ESTIMATING TIGER Panthera tigris POPULATIONS FROM CAMERA-TRAP DATA USING CAPTURE—RECAPTURE MODELS

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Abstract
The applicability of capture–recapture models for estimating tiger Panthera tigris numbers from camera-trap data was investigated in a part of Nagarabahole National Park, India during 12 months (387 trap-nights) in 1991–92. Camera-traps were placed along regular travel routes of tigers to obtain 31 photographic ‘captures’ of individual tigers in a 15 km² study area, during nine sampling occasions. Tigers could be identified unambiguously from photographs, and capture histories of 10 different animals were obtained. The data were analysed in the conceptual framework of capture–recapture theory, using probabilistic models. The results suggest that the closed capture–recapture model M₀, which allows for heterogeneity of capture probabilities among individual animals was appropriate for estimating tiger population size. The mean tiger numbers and their 95% confidence intervals were estimated at 11 (10–22) and 10 (10–15), respectively, with the M₀ (Jackknife) and M₀ (Chao) estimators. Considering the prey biomass available in the study area, the mean tiger densities of 13.3–14.7 adult/subadult tigers per 100 km² estimated from the above data appear to be reasonable. Capture–recapture models using camera-trap data offer scope for estimating objectively parameters such as size, density, survival, and recruitment for populations of tigers and other secretive animal species.

Keywords: tiger, population estimation, capture–recapture models, camera-traps, India.

INTRODUCTION AND OBJECTIVES
The tiger Panthera tigris has been used as a charismatic flagship species in the efforts to protect overall biodiversity in several Asian countries. Despite this, threats to its survival appear to have increased in recent years due to widespread overhunting of its prey (Karanth, 1991; Rabinowitz, 1991), poaching of tigers for commercial reasons (Jackson, 1993; Rabinowitz, 1993), and from habitat destruction (Seidensticker, 1986), combined with slackening protection efforts for socio-political reasons (Ghosh, 1993). However, despite the obvious importance of monitoring tiger populations in the protected areas, the approaches adopted by Asian wildlife managers to estimate tiger numbers have so far been totally divorced from the conceptual framework of modern population sampling methods. A partial exception to the above generalization has been the effort of Smith et al. (1987a), which synthesized prior information on tiger densities derived from radiotelemetry in Chitwan Park, Nepal, with assessments of habitat quality and prey abundance, using a GIS approach. Griffiths (1993) derived rough home-range size estimates for some tigers in Gunung Leuser Park, Indonesia from camera-trap photos. Rabinowitz (1993) assessed tiger populations in Thailand by combining subjective categorizations of habitat quality with arbitrarily assumed tiger densities. Most other tiger population estimates (e.g. Seal et al., 1987; Jackson, 1993) are based largely on unsubstantiated guesswork. The population estimates for India, which harbours a substantial proportion of surviving wild tigers, are derived from the demonstrably failure-prone and unvalidated (Karanth, 1987, 1988, 1993a, b) ‘pug-mark census’ method (Panwar, 1979) or its untested variants (Gore et al., 1993). Consequently, the resulting tiger population estimates do not appear to be meaningful in the light of what is known about tiger ecology (Schaller, 1967; Sunquist, 1981; Smith et al., 1987a; Karanth, 1993c). Further, because the above estimates are neither total counts nor sample statistics, they bear no logical or consistent relationship to the actual size of tiger populations. Therefore, they cannot be considered as indices of relative abundance.

Radiotelemetry provides data on tiger home range size and social organization, which can be used to derive estimates of densities (Sunquist, 1981; Smith et al., 1987a,b; Quigley, 1993; Karanth & Sunquist, unpublished data). However, the presence of untagged animals in the population, and the excessive effort involved in capture and radiotracking operations, limit the usefulness of this approach for estimating tiger population size.

Traditionally, capture–recapture techniques (Seber, 1982) have been employed to estimate population parameters for fish, birds and small mammals which cannot be easily counted using distance sampling methods, such as point and line transects (Buckland et al., 1993).
The theory and practice of capture-recapture methods have progressed far beyond the Peterson-Lincoln estimator and have recently undergone considerable development, as summarized by Nichols (1992). Recent probabilistic capture-recapture estimators can model a biologically important factor like capture probabilities being heterogeneous among individual animals in a population as a result of social structure. Current capture-recapture models also permit incorporation of other biologically relevant factors, such as behavioural response to trapping or temporal variation in capture probabilities. Recent comprehensive treatment of capture-recapture methods can be found in Otis et al. (1978), Seber (1982), White et al. (1982), Brownie et al. (1985), Nichols (1990), Pollock et al. (1990) and Lebreton et al. (1992). These analytical advances, coupled with the availability of user-friendly microcomputer software, now enable wildlife biologists to estimate the size and other parameters of animal populations with increased accuracy, precision and efficiency, using capture-recapture methods (Nichols, 1992).

Tigers are known to be individually identifiable from their stripe patterns (Schaller, 1967). They can also be photographed using camera-traps activated by the animals themselves (Champion, 1927; McDougal, 1977; Griffiths, 1993; Karanth, this study). However, obtaining a total count (census) of tigers using such pictures may involve excessive effort and still be dogged by uncertainty as to the completeness of the count. On the other hand, if a tiger population can be sampled by obtaining photographs of individual animals periodically within the framework of capture-recapture theory, it should be possible to estimate capture probabilities and population size with some degree of statistical rigor. This paper presents a preliminary appraisal of the first such attempt, based on data from a high-density tiger population in Nagarhole National Park, India. The objective of this appraisal was to provide preliminary answers to the following questions: (1) Can tiger populations be adequately sampled using camera-traps? Are capture-recapture model assumptions generally satisfied by camera trapping, and which models are most appropriate for tigers? (2) Can capture-recapture models be applied to camera-trap data to derive reasonable estimates of tiger population size? (3) Under which field conditions is this approach practical for estimating tiger numbers? Do camera-trap based capture-recapture models have further potential for estimating other population parameters such as density, survival and recruitment in tiger populations?

MATERIALS AND METHODS

The study area

This study was ancillary to a research project examining predator-prey relationships among large mammals in the tropical deciduous forests of the 644-km² Nagarhole National Park in southern India (11°50'-12°15' N Lat. and 76°0'-76°15' E. Long.). The bioclimate, soil, vegetation and wildlife communities of the area and of the surrounding regions have been described earlier (Meher-Homji, 1990; Karanth & Sunquist, 1992). Within the park, a 15-km² area, in and around the home range of a radiocollared tigress (Karanth & Sunquist, unpublished data) was selected for this study during the period February 1991–January 1992. Because of the high biomass of wild ungulate prey (about 5667 kg/km², Karanth 1993c), the tiger densities were also high in this study area.

Equipment

I used TrailMaster brand camera-trap units (manufactured by Goodson Associates, Lenexa KS 66215, USA), each consisting of one or two TM-35 camera kits (35 mm, autofocus, rangefinder type) triggered by one TM-1500 active infra-red trail monitor, for obtaining close-up photographs of tigers on 100 ASA colour print film. These units can be programmed to take pictures only between specified hours and only of animals above a predetermined body size. The unit also records the date and time for each exposure.

Field study design

Because tigers regularly used some forest roads and trails in the study area, as observed at other sites also (Panwar, 1979; Sunquist, 1981), camera traps were set at such optimal sites, after judging their frequency of use by tigers from tracks, scrapes, and scat deposition. The unit was mounted on wooden posts 3 m from the path, with the electronic beam set 45 cm above the ground. Although earlier workers (Schaller, 1967; McDougal, 1977) have used facial markings to distinguish individual tigers, because I was interested in noting the sex and age-class of the ‘trapped’ tigers by observing their relative body sizes and genitalia, an attempt was made to obtain broadside photographs. Since the flanks present a bigger and clearer target, I used body stripe patterns for identification, with the stripes on limbs, face, and tail providing additional supplementary information.

I used 15 different camera-trap sites spread throughout the area to ensure potential trap access to all transiting tigers. Since there were only two or three camera-traps, these were periodically moved among the

<table>
<thead>
<tr>
<th>Occasion</th>
<th>Period</th>
<th>Effort (trap-nights)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>February 1991</td>
<td>36</td>
</tr>
<tr>
<td>2</td>
<td>1–16 March 1991</td>
<td>36</td>
</tr>
<tr>
<td>3</td>
<td>17–31 March 1991</td>
<td>39</td>
</tr>
<tr>
<td>4</td>
<td>1–14 April 1991</td>
<td>46</td>
</tr>
<tr>
<td>5</td>
<td>15–30 April 1991</td>
<td>45</td>
</tr>
<tr>
<td>6</td>
<td>May 1991</td>
<td>45</td>
</tr>
<tr>
<td>7</td>
<td>June/July 1991</td>
<td>58</td>
</tr>
<tr>
<td>8</td>
<td>October/November 1991</td>
<td>47</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>387</td>
</tr>
</tbody>
</table>
sites. The total trapping period was partitioned into nine sampling occasions (White et al., 1982). Due to climatic and logistical constraints, the trapping efforts in each sampling occasion were not exactly equal. The details of the sampling scheme are in Table 1.

Assumptions and data analysis
Capture-recapture models can estimate parameters for both demographically closed and demographically open populations, but both types of models assume geographic closure. The assumption of demographic closure can be relaxed if mortality rates do not differ between marked and unmarked animals (White et al., 1982). For estimating the tiger population size (N) in this pilot study, I have assumed geographic closure around the sampled site, and demographic closure during the study period. The analysis was carried out using the computer program CAPTURE (White et al., 1982, updated version by Rexstad & Burnham, 1991). Since use of a typical trapping-grid (White et al., 1982) was not feasible in view of the need to select optimal trap locations, I could not use the density estimation options available in the program. I used CAPTURE to test statistically the closure assumption, to test the fit of the data to different estimators, and to compare models using the program's model selection procedure (White et al., 1982). Several estimators of population size are offered by program CAPTURE. The simplest is for the null model (M₀), which assumes that the time of capture, heterogeneity among individuals, or trap-response (behaviour) do not affect capture probabilities of animals in the population being sampled. In addition, there are two estimators for models of time effects on capture probability (M₁); two for models of heterogeneity effects (M₂); and one estimator each for models of behaviour effects (M₃), time and heterogeneity effects (M₄), and for time and behaviour effects (M₅). There are two estimators modeling the effect of behaviour and heterogeneity effects (M₆). Detailed accounts of the theory and analytical procedures involved have been published by Otis et al. (1978), White et al. (1982) and Rexstad and Burnham (1991).

RESULTS AND DISCUSSION

Sampling effort
A total of 387 trap-nights of sampling effort was expended spread over 12 months (Table 1). Despite the high density of tigers in the area, about 15 rolls of 36-exposure film were expended to obtain 31 usable pictures (captures) of tigers. The average trapping effort was 12.5 trap nights per capture, and the quantity of film expended was about 18 frames per capture. The film expenditure was high because of frequent tripping of cameras by other mammal species, particularly elephants Elephas maximus. Since I was using only two or three units at any given time, it appears that if a larger number of camera-traps could be deployed, sampling intensity could be increased to enable greater area coverage or to sample tiger populations at lower densities with adequate intensity. Unlike in Nagarahole, if interference from other animals or humid weather are not problems, less expensive, pressure-pad activated camera-traps can be used.

Identification of individual tigers
The photos obtained were of high quality, and were useful for distinguishing different individual tigers unambiguously, even when partial photos where obtained (Fig. 1). Tigers could be identified clearly even when the same animal was photographed in varying postures or from very different angles (Fig. 2). The stripe patterns were asymmetrical on two flanks of the same animal (Fig. 3). However, I was able to link the left and right profiles of some tigers with the help of additional daylight photos and videotapes of animals obtained by chance, and in other cases by eliminating duplication based on size, sex, or by the presence of radiocollars. However, because of the marked asymmetry in stripe patterns, in any future study it is essential to identify tigers by obtaining pictures of both flanks simultaneously. This can be a problem due to mutual interference between the camera flashes. Another approach would be to photograph one flank, and simultaneously a frontal photo. Otherwise, two separate data-sets consisting of 'captures' of left and right profiles will be obtained, with the attendant sample size reduction and related statistical problems. Another alternative is to only use frontal pictures, but this entails losing information on

Fig. 1. Example of unambiguous individual identification of tigers T-108 (top) and T-105 (bottom) using camera-trap photos of stripe patterns on the flanks. Note the usefulness of even partial photographs.
sex and size of the animal. In addition to camera-trap photos, I was able to use three instances of 'recaptures' of two individual tigers from daylight photos obtained during chance encounters, based on the reasonable assumption that all animals in the area have similar probabilities of being encountered casually.

Capture histories and sample statistics
The capture histories of the ten individually identified tigers which used the study area are given in Table 2, and the summarized capture statistics (Otis et al., 1978), in Table 3. These data enable computation of capture frequencies which show that two individual tigers were captured only once, five were caught twice, two were caught five times, and one animal was caught six times during the sampling period.

The null hypothesis assumes that population closure could not be rejected (z=-1.18, p=0.12). White et al. (1982) recommend that closed capture-recapture models should ideally not be used to estimate the size of small populations (n<20), a condition which was probably not met in this pilot study.

Model selection
The hypothesis that the above capture-recapture statistics come from an underlying null model $M_0$ could not be rejected in contrast to the alternative hypotheses of the underlying models being, respectively, $M_1 (x^2=8.14$, Table 2. Capture histories of individually identified tigers in Nagarahole, India

<table>
<thead>
<tr>
<th>ID no.</th>
<th>Capture history*</th>
</tr>
</thead>
<tbody>
<tr>
<td>T-002</td>
<td>Adult female, radiocollared 0111110101</td>
</tr>
<tr>
<td>T-003</td>
<td>Adult male, radiocollared 0001100000</td>
</tr>
<tr>
<td>T-004</td>
<td>Adult male, radiocollared 0010111011</td>
</tr>
<tr>
<td>T-102</td>
<td>Subadult female 1000000000</td>
</tr>
<tr>
<td>T-103</td>
<td>Adult male 1100011010</td>
</tr>
<tr>
<td>T-104</td>
<td>Subadult male 1000000000</td>
</tr>
<tr>
<td>T-105</td>
<td>Adult female 1010000000</td>
</tr>
<tr>
<td>T-107</td>
<td>Subadult female 0001100000</td>
</tr>
<tr>
<td>T-108</td>
<td>Adult female 0000001011</td>
</tr>
<tr>
<td>T-110</td>
<td>Adult male 0000000111</td>
</tr>
</tbody>
</table>

*1, capture; 0, no capture. The nine sequential positions of these notations represent the successive sampling occasions during 1991–92.

Table 3. Summary of capture-recapture statistics for tigers obtained from camera-trap sampling in Nagarahole, India, during 1991–92

<table>
<thead>
<tr>
<th>Sampling occasion (j)</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Animals caught ($n_j$)</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Total caught ($m_j$)</td>
<td>0</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>Newly caught ($\mu_j$)</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

$n_j$, no. of animals captured on the $j$th sampling occasion.
$m_j$, no. of previously caught animals before the $j$th sampling occasion.
$\mu_j$, no. of new animals captured in the $j$th sample.
Tiger populations in Nagarahole

Since population size (N) is not normally distributed, it may not be appropriate to use the estimated mean and its standard error (SE) to construct the usual asymptotic 95% confidence intervals. Further, such an approach can sometimes lead to an illogical situation where the lower bound of the confidence interval is less than the number of distinct individuals captured during the study. To overcome this problem, the confidence intervals constructed by CAPTURE assume a log-normal distribution for the number of animals not captured at all during sampling (Rexstad & Burnham, 1991). The lower bound of this log-normal based confidence interval (N_10) equals the number of distinct animals captured, but the upper bound may sometimes be higher than N+1-96 SE. The estimates of population size along with the standard error, 95% confidence interval, and the average capture probability (p), derived using models M_n, M_h (Jackknife) and M_a (Chao) are shown in Table 4. It can be seen that all three estimates of N are similar (10-11), and in this case, close to the number of distinct tigers identified. As argued earlier, the extremely narrow confidence interval estimated under model M_n is likely to be an artifact of small sample size, and the confidence intervals under model M_h are most likely to include the true value of N. The interval estimated by estimator M_a (Chao) as 10–15 is narrower than the interval of 10–22 generated by M_h (Jackknife) estimator.

To obtain a preliminary estimate of tiger densities in the study area, I have assumed that although the traps were set within a 15-km² area, the estimated population size pertains to a 'catchment' area which includes the home ranges of five resident females (the radiocollared female T-002 and her four neighbours) or about 75 km², which also contains other transient tigers which had some probability of being captured in camera-traps. Based on the estimated mean values of population size from M_n (Chao) and M_h (Jackknife), respectively, densities in the study area appear to be about 13.3–14.7 tigers per 100 km² (6.8–7.5 km² per tiger). Considering the available ungulate prey biomass density of 5667 kg/km² (Karanth, 1993c), and, assuming an annual biomass cropping rate of 8% by tigers together with an average kill rate of 3000 kg/year per tiger (Sunquist, 1981), the Nagarahole study area seems to be capable of supporting densities of up to 15–100 tigers/100 km², suggesting that tiger density estimates derived from capture–recapture model M_n are not unreasonable.

However, it should be noted that the capture records from camera-traps do not appear to include tigers less than 8–10 months of age. The capture probabilities for small cubs in particular may be very low or even zero, requiring separate estimates based on numbers and reproductive status of resident females. However, this pilot study suggests that the camera-trap based capture–recapture methodology offers a promising new approach to obtain objective estimates of population size for adult and subadult tigers. The method also has potential applicability to the study of other secretive animals which have distinctive natural markings. Such species include leopard, jaguar, snow-leopard, clouded leopard and perhaps other spotted or striped carnivores.

Capture–recapture models have also been developed for estimating parameters such as population size, survival and recruitment in demographically open populations (Seber, 1982) through long-term studies. Therefore, there appears to be scope for expanding camera-trap based capture–recapture studies of tigers (and of other species with distinctive markings) to incorporate robust study designs which combine the best features of both closed and open models (Nichols, 1990, 1992; Pollock et al., 1990; Lebreton et al. 1992). Such an approach seems to offer considerable potential for estimating several problematic population parameters for many secretive animal species.

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