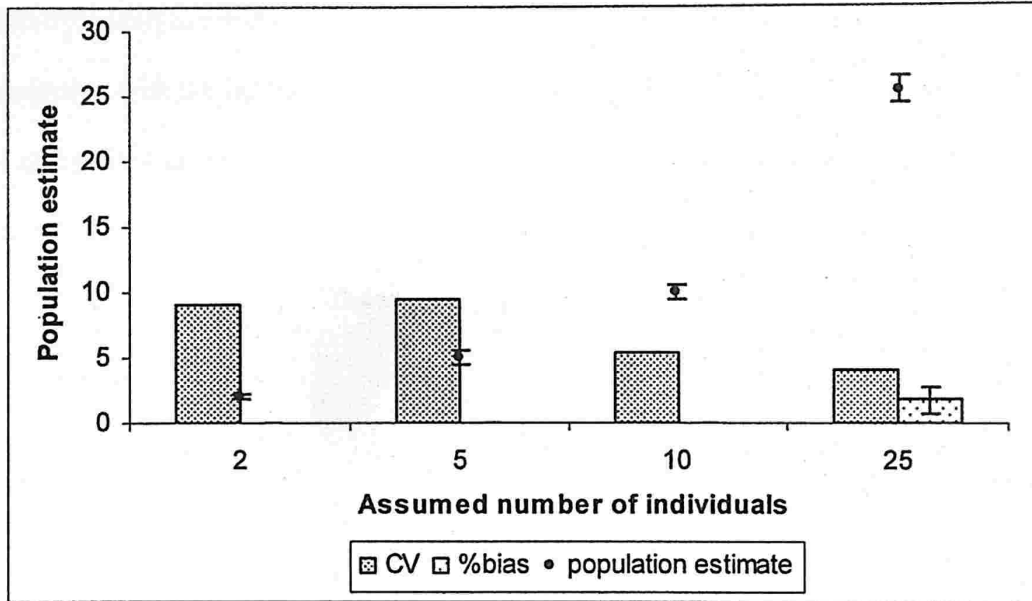
**Figure 4.6c** Population estimate of simulated / assumed population of 10 tigers plotted against trap density.



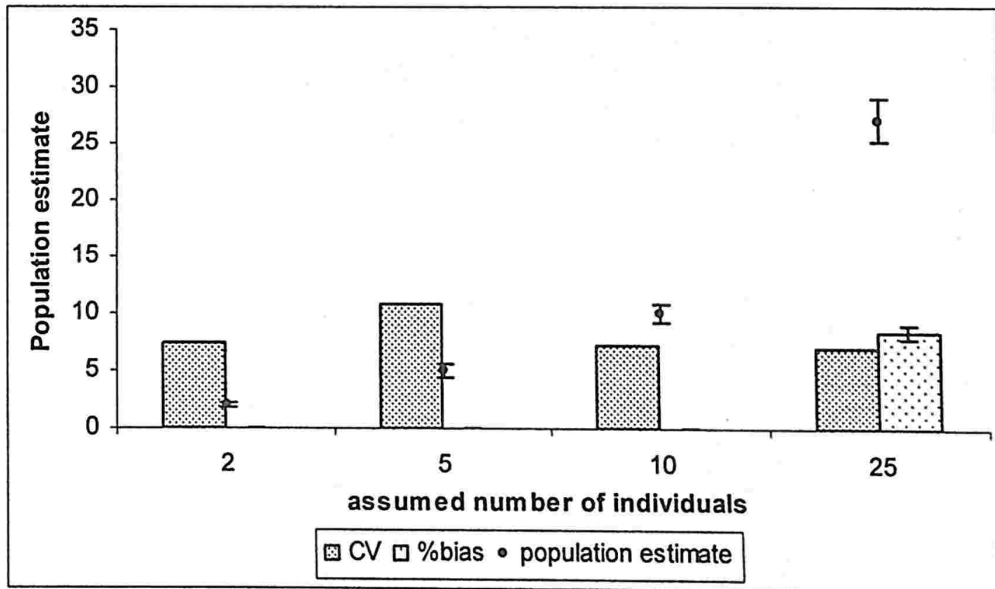
**Figure 4.6d** Population estimate of simulated / assumed population of 25 tigers plotted against trap density.



**Figure 4.7a** Population estimate and associated bias calculated using high trap density of 28 cameras/100 sq. km.



**Figure 4.7b** Population estimate and associated bias calculated using medium trap density of 14 cameras/100 sq. km.



**Figure 4.7c** Population estimate and associated bias calculated using low trap density of 7 cameras/100 sq. km

The effect of trap density does not seem to affect the estimates of population so much that it becomes difficult to detect the changes in the population. But, on the other hand population estimates at low trap densities have an associated positive bias and poor precision with the increase in the number of animals (Figure 4.7a , 4.7b and 4.7c) This suggests that using higher trap densities is advisable where animal densities are high to arrive at reliable population estimates which are ecologically relevant. This will further aid in detecting changes in the overall population.

## 5. DISCUSSION

Discrepancies in the sampling technique make estimates erroneous or highly site specific. This limits the ability of a study for practical use with respect to delineating conservation strategies and making important management decisions. By intensively sampling in a large area (MCP = 420.86 sq.km) through systematic sampling, an attempt was made to arrive at reliable population and density estimates for tigers in Corbett NP. The study was also aimed at answering some key questions regarding the importance of sampling effort required for arriving at reliable estimates as well as problems put forth due to the discrepancies in the effective sampling area, which often arises as an artifact of the sampling design and choice of analytical techniques.

### 5.1 Population closure

A critical assumption of closed population models is the closure assumption where it is assumed that the population is geographically closed i.e. there is no immigration or emigration, as well as demographically closed i.e. there is no recruitment (births or deaths) throughout the sampling period (Otis *et al* 1978, White *et al* 1982). The statistical test for population closure using program CAPTURE (Otis *et al.*, 1978; Rexstad & Burnham 1991) rejected the closure assumption for the sampled population (section 4.1). The sampling was carried out for a span of 65 days which is considerably small in keeping the longevity of the animal in mind. Also, individual tigers less than 1 year of age were not considered for population estimation. So it is safe to assume that the population was demographically closed. Tigers are highly territorial animals and so the assumption of geographical closure can also be made but it may need further investigation. The inclusion of a new individual at the end of the study period (Figure 4.1) makes it questionable. It should be kept in mind

that closure is difficult to ascertain in biological population especially in non – controlled situations (Soisalo and Cavacanti 2006). Closure is affected by trap response (trap shyness) if the animal becomes trap shy and uncatchable it is difficult to differentiate it from death or emigration of the animal. Since model Mtb was selected for the population in Corbett NP, the test for closure in CAPTURE may have been unable to distinguish failure of closure from any behavioural change in capture probabilities. Moreover, closure assumes equal catchability. So closure may be rejected in certain cases where it is actually true but the animals have unequal catchability (Pollock et al 1990). It is necessary to meet the closure assumption for closed population models. As this closure test is poor, Soisalo and Cavalcanti (2006) suggested sampling in a short period relating to the life history of the study animal which was done in this study.

## **5.2 Model selection**

Model Mtb was identified as the appropriate model (by programs CAPTURE, CARE-2 and CARE-3 Section 4.2). Model Mtb is generalization of model Mt for the effect of behaviour (Otis et al 1978, Chao and Huggins 2005), an estimator which assumes that capture probabilities vary by behavioural response as well time of capture, which suggests that the tigers may have responded behaviourally and to the time of capture. Burnham derived the MLE for Mtb, under the assumption that recapture probability is a power function of the initial capture probability for a parameter  $\theta$  (Rexstad and Burnham 1991). If  $\theta > 1$  animals exhibit trap happy behaviour and animals are trap shy if  $\theta < 1$ . The  $\theta$  value for the population estimate of this dataset is  $\theta = 1.043$ , which means the animals exhibit trap happiness. Such positive response to trapping occurs where animals have a favourable experience at the time of the first capture e.g. when a bait or lure is used. No such baits were used

for this study, so there is a reason to believe the animals were not trap happy. The increased recapture probability may have been an artifact of the selection of sites for laying camera traps as these were selected on the basis of presence of signs and may have led to placing of traps in established routes of habitual movement and regular usage by tigers.

According to Otis et al 1978, a robust estimator is one which is not sensitive to breakdown of particular assumption. Since a specific measure of robustness is difficult to define, the robustness of estimator determined is subjective based on the general performance of the estimator. Model Mo is the simplest and the only model which meets all the assumptions of capture recapture. Model Mt performs poorly when heterogeneity is present in the population. Model Mh jackknife is reasonably robust with respect to the essential criteria of bias, precision and confidence interval coverage. Therefore, for most part of the study involving evaluation of required sampling effort and effect of camera density, the above mentioned models were used.

### **5.3. Density estimation**

Density is an ideal instrument for studying animal population (Greig - Smith 1983). A large part of ecological theory has been developed with the assumption that intra and inter specific patterns of density and spatial distribution can be consistently and accurately compared, and these patterns represent populations across non studied landscape. This assumption is erroneous (Smallwood and Schonewald 1996). Scientists fail to realize that information may change due to study design and perception of the investigator (while comparing studies) and the concerned species (Levin 1992). There is unevenness in the distribution of animals which can be explained ecologically as an effect of clumped distribution. The patchy availability of resources (food water etc) will lead to clumped distribution of prey and tigers will

follow their distribution is highly influenced by prey availability (Karanth 1995). Without accounting for such unevenness in the distribution when density is estimated with the help of mark recapture framework, it leads to estimates which are much less reliable and minimizes their utility in practice (Smallwood and Schonewald 1996).

In mark recapture studies, especially for large mammals, the trapping is done in a small area and a buffer strip is added to it to account for the space use by animals trapped at the periphery. The strip width is calculated, most often through the MMDM (mean maximum distance moved) between recaptures and a strip of half the size of MMDM is added to the intensively sampled area. The half MMDM method ends up giving overestimates of density as a consequence of underestimate of effectively sampled area (Soisalo and Cavalcanti 2006). Full MMDM as well RPSV methods were used to derive the density estimates for Corbett NP (Table 4.2). Further the areas which may act as hard boundaries for tigers were removed from the calculation of the effectively sampled area. Since the trapping was carried out on almost the whole of the park, this density estimate can be used to extrapolate and arrive at a population figure for the park; however it will be advisable to use it with caution. The new approach of using RPSV for the calculation of effectively sampled area does not restrict the density to the sampled area but is globally applicable (Efford 2004). The RPSV density figure of 16 tigers/100 sq. km coincides with the one estimated through MMDM excluding the possible hard boundaries (section 4.1). Even if the density is slightly underestimated through full MMDM method, it is better than presenting an over estimate as such a high level of error can wrongly influence management decisions made on the basis of this estimate (Soisalo and Cavalcanti 2006).

## **5.4 Sampling issues**

### ***5.4.1. Effort required in terms of sampling occasions***

Results from section 4.3 suggest that trapping effort (number of sampling occasions) plays a significant role in estimating population size accurately with good precision. From the present data it appears that a minimum of 35 – 40 sampling occasions are required to get a reliable estimates of the population..

The effect of pooling the sampling days (resulting in decrease in the number of sampling occasions) on the accuracy and precision of population estimate was also evaluated. It was found that pooling days resulted in higher capture probability, but the population estimates seem unaffected. Pooling days neither affects the accuracy or the precision of the estimate using model Mh. Estimates from model Mo show that accuracy and precision improve when the number of days pooled decreases and is best when the session comprises of one or two sampling days. This suggests that it is better to capture the maximum information by keeping the number of days per sampling occasion to a minimum (thus resulting in increase in sampling occasions) while analyzing populations using capture-recapture sampling.

### ***5.4.2. Effort required in terms of camera trap density***

Trapping was carried out with a camera trap density of 1 camera in every 3.4 sq.km. When trap locations and associated individual capture histories were selectively dropped from the analysis it was observed that the population estimates decline drastically. Not only does one get an underestimate (reduced accuracy) of the true population at lower camera densities, but the estimates are poor in terms of precision too making the estimates unreliable for making important consideration in terms of conservation as well as management strategies. The same trend is reflected in the density estimates. Density estimates were calculated using the full MMDM

method (Parmenter 2003) as well RPSV (Efford 2004) and both estimates showed a clear pattern of underestimates of density and poorer precision. This suggests that it is of considerable significance to have a density of traps high enough so that it covers the area fairly well. In a high density area, the animal home ranges are likely to be compact resulting in limited movement compared to an area where animal densities are lower. In such a scenario the trap density should be high in order to maximize captures as well as recaptures in the area. A comparison of (%CV) from published camera trap studies further emphasizes this. Table 5.1 summarizes 15 studies carried out on tigers across Southeast Asia.

Comparing the CVs of various studies reported here with this study, for both population as well as density estimates, clearly indicates that the present study has superior precision. The estimates present here are arrived at by putting Mh estimator to use, while the estimates for the current study presented here are calculated for Model Mtb. One may argue that the use of different model for estimation has led to a lower CV. But the estimates for model Mh for the population estimate of Corbett NP also has a CV lower than that of the studies present here ( $N^{\wedge} = 131$  CV = 8.38 (Table 4.1)). None of the studies have mentioned a use of a systematic grid or an overall high and homogeneous density of camera traps, like the one used in Corbett NP for this study, in their methodology (See Chauhan et al (2005), Kawanishi (2002), Karanth and Nichols (1998), Karanth et al (2004), O' Brien et al (2003)).

This could have been one of the contributors to the high CVs associated with the estimates. Of course, one cannot deny that there might be a distribution of tigers which is so patchy that it contributes to low precision. Even in such case, it would be advisable to use a high density of camera traps to smoothen out any discrepancies which may arise as an artifact of trap placement or trap numbers per unit area.

**Table 5.1** Tiger population and density estimates from some of the studies carried out in SE Asia

Location	<i>A (W)</i>		CV (N)	D	CV (D)
	MMDM/2	N <sup>^</sup>			
Ranthambore, India	360	21	29.14	5.83	34.48
Taman Negara, Malaysia	376	6	37.00	1.66	12.65
Bukit Barisan Selatan, Indonesia	836	13	28.15	1.56	27.56
Tadoba, India	367	12	16.42	3.27	18.04
Bhadra, India	263	9	21.44	3.42	24.56
Pench, India	122	6	23.50	4.94	27.73
Melghat, India	360	24	25.38	6.67	27.74
Panna, India	418	29	33.28	6.94	46.54
Pench - M'rashttra, India	274	20	22.05	7.29	34.84
Ranthambore, India	244	28	26.04	11.46	36.65
Kanha, India	282	33	14.21	11.70	16.50
Nagarhole, India	243	29	13.00	11.92	14.35
Bandipur, India	284	34	29.12	11.97	30.99
Kaziranga, India	167	28	16.11	16.76	17.66
Corbett, India*	562	108	4.21	19.20	8.33

Where

*A(W)* MMDM/2 = Effectively sampled area calculated using half MMDM

N<sup>^</sup> = Population estimate

D = Density estimate

\* = This study

**Sources:** Chauhan et al (2005), Kawanishi (2002), Karanth and Nichols (1998), Karanth et al (2004), O' Brien et al (2003)

Results from the simulation experiment where population levels are assumed to be as low as 2 and 5 individuals and medium with 10 and 25 individuals, exhibit the effect of trap density on population estimates. At low levels of population, the population estimates have poor precision in terms of CVs. It is advisable to use high trap density even if population levels are low. Silver et al (2004) made a similar suggestion about keeping trap densities adequate enough where population is low. They suggested that at a sufficiently high density of subject animals, a small number of camera trap sites functioning for a short period of time may produce sufficient observations to generate an abundance estimate. This suggestion proves to be

disputable based on the results of section 4.3 (figure 4.7a, 4.7b and 4.7c). At low levels of population the estimates have poor precision with low trap density. But, as the number of individuals increases, the estimates become both biased and with poor precision. This clearly indicated the use of a good sampling approach in terms of trap layout as well as trap density to arrive at reliable population estimates.

It is worth considering that the population estimates generated through simulation for low number of tigers are superior in terms of bias and precision compared to other studies with such low numbers. Kawanishi (2002) reported an estimate of 6 with a CV of 37% ca. and an estimated 5 tigers with a CV of 28% were reported by Karanth and Nichols (1998) from Pench, India. Both studies gave the estimate for model Mh. For this study the simulated samples gave an estimate of 5 tigers with a CV of 21% with model Mh and the same estimate with a CV of 6% with model Mo using a trap density of 28 traps/100 sq.km. Comparing results of this study with the former clearly points at the advantage of using high density of traps as at medium (14 traps/100 sq.km) and low trap density (7 traps/100sq.km.) the CV is as high as 45% and 59% respectively. It is evident that for accurate and precise estimates of the true population one must maximize the sampling effort in terms of number of terms per unit area irrespective of the underlying density/population gradient.

To ensure the normal functioning of the various forest ecosystems, it is critical to ensure the continued survival of the tiger. Its role as a flagship as well as umbrella species cannot be overlooked when evaluating or planning a conservation scenario. For this purpose, the need of reliable estimates of tigers has arisen. Despite all the developments in methodologies, we still seem to suffer from discrepancies when it comes to providing reliable estimates of tigers. Due to the lack of reliable estimates, it becomes extremely difficult to monitor changes in the numbers. If one is able to

arrive at accurate estimates of individuals in a given area, than this population becomes much easier to monitor, which in turn can help to identify drastic declines in numbers of tigers. In the current scenario where tiger poaching is one of the biggest threats to its existence, such a method may prove to be instrumental in preventing another disaster, like the one in Sariska, from happening.

## LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pages In: B.N.Petran and F.Csaaki *International symposium on Information Theory*, 2<sup>nd</sup> ed. Akadeemiai Kiado, Budapest, Hungary. pp 267-281 p
- Anderson, D.R., Burnham, K.P., White, G.C. and Otis, D.L. 1983 Density estimation of small mammal populations using trapping web and distance sampling methods. *Ecology* 64: 674- 680.
- Bailey, N.T.J. 1952 Improvements in the interaction of recapture data. *Journal of Animal Ecology*. 21: 120 -127.
- Bertram, B. C. R. 1979. *Studying predators*. Second edition. African Wildlife Leadership Foundation, Nairobi.
- Bharthari 1999 *Management plan for Corbett National Park (Ramnagar Tiger Reserve Division)* Part I. pp 1-11.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist*. 124: 255-279
- Burnham, K.P., and Anderson D.R. .2002. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Burnham, K. P. and Overton, W. S. 1978. Estimation of the size of a closed population when capture probabilities vary among animals *Biometrika* 65: 625- 633.
- Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J. R., Griffiths, M., Holden, J., Kawanishi, K., Kinnard, M., Laidlaw, R., Lynam, A., Macdonald, D. W., Martyr, D., McDougal, C., Nath, L., O' Brien, T., Seidensticker, J., Carothers, A. D. 1973. Capture-recapture methods applied to a population with known parameters. *Journal of Animal Ecology* 42: 125-146.
- Chao, A and Higgins, M. 2005. Modern closed - population capture – recapture models. In *Handbook of capture –recapture analysis* Eds. Amstrup S.C., McDoanld T.L. and Manly, B.J.F. Princeton University press, Princeton, New Jersey

- Champion, F.W. & Seth, S.K. 1968. *A revised survey of the forest types of India*. Govt of India, New Delhi, pp 234 -238
- Choudhury, S. R. 1970. Let us count our tigers. *Cheetal*. 14: 41-51.
- Choudhury, S. R. 1972. Tiger census in India. *Cheetal*. 15: 67-84.
- Cooch, E. & White, G. 1995 . Program MARK. Analysis of Data from Marked Individuals. "A Gentle Introduction" 2nd Edition. Internet URL <http://www.phidot.org/software/mark/docs/book>
- Craig, C.C. 1953 On the utilization of marked specimens in estimating population of flying insects. *Biometrika*. 46: 336 - 351.
- Dahl, K 1918-19 Studies of trout and trout waters in Norway. *Salm. trout. Mag* 17:58-59 and 18:16-33.\*
- Darroch, J.N. 1958. The multiple-recapture census, I: estimation of a closed population. *Biometrika* 46: 343-359.
- Dice, L. 1938. Some census methods for mammals. *Journal of Wildlife Management*. 2: 119-130.
- Edwards, W.R., and Eberhardt, L.L. 1967 Estimating cottontail abundance from live trapping data. *Journal of Wildlife Management*. 31: 87 - 96.
- Efford M. 2004. Density estimation in live-trapping studies. *Oikos* 106: 598 - 610.
- Franklin, N., Bastoni, Sriyanto, Siswomartono, D., Manansang, J. & Tilson, R.(1999). Using tiger stripes to identify individual tigers. In *Riding the Tiger: Tiger Conservation in Human Dominated Landscapes*: 138-139. Seidensticker, J., Christie, S. & Jackson, P. (Eds). Cambridge University Press, Cambridge, United Kingdom
- Gaston K.J., Blackburn, T.M. and Gregory, R.D (1999) . Does Variation in census area confound density comparisons? *Journal of Applied Ecology* 36: 191 - 204.

- Greig – Smith, P. 1983 *Quantitative plant ecology*. University of California Press, Berkeley.
- Huggins, R.M. 1989. On the statistical analysis of capture experiments. *Biometrika* 76:133-140.
- Huggins, R.M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrika* 47: 725-732.
- Jett, D. and Nichols, J. D. 1987. A field comparison of nested grid and trapping web density estimators. *Journal of Mammology*. 68: 888-892.
- Johnson, D. H. 1994. Population analysis. In: T. Bookout, editor. In *Research and management techniques for wildlife and habitats*. The Wildlife Society, Bethesda, Maryland, USA. pp 419-444
- Karanth, K. U., 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological conservation*. 71: 333-338.
- Karanth, K.U., Chundawat, R.S., Nichols, J.D., & Kumar, N.S. 2004 Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture-recapture sampling. *Animal Conservation* 7: 285-290.
- Karanth, K. U. and Nichols, J. D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79: 2852-2862.
- Karanth, K. U. and Nichols, J. D. 2000. *Ecological Status and Conservation of Tigers in India*. Final Technical Report to the Division of International Conservation, US Fish and Wildlife Service, Washington DC and Wildlife Conservation Society, New York. Centre for Wildlife Studies, Bangalore, India.
- Karanth, K.U., Kumar S.K. & Nichols, J.D. (2002). Field Surveys: Estimating absolute densities of tigers using capture-recapture sampling. In *Monitoring Tigers and their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia* :139-152. Centre for Wildlife Studies, Bangalore, Karnataka, India.

Karanth, K.U., Nichols, J.D., Seidensticker, J., Dinerstein, E., Smith, J.L.D., McDougal, C., Johnsingh, A.J.T., Chundawat, R.S., Thapar, V., 2003. Science de.ciency in conservation practice: the monitoring of tiger populations in India. *Animal Conservation*. 6:1–10.

Karanth, K. U. & Stith, B. M. 1999. Prey depletion as a critical determinant of tiger population viability. In: Siedensticker, J., Christie, S. & Jackson, P *Riding the tiger: tiger conservation in human-dominated landscapes*. Cambridge: Cambridge University Press.  
pp 100–113.

Kawanishi, K., 2002. *Population status of tigers (Panthera tigris) in a primary rainforest of Peninsular Malaysia*. Ph.D. Dissertation. University of Florida, Gainesville, USA.

Kelly, M.J., Laurenson, M.K., FitzGibbon, C.D., Collins, D.A., Durant, S.M., Frame, G.W., Bertram, B.C.R., Caro, T.M., 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. *Journal of Zoology*. 244: 473–488

Kenny, J.S., Smith J.L.D. Starfield, A.M. and McDougal, C. 1995 The long – term effects of tiger poaching on tiger population viability. *Conservation Biology*. 9: 1121 – 1133

Kitchner, A.C. (1999). Tiger distribution, phenotypic variation and conservation issues. In *Riding the Tiger: Tiger Conservation in Human Dominated Landscapes*: 19–39. Seidensticker, J., Christie, S. & Jackson, P. (Eds).Cambridge University Press, Cambridge, United Kingdom

Lancia, R. A., Nichols, J. D. & Pollock, K. N. 1994. Estimation of number of animals in wildlife populations. In: Bookhout, R. *Research and management techniques for wildlife and habitats*. Bethesda: The Wildlife Society. pp 215–253

LeCren, E. D. 1965 A note on the history of mark - recapture population estimation. *Journal of Animal Ecology*. 34: 453 – 454.

- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology*. 73: 1943 – 67.
- Lincoln, F.C (1930). Calculating waterfowl abundance on the basis of banding returns. *Circular of U.S. Department of Agriculture*. No.118
- Mace, R.D., Minta, S.C., Manley, T.L., Aune, K.A., 1994. Estimating grizzly bear population size using camera sightings. *Wildlife Society Bulletin* 22, 74–83.
- Manly, B.J.F, Amstrup S.C and McDoanld T.L 2005. Capture- recapture methods in practice. In: Amstrup S.C., McDoanld T.L. and Manly, B.J.F *Handbook of capture – recapture analysis*. Princeton University press, Princeton, New Jersey
- McDougal, C. 1977. *The Face of the Tiger*. London: Rivington Books.
- Nichols, J.D. 1992. Capture-recapture models: using marked animals to study population dynamics. *Bioscience*. 42: 94-102.
- Nichols, J.D. & Karanth. K.U. (2002). Statistical concepts: Estimating absolute densities of tigers using capture-recapture sampling. In *Monitoring Tigers and their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia*:121-138. Centre for Wildlife Studies, Bangalore, Karnataka, India.
- Nowell, K. & Jackson, P. 1996. *Wild Cats: Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland.
- O'Brien, T.G., Kinnaird, M.F., Wibisono, H.T., 2003. Crouching mtigers, hidden prey: Sumatran tiger and prey populations in a t tropical forest landscape. *Animal Conservation* 6: 131–139.
- Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monograph* 62: 1–35.
- Pant, P.C 1986 *Flora of Corbett National Park*,. Botanical Survey of India, Howrah, India pp 4-17

- Panwar, H. S. 1980. A note on tiger census technique based on pugmark tracings. *Cheetal* 22: 40-46.
- Parmenter, R. R., Yates, T. L., Anderson, D. R. et al. 2003. Small-mammal density estimation: a field comparison of grid-based vs web-based density estimators. *Ecological Monographs*. 73: 1-26.
- Peters, D.P.C and Herrick J.E. 2004 Strategies for ecological extrapolation *Oikos* 106: 627 - 636
- Peterson C.G.J (1889) Fisk. Bretn. Kbh, 1889-9. \*
- Pollock, K.H. and M.C.Otto. 1983. Robust estimation of population size in closed animal populations from capture-recapture experiments. *Biometrics* 39:1035-1049.
- Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. 1990 .Statistical inference for capture recapture experiments. *Wildlife Monographs*107:1-97.
- Qureshi, Q., Gopal R, Kyatham, S., Basu, S., Mitra, A., Jhala, Y.V. 2006. *Evaluating tiger habitat at Tehsil level*. Project Tiger Directorate, Govt. of India, New Delhi, and Wildlife Institute of India, Dehradun pp 162
- Rexstad, E., Burnham, K.P., 1991. *Use's Guide for Interactive Program CAPTURE Abundance Estimation of Closed Animal Populations*. Colorado State University, Fort Collins.
- Schaller, G.B., 1967. *The Deer and the Tigers: A Study of Wildlife in India*. University of Chicago Press, Chicago.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters* (2nd. edn). New York: Macmillan.
- Seidensticker, J. & McDougal, C. 1993. Tiger predatory behaviour, ecology and conservation. *Symp. Zool. Soc. Lond.* 65: 105-125.
- Sharma, S. Jhala, Y.V.&. Sawarkar, V.B 2005 Identification of individual tigers (*Panthera tigris*) from their pugmarks. *Journal of Zoology* 266: 1-10

Schnabel, Z.E. 1938. The estimation of the total fish population of a lake. *American Mathematical Monthly* 45:348-352.

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gomez, H., & Ayala, G. 2004. The use of camera traps for estimating jaguar (*Panthera onca*) abundance and density using capture/recapture analysis. *Oryx* 38: 148-154.

Silveira, L., Jácomo A.T.A. & Diniz-Filho, J.A.F 2003 Camera trap, line transect census and track surveys: a comparative evaluation *Biological Conservation* 114: 351-355

Singh, L. A. K. 1999. *Tracking tigers: guidelines for estimating wild tiger populations using the pugmark technique*. New Delhi: World Wide Fund for Nature-India.

Smallwood, K.S. & Fitzhugh, E.L. (1995). A track count for estimating mountain lion *Felis concolor californica* population trend. *Biological Conservation* 71: 251-59.

Smallwood K.S.& Schonewald C. 1996 Scaling population density and spatial pattern for terrestrial, mammalian carnivores. *Oecologia* 105:329-335

Smallwood K.S.& Schonewald, C. 1998 Study design and interpretation of mammalian carnivore density estimates. *Oecologia* 113: 474 - 491

Smith, J.L.D. 1993. The role of dispersal in structuring the Chitwan tiger population. *Behaviour* 124: 165 - 195

Smith, D. J. L., Sunquist, M., Tilson, R. & Wan Shahrudin, W. N. 2001 The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation* 4:75-79.

Soisalo, M. K. and Cavalcanti S, M. C. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*. 29: 487-496.

Sunquist, M. E., 1981. The social organization of tigers (*Pantheratigris*) in Royal Chitawan National Park, Nepal. *Smithsonian Contribution to Zoology*, 336:1-98

Sunquist, M. E., K. U. Karanth and F. Sunquist. 1999. *Ecology, behaviour and resilience of the tiger and its conservation needs*. In: Seidensticker, J., S. Christie and P. Jackson. *Riding the tiger. Tiger conservation in a humandominated landscape*. Cambridge, Cambridge University Press.

Thompson, W. L., G. C. White, and C. Gowan. 1998. *Monitoring vertebrate populations*. Academic Press, San Diego, USA.

Upreti, D. K. Chatterjee, S. 1999, A Preliminary Survey of Lichens From Corbett National Park Journal- *Bombay Natural History Society*. 96: 88-92

Wegge, P., Pokheral, C . Pd., Jnawali, S.R. 2004 Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. *Animal Conservation* 7: 251-256

White, G.C., Anderson, D.R., Burnham, K.P., Otis, D.L., 1982. *Capture-recapture Removal Methods for Sampling Closed Population*. Los Almos National Laboratory Publication LA-8787- NERP, Los Alamos.

Wikramanayake, E. D., Dinerstein, E., Robinson, J. G., Karanth, K. U., Rabinowitz, A. R., Olson, D., Mathew, T., Hedao, P., Conner, M., Hemley, G. & Bolze, D. 1998. An ecology based method for defining priorities for large mammal conservation: the tiger as a case study. *Conservation Biology*. 12: 865-878.

Wilson, K. R. and Anderson, D. R. 1985. Evaluation of two density estimators of small mammal population size. *Journal of mammology* 66: 13- 21

\* Secondary reference, original not seen.