# Assessing the viability of tiger subpopulations in a fragmented landscape

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## Summary

**1.** Conservation managers require accurate and timely information on the occurrence, size and viability of populations, but this is often difficult for cryptic species living at low densities over large areas. This study aimed to provide such information for tigers in the 36 400-km$^2$ Kerinci Seblat (KS) region, Sumatra, by identifying and assessing subpopulation viability under different management strategies.

**2.** Tiger occurrence was mapped within a geographical information system (GIS) using repeat detection–non-detection surveys to incorporate a function of detection probability into a logistic regression model. The landscape variables that influenced tiger occupancy were then used to construct a spatially explicit habitat model to identify core areas.

**3.** The number of tigers within each core area was estimated by calculating the area of different forest types and their respective tiger densities as determined through camera trapping. The viability of each subpopulation was then assessed under different management scenarios using a population viability analysis (PVA).

**4.** Tiger occurrence was negatively correlated with distance to public roads. Four core tiger areas were identified, all predominantly located within KS National Park, estimated to support subpopulations of 21, 105, 16 and three adult tigers, respectively. PVA showed that the three larger subpopulations could be demographically viable if well protected. However, if poaching removed ≥ 3 tigers per year, then only the largest subpopulation would not reach extinction within 50 years. Connectivity to this large subpopulation would ensure survival of the smaller subpopulations, through providing a source of tigers to offset poaching losses.

**5.** *Synthesis and applications.* Our key management recommendations for tigers in the Kerinci Seblat region of Sumatra stress the importance of maintaining connectivity between the smaller areas and the larger area, and minimizing poaching within these smaller areas. More widely, our research has shown the feasibility of using detection–non-detection surveys combined with spatial modelling to provide timely information for conservation management.

*Key-words*: detection probability, GIS, logistic regression, population viability, spatially explicit habitat model, Sumatran tiger

## Introduction

Conservation managers often need to determine the occurrence, number and population viability of cryptic species living at low densities and over large areas. However, this can present a dilemma. On the one hand, conservation managers may begin to implement strategies based, at best, on crude population estimates or guesses, which in turn may lead to the wrong management approach (Blake & Hedges 2004). On the other hand, by stressing the need for accurate information requiring investment of substantial time and money,

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conservation managers may procrastinate before taking any management action. Therefore, conservation managers require rapid yet rigorous population census methods, and the means to model the results in a meaningful and pragmatic way that leads to improved and timely species management strategies. Such requirements are pertinent for many top terrestrial carnivores.

To overcome these management problems, previous studies on large carnivores have used presence–absence data within logistic regression modelling to investigate factors that determine species occurrence, and a geographical information system (GIS) to construct spatially explicit habitat models (SEHM) (Palma, Beja & Rodrigues 1999; Schadt *et al.* 2002). Using emerging techniques, biases associated with a failure to differentiate 'absent' and 'undetected' can be avoided by explicitly incorporating detection probability estimates through repeated detection–non-detection surveys (MacKenzie *et al.* 2002; Tyre *et al.* 2003).

The detection–non-detection method assumes that all cells are either occupied or unoccupied. Ideally, three cases would be distinguished, true absences (where no sign is detected because the cell is not within an animal's home range), false absences (where no sign is detected even though a sign exists within the cell) and pseudo-absences (where no sign exists within the cell but, none the less, the cell occurs within an individual's home range). The latter situation is likely to arise when cells are small compared with a large carnivore's home range, as a cell may be occupied (i.e. within an individual's home range) but may contain no sign if that individual has not passed through recently. Of these three cases, false absences can be differentiated from true or pseudo-absences by surveying each cell more than once, ideally within a short time period (i.e. a few days) (MacKenzie & Royle 2005). If the interval between surveys is short, the probability with which a sign is detected when present can be estimated from the frequency with which a sign is recorded in a given cell in some surveys but not in others. True absences and pseudo-absences cannot be differentiated and so 'occupancy' measured in these studies may be more usefully thought of as 'usage' (MacKenzie 2005). By surveying large areas in this way, relative use of different habitat types can still be estimated because cells in better quality habitat would still be expected to be visited more often and have a greater likelihood of containing a sign than cells located in poorer quality habitat.

Construction of a SEHM using the detection–non-detection approach can identify habitat suitability and the proportion of a species' range actually occupied, rather than assigning arbitrary cut-off values for habitat suitability (Lennon 1999). Furthermore, SEHM can be used to estimate carnivore population sizes, and these may be combined with population viability analyses (PVA) to determine extinction risks under different management strategies and scenarios (Coulson *et al.* 2001; Carroll *et al.* 2003).

The tiger *Panthera tigris* is a cryptic top predator that lives in diverse environments. Three out of eight tiger subspecies have already been driven to extinction by widespread habitat clearance, human over-hunting of prey and use of tiger parts in traditional Chinese medicine and other trade (Nowell & Jackson 1996). To prevent further losses of tigers across Asia, conservationists have focused funds and effort on tiger conservation units (TCU) (Wikramanayake *et al.* 1998). Yet, there is little or no detailed monitoring information on tiger populations in many of the most important level 1 TCU, making it difficult to evaluate tiger conservation strategies systematically. While camera trapping has provided reliable and detailed information on tiger densities (Karanth & Nichols 1998; Kawanishi & Sunquist 2004), it is expensive, requires skilled personnel and can only cover a small area (< 400 km$^2$) over a relatively long time period (4–6 months). Through camera trapping alone, it would take many years to obtain sufficient monitoring data for tiger populations over large (> 10 000-km$^2$) TCU. Therefore, it is critical to develop a rapid, accurate and comparable survey method that all field staff can use to determine the occurrence of tigers across key TCU.

In this study, we combined a rapid census method with a spatial and population modelling approach to identify tiger subpopulations and assess their viability in the Kerinci Seblat (KS) region, Sumatra, a level 1 TCU for which limited information on tiger populations had been previously available. Specifically, we aimed to (i) use field data on tiger distributions analysed with logistic regression modelling to map probabilities of tiger occurrence throughout the KS region, and (ii) parameterize a PVA, to assess the consequences of different management strategies for the viability of these tiger subpopulations.

## Methods

### STUDY AREA

Located in west-central Sumatra, Indonesia (−3°57′ to −0°53′, 100°38′ to 102°95′), the KS region covers an area of some 36 400 km$^2$ (Fig. 1). It lies within a warm per-humid bioclimate (Whitmore 1984) that supports four broad forest types: lowland hill (0–300 m a.s.l.), hill (300–800 m a.s.l.), submontane (800–1400 m a.s.l.) and montane (1400 + m a.s.l.) (adapted from Laumonier 1994). The 13 300-km$^2$ KS National Park (KSNP) contains large blocks of forest that extend outside to form a level 1 TCU. Nevertheless, agricultural expansion has fragmented KSNP into two parts and poaching of tiger prey has degraded habitat quality in sections of KSNP (Linkie *et al.* 2003).

### FIELD DATA COLLECTION

The KS region was divided into a 2 × 2-km grid of 5262 cells. A stratified sampling approach was used to select 200 cells representing the main habitat types and various distances from the forest–non-forest edge. Detection of tigers (defined as presence of tracks and/or faeces) was
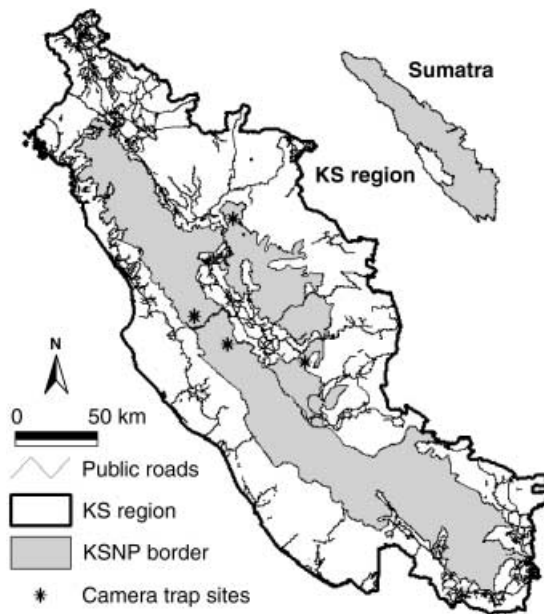
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Ecological Society,
*Journal of Applied
Ecology*, **43**,
576–586

**Fig. 1.** The Kerinci Seblat (KS) region of Sumatra, showing the position of the KS National Park (KSNP) boundary, public roads and camera trap sites.

determined from transects walked by three independent teams consisting of field researchers and KSNP staff during the rainy seasons of 2001 and 2002. Each cell that was resurveyed was re-entered within 1 week of the first survey in that cell. Forty cells were resurveyed on a third occasion, but the remaining 160 cells were not resurveyed for a third time because of field personnel constraints.

Within each selected cell, transects averaging 2·47 km in length were surveyed. To maximize the probability of encountering tiger signs, transects followed pre-existing animal trails or topographic features such as mountain ridges, which tigers often use as travel corridors (O'Brien, Wibisono & Kinnaird 2003). The location of each transect was recorded in universal transverse mercator (UTM) coordinates using a Garmin 12XL global positioning system (GPS) (Garmin Corp., Ulathe, KA) and compass bearings with 1 : 50 000 topographic paper maps.

### GIS DATABASE AND PREPARATION

Although prey abundance is likely to be a primary determinant of tiger abundance (Karanth *et al.* 2004), data on prey densities were unavailable for the KS region. We therefore assessed seven other parameters as potential predictors of tiger occurrence: mean proximity to public roads, logging roads, settlements and rivers, as well as altitude, slope and protected status.

The 2 × 2-km sampling grid was superimposed onto a forest cover map developed for the KS region by on-screen digitizing five corresponding Landsat 7 ETM+ satellite image scenes from 2001. For each grid cell, altitude, slope, rivers, public roads, settlements and boundaries of KSNP were obtained from 1 : 50 000 maps

produced by the Indonesian National Coordination Agency for Surveys and Mapping (Bogdor, Indonesia). Grid cells of which more than 50% was occupied by KSNP were classified as protected. The position of logging roads was identified from GPS location data collected from field surveys and on-screen digitizing of satellite images from 2000 to 2002, verified from field surveys using GPS units. These data were imported into an ArcView v3·2 GIS software package (ESRI Inc., Redlands, CA) and converted into a 100-m$^2$ raster format.

The continuous data were extracted for each cell, logarithmically transformed and imported into PRESENCE software (Proteus Wildlife Research Consultants, New Zealand). Tiger detection (1) and non-detection (0) data were then entered to provide information on the detection history of each sampling cell for each sampling occasion.

### STATISTICAL ANALYSIS AND MODEL DESIGN

#### Mapping probability of tiger occurrence

Three sequential steps were used to obtain unbiased estimates of the proportion of area occupied (PAO) by tigers in the KS region. First, from the observed data (440 cells surveyed) PRESENCE predicted a tiger detection probability, as tigers will not always be detected within a cell that they have been using during the survey period. Secondly, this detection probability ($p$) was incorporated into a logistic regression analysis to determine which of the seven landscape factors, individually or in combination, best explained the probability of tiger presence ($\psi$). Thus, in PRESENCE, different models to explain detection probabilities were compared. Models included detection probability as a constant, $p(\cdot)$, or as affected by different combinations of site-specific covariates, such as altitude, $p$(Elevation) (MacKenzie *et al.* 2002). Candidate models were ranked by their Akaike information criterion (AIC) values (Burnham & Anderson 1998). Thirdly, the best candidate model was used to determine the PAO by tigers for the KS region. The presence of spatial auto-correlation in the final model was then tested by calculating Moran's *I* statistic (Cliff & Ord 1981) using the Crime-Stat v1·1 software (N Levine & Associates, Annadale, VA).

From the final logistic regression model the probability of tiger presence ($P$) was constructed by:

$$P = e^{Y}/(1 + e^{Y}) \qquad \text{eqn 1}$$

where:

$$Y = \beta_0 + \Sigma \beta_i X_i \qquad \text{eqn 2}$$

$\beta_0$ is the constant coefficient (intercept); $\beta_1$, $\beta_2$ … $\beta_i$ represent selected independent variable coefficients; $X_1$, $X_2$ … $X_i$ represent their associated independent variables.

The SEHM predictions of the probability of tiger presence were validated using tiger encounter rate data derived from an independent camera trapping survey

(see below). To minimize problems with spatial auto-correlation, 50 camera traps, greater than 2 km apart, were randomly selected and their respective tiger encounter rate calculated (tiger photographs/100 days) and SEHM score extracted from the corresponding cell. Spearman's rank correlation ($r_s$) was used to test whether observed tiger encounter rates were correlated with expected SEHM scores.

Next, the tiger SEHM was reclassified to include only those cells with the highest habitat suitability values, which corresponded to the PAO by tigers (previously estimated in PRESENCE). This showed the locations of discrete tiger subpopulations, which we defined as core habitat areas and treated independently thereafter. We excluded areas of less than 200 km² and areas that were not connected to KSNP (and therefore not under park management jurisdiction). Tiger density varies with prey biomass (Karanth *et al.* 2004). We did not have estimates of prey biomass but this factor was assumed to vary with habitat type. Consequently, the amount of lowland hill, hill, submontane and montane forest in each core area was calculated to allow an estimation of tiger carrying capacity in each core, as described in the next section.

### Estimating tiger subpopulation sizes

For each core area, cameras were placed within a grid formation at 1–4-km spacing for 4–5 months. To increase the chances of photographing every tiger that entered the study site, placements covered all main ridge and animal trails, leaving no apparent gaps in the trapping area. Camera placements recording few or no tiger photographs were moved to another location within the same cell. Respectively, in the lowland hill, hill, submontane and montane sites, 29, 28, 33 and 16 camera stations operated for a total of 762, 1848, 950 and 958 trap nights. All study sites had evidence of human disturbance, i.e. human signs (footprints and litter) and snare traps set for tiger prey. These sites were considered to be representative of other forest patches in KSNP. Two methods were then used to estimate tiger density in the four different habitat types.

First, tiger density in lowland hill, hill and submontane forest was estimated using a capture–recapture method (Karanth & Nichols 1998). Closure tests were performed using CAPTURE software to verify that each tiger population was closed (i.e. no births, deaths, immigrations or emigrations) during the duration of the respective camera trap surveys. In CAPTURE, tiger capture probability ($\hat{p}$) and abundance ($\hat{N}$) were estimated using model $M_h$ because it is more robust and, by incorporating heterogeneous capture probabilities, produces more realistic estimates than the six other models (Rexstad & Burnham 1991; Karanth & Nichols 1998). Tiger density was then calculated by dividing the $\hat{N}$ by the effective sampling area, calculated within the GIS as the camera trapping area plus a boundary strip width around the outermost cameras (Wilson & Anderson 1985).

Second, because of the lower number of individual tigers photographed ($M_{t+1}$) in montane forest, it was not appropriate to apply the capture–recapture method because surveying in habitats where tiger population densities are very low would have required an unrealistically large amount of time and funds. Instead, an empirical relationship between camera trap-derived encounter rates ($x$) and tiger density ($y$), based on 19 studies throughout the tiger's range, was used (Carbone *et al.* 2001):

$$y = 133 \cdot 89x^{-0 \cdot 971} \qquad \text{eqn 3}$$

This method, whilst not as statistically robust as the capture–recapture method (Jennelle, Runger & MacKenzie 2002; but see Carbone *et al.* 2002; O'Brien, Wibisono & Kinnaird 2003), enabled an assessment of tigers in the montane forest study area. For this empirical relationship, it was necessary to estimate 95% prediction intervals (PI), using a standard quadratic formula (Snedecor & Cochran 1989; as in Jennelle, Runger & MacKenzie 2002) instead of 95% confidence intervals (CI) because the density value was derived from an equation of which it was not originally a part.

Finally, this encounter rate method was also used to estimate tiger densities in the lowland hill, hill and submontane sites for comparison with their previously estimated CAPTURE-derived densities.

Using the tiger density estimates from each habitat type and the amount of habitat type in each core area, the number of individual adult tigers that could be supported in each core area was estimated.

### Population viability model design

The viability of different sized tiger subpopulations to demographic stochasticity and varying poaching pressures was calculated by developing a tiger-specific stage-structured model with a 1-year step using unified life models software (Legendre & Clobert 1995). This model considered a population as viable if its extinction probability was lower than 5% within 50 years of simulation (Tufto *et al.* 1999; Chapron *et al.* 2003).

### Population viability model parameters

Our model was based on the same life-history attributes and stages as Karanth & Stith (1999), which included male and female cubs, juveniles, transients and territorial breeders (Table 1). Young male and female tiger cubs dispersed and became transients at age 2, when they started searching for a vacant territory to occupy for breeding. Thus, only adult individuals that had already settled in a territory could reproduce. Transients initially tried to settle within territories in their natal core subpopulation area but, if there were no territories available, then they would disperse and search in connected core areas. Transients died if they failed to settle in their natal core area or subsequently in adjacent, connected areas that were fully occupied. Hence density-independent

**Table 1.** Tiger life-history attributes used in the simulation model, based on field data on tigers (Sunquist 1981; Smith, Wemmer & Mishra 1987; Smith & McDougal 1991; Smith 1993). Leopards (Martin & de Meulenaer 1988; Bailey 1993) and cougars (Lindzey *et al.* 1992; Laing & Lindzey 1993; Lindzey *et al.* 1994)

| Class | Yearly survival probability |
| --- | --- |
| Cub (0–1 years) | 0·6 |
| Juvenile (1–2 years) | 0·9 |
| Transient female (2–3 years) | 0·7 |
| Transient male (2–3 years) | 0·65 |
| Breeding female (> 3 years) | 0·9 |
| Breeding male (> 3 years) | 0·8 |

population growth was assumed up to the maximum number of tigers in a subpopulation. We assumed density independence below the ceiling because there were no data available to parameterize a density-dependence function (Wielgus 2002).

Karanth & Stith (1999) modelled male density as a function of female density. In contrast, in our model male density was an emergent property of the number of occupied and vacant territories and incoming transients. That male numbers could fluctuate because of intraspecific competition was not considered because the number of females in a population is usually the limiting resource (Kenney *et al.* 1995).

The demographic parameters used for the model comprised an age of first reproduction of 3 years, equal sex ratio at birth, mean litter size of three cubs and interbirth interval of 2·5 years. By dividing mean litter size (3) by mean interbirth interval (2·5), we calculated the annual mean litter size (1·2). Demographic stochasticity was applied to both survival and fecundity. Class survival followed a binomial distribution, where class survival was parameterized and a random number was drawn from a Bernoulli trial resulting in a tiger surviving if the result was '1' and dying if the number was '0'. Fecundity followed a Poisson distribution with mean litter size as a parameter. Our model did not consider environmental stochasticity because there were no available data to parameterize this.

The model considered the spatial arrangement of subpopulations but did not mimic a spatial arrangement of territories within subpopulations. Each subpopulation was characterized by a maximum number of territorial breeders and a maximum number of tigers. The female : male ratio was 3 : 1 among breeder territories (Sunquist 1981). We assumed that only the proportion of the best habitats indicated by the estimate of PAO were occupied. Combining that proportion with the probability of tiger presence gave estimates of current core population sizes. Clearly, however, ceiling subpopulation sizes would only be reached if all available habitat was occupied. Consequently, to derive theoretical ceiling subpopulation sizes for the PVA, we used PAO = 1·0 and estimated potential subpopulation sizes accordingly.

Tiger poaching was modelled randomly and specified that all life stages except cubs could be poached (Table 1). Survival of these stages was determined by multiplying them by the probability of not being poached $(1 - po)$, where $po$ is the number of poached tigers divided by the number of individuals in the targeted classes. Poaching was modelled as being completely additive to initial mortality, resulting in more conservative estimates of viability. When a tigress with cubs aged 0–1 years died (either naturally or through poaching), her whole litter died.

### ASSESSING MANAGEMENT ALTERNATIVES

The tiger subpopulations identified in each core area were used to model three scenarios to generate predictions of extinction probabilities when subpopulations were (i) isolated with varying poaching pressures, (ii) connected with varying poaching pressures and (iii) connected with varying poaching pressures, with adjacent subpopulations completely protected from poaching. For each scenario, Monte Carlo simulations were run with 1000 repetitions for a duration of 50 years. A subpopulation qualified as extinct once all classes were empty.

#### *Scenario 1: isolation*

The viability of each subpopulation was determined under poaching pressures ranging from no to five tigers removed per year. There was no dispersal among subpopulations.

#### *Scenario 2: connectivity*

The viability of each subpopulation was determined under poaching pressures ranging from no to five tigers removed per year but subpopulations were assumed to be connected (by dispersal) to the nearest neighbouring subpopulation. Interconnection was modelled by corridor permeability, which allowed either 25% or 50% of transients from one subpopulation to search and settle within territories in an adjacent and connected subpopulation, if no vacant territories were available in their own area.

#### *Scenario 3: connectivity with anti-poaching measures*

The PVA models were repeated as for scenario 2, but anti-poaching measures were incorporated into the models. Using different combinations of connectivity with the different levels of poaching, each of the connecting core areas was designated as having no poaching, i.e. being the focus of successful anti-poaching measures.

### Results

#### MAPPING PROBABILITY OF TIGER OCCURRENCE

From the three occasions ($n$ = 440 cells), tigers were detected in 16·5% of sampling cells on the first occasion,

**Table 2.** Summary of model selection procedure and parameter estimate (with 1 SE in parentheses) for tigers in the Kerinci Seblat region using three sampling occasions

| Model no. | Model | $K$ | AIC | $\Delta$AIC | $w_i$ | PAO ($\pm$ SE) |
|---|---|---|---|---|---|---|
| 1 | $\Psi$(Dist. public roads)$p$(Dist. public roads) | 4 | 370·20 | – | 0·61 | 0·442 (0·053) |
| 2 | $\Psi$(Dist. public roads)$p(\cdot)$ | 3 | 371·11 | 0·91 | 0·39 | 0·435 (0·054) |
| 3 | $\Psi$(Dist. settlements)$p(\cdot)$ | 3 | 394·71 | 24·51 | 0·00 | 0·427 (0·056) |
| 4 | $\Psi$(Dist. settlements)$p$(Dist. public roads) | 4 | 396·11 | 25·91 | 0·00 | 0·422 (0·054) |
| 5 | $\Psi(\cdot)p(\cdot)$ | 2 | 407·15 | 36·95 | 0·00 | 0·427 (0·059) |
| 6 | $\Psi(\cdot)p$(Dist. public roads) | 3 | 409·14 | 38·94 | 0·00 | 0·425 (0·060) |

$\Psi$ is the probability a site is occupied by tiger and $p$ is the probability of detecting tiger in the $j$th survey where $\Psi(\cdot)p(\cdot)$ assumes that tiger presence and detection probability are constant across time and sites, $t$ is the survey effects, $K$ is the number of parameters in the model, $\Delta$AIC is the difference in AIC values between each model with the low-AIC model and $w_i$ is the AIC model weight. Dist. distance.

in 21% of sampling cells on the second occasion and in 20% of sampling cells on the third occasion. Only two models explaining tiger detection received strong support (models 1 and 2; Table 2) and together these had an Akaike weight of 1·0. Both of these models included distance to roads as an important parameter. Model 1 had the highest Akaike weight and suggested that tiger occupancy rates were higher further from public roads, while detection rates were also influenced by proximity to roads. Model 1 had a tiger detection probability of 0·51 ($\pm$ 0·02 SE), the most precise PAO estimate, indicated by having the smallest SE, and was not affected by spatial autocorrelation (Moran's $I = 0·04$, $P > 0·1$). The result of this model was used to construct the SEHM.

The tiger SEHM was constructed from a single factor, $\log_{10}$ distance to public roads. It showed that good-quality tiger habitat predominantly occurred inside KSNP (Fig. 2). Although large blocks of forest habitat did occur outside KSNP, particularly in the north, the position of this forest in relation to public roads reduced it to poor-quality tiger habitat.

The SEHM predictions of the probability of tiger presence were positively correlated with tiger encounter rates that were derived from independent camera trap data ($n = 50$, $r_s = 0·398$, $P = 0·004$).

### ESTIMATING TIGER SUBPOPULATION SIZES

The final logistic regression model gave an overall estimate for the PAO by tigers of 0·442 ($\pm$ 0·053 SE), which represented 44·2% or 9344 km$^2$ of the 21 141 km$^2$ of forest remaining in the KS region. Using the SEHM, 9344 km$^2$ of the most suitable forest habitat was selected from the KS region. This identified seven core areas. However, by then excluding those patches < 200 km$^2$ or not connected to KSNP, only four isolated patches, or core areas, remained (Fig. 3).

The distribution of different forest types showed that core 2 not only had the largest blocks of forest (5712·6 km$^2$) but these were mainly composed of lowland hill and hill forest tiger habitat. In contrast, cores 1 (1574·6 km$^2$), 3 (1198·3 km$^2$) and 4 (206·7 km$^2$) were predominantly submontane and montane forest habitat.

KS region
KSNP border
Probability of tiger occupancy
0–0·1
0·1–0·2
0·2–0·3
0·3–0·4
0·4–0·5
0·5–0·6
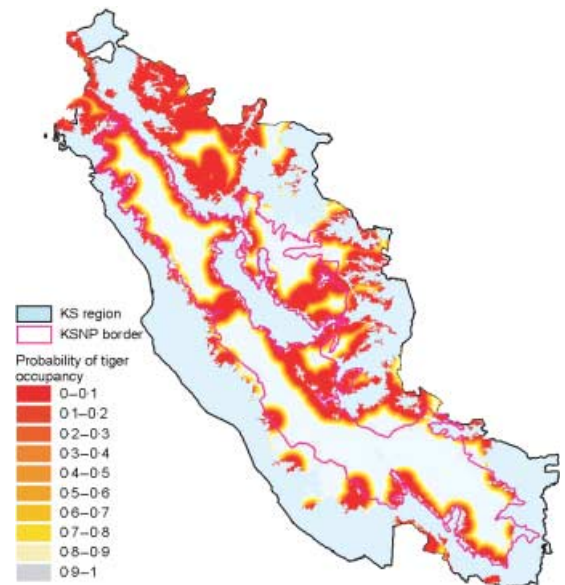0·6–0·7
0·7–0·8
0·8–0·9
0·9–1

**Fig. 2.** Tiger habitat suitability for forested areas in the Kerinci Seblat (KS) region.

From camera trapping in the lowland hill, hill and submontane study sites, respectively, closure tests did not reject the null hypothesis that the population was closed during the period of camera trapping ($z = -1·107$, $-1·048$ and $1·113$, $P = 0·134$, $0·147$ and $0·867$). Respectively, six individual tigers were identified from 15 tiger photographs, five individuals from 50 tiger photographs and five individuals from 12 tiger photographs, with estimated capture probabilities of 0·1633, 0·3611 and 0·2143 and tiger abundances of $7 \pm 2·65$ (SE), $6 \pm 1·28$ and $6 \pm 1·87$ (Table 3). Model M$_h$ in CAPTURE was ranked second to the null model M$_o$ in all sites. However, model M$_h$ was selected in preference because it was a more realistic model that assumed each individual tiger had a unique capture probability (Karanth & Nichols 1998; Kawanishi & Sunquist 2004). These tiger densities were similar to those derived using the encounter rate indices method (Table 3).

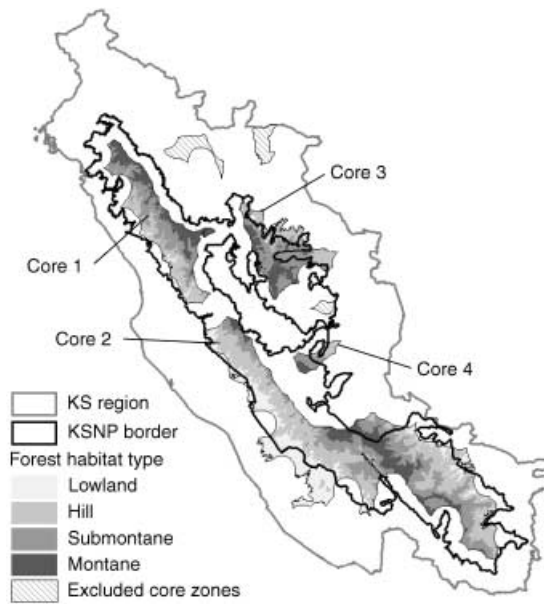The different combinations of size and habitat types for each core area resulted in a total population of 145

**Fig. 3.** Core tiger habitat representing four tiger subpopulations and the distribution of their forest types in the Kerinci Seblat (KS) region.

adult tigers, with individual subpopulations that comprised 21 (core 1), 105 (core 2), 16 (core 3) and three adult tigers (core 4) (Table 4).

### ASSESSING MANAGEMENT ALTERNATIVES

For the PVA modelling, the ceiling adult tiger subpopulations, which assumed that all tiger habitat was occupied (PAO = 1·0), were set at 42 (core 1), 164 (core 2), 38 (core 3) and 15 adult tigers (core 4). The PVA modelling of

various scenarios of poaching rate, from no to five tigers per year, and connectivity between core subpopulations at 0%, 25% and 50%, produced different predicted probabilities of extinction during simulations over 50 years (Fig. 4a–d). For example, under the worst scenario, where the smallest subpopulations in cores 1, 3 and 4 were subjected to five tigers poached per year and 0% connectivity, the predicted probabilities of these subpopulations going extinct were all $P > 0.98$ (Fig. 4a). In contrast, under the best scenario, where the largest subpopulation of core 2 had poaching eliminated (i.e. #2) and was connected at 50% to core 1 or 4 (i.e. '1→#2; at 50%' and '4→#2; at 50%', respectively), the predicted probability of extinction in cores 1 and 4 was greatly reduced ($P < 0.01$ for both; Fig. 4d).

The most substantial change in subpopulation viability was predicted to occur on cores 1 and 3. If subjected to poaching levels of $\geq 3$ tigers year$^{-1}$, neither subpopulation was viable. However, if poaching was eliminated from core 3 then the tiger subpopulation in core 1, connected at 25% to core 3 (i.e. '1→#3; at 25%') and with two tigers poached per year, was less likely to reach extinction ($P = 0.17$; Fig. 4d) than without anti-poaching measures on core 3 ($P = 0.57$; Fig. 4b). Equally, if core 3 was connected at 25% to core 1, from which poaching was eliminated (i.e. '3→#1; at 25%'), the subpopulation in core 3 was less likely to reach extinction if two tigers were poached per year ($P = 0.30$; Fig. 4d) than without anti-poaching measures on core 1 ($P = 0.84$; Fig. 4c).

## Discussion

This study has shown the potential of new statistical and spatial mapping techniques for deriving accurate

**Table 3.** Tiger density for different forest habitat types in the Kerinci Seblat region, shown with methods used to estimate density

| Forest type | $M_{t+1}$ | $\hat{N}$ (± SE) | Effective sampling area (km²) | Tiger density (tigers/100 km²) | |
|---|---|---|---|---|---|
| | | | | Capture–recapture method (95% CI) | Encounter rate method (95% PI) |
| Lowland hill | 6 | 7·0 (± 2·65) | 212·2 | 3·3 (3·3–9·9) | 2·5 (0·5–11·2) |
| Hill | 5 | 6·0 (± 1·28) | 294·1 | 2·0 (2·0–4·1) | 3·3 (0·7–15·4) |
| Submontane | 5 | 6·0 (± 1·87) | 396·5 | 1·5 (1·5–4·0) | 1·7 (0·4–7·3) |
| Montane | 1 | NA | NA | – | 0·3 (0·1–1·4) |

**Table 4.** Habitat characteristics and estimated numbers of tigers in each core area

| Forest type | Core 1 | | Core 2 | | Core 3 | | Core 4 | |
|---|---|---|---|---|---|---|---|---|
| | Area (km²) | Estimated no. of tigers | Area (km²) | Estimated no. of tigers | Area (km²) | Estimated no. of tigers | Area (km²) | Estimated no. of tigers |
| Lowland hill | 36·3 | 1·2 | 830·6 | 27·4 | 17·3 | 0·6 | 0·0 | 0·0 |
| Hill | 471·8 | 9·4 | 2610·8 | 52·2 | 344·5 | 6·9 | 67·9 | 1·4 |
| Submontane | 624·2 | 9·4 | 1616·0 | 24·2 | 563·4 | 8·5 | 101·9 | 1·5 |
| Montane | 442·3 | 1·3 | 655·2 | 2·0 | 273·1 | 0·8 | 36·8 | 0·1 |
| Total* | 1574·6 | 21 | 5712·5 | 105 | 1198·3 | 16 | 206·7 | 3 |

*Tiger estimates rounded down.

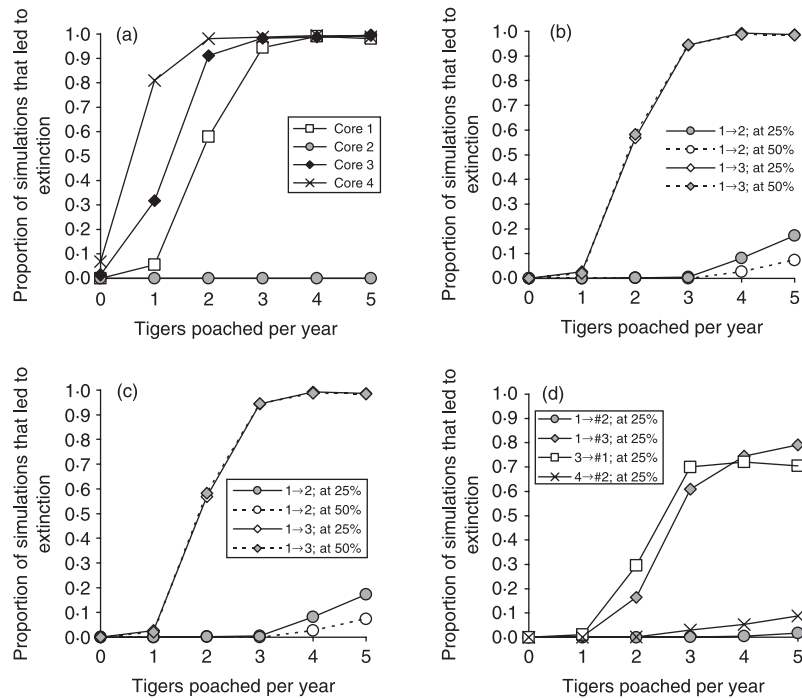**Fig. 4.** Extinction probabilities over 50 years, with varying poaching rates and connectivity (→) for (a) isolated tiger subpopulations, (b) the core 1 subpopulation connected to adjacent core areas at 25% or 50% (c), core 3 and 4 subpopulations connected to adjacent core areas at 25% or 50%, and (d) core 1, 3 and 4 subpopulations connected at 25% and with successful anti-poaching measures focused on specific core areas (#).

population estimates, and for evaluating appropriate and practical options for future management of a cryptic and critically endangered large carnivore. The SEHM identified the negative effect of public roads on tiger distribution and habitat quality in the KS region, which results in the isolation of four core tiger areas. Linking the SEHM with the PVA allows the prioritization of conservation management interventions, which showed the effectiveness of focusing anti-poaching strategies on the smaller core areas. It also showed that maintaining connectivity between the largest core area, and either one of the two smaller adjacent core areas, greatly improved the long-term persistence of tigers in KSNP.

### SEHM VALIDATION

The value of our conclusions should be set in the context of possible limitations of the likelihood-based modelling framework we used. As field survey effort is usually constrained by the resources of time, money and personnel, there is a trade-off between surveying a greater number of sampling units with fewer repeat surveys (occasions) or fewer sampling units with more repeat surveys. For cryptic species that occur at low densities, it is probably more effective to survey fewer sampling units ($\approx 80$ cells) more intensively ($\geq 3$ times) to overcome problems of a low number of detections (MacKenzie & Royle 2005). With hindsight, all 200 cells in this study should have been surveyed at least three times (rather than 40 cells on the third occasion). However, we have confidence in our final model because

as the detection–non-detection method tends to over-estimate occupancy and underestimate detection probability for data with few detections, models generated with small PAO estimates, as for KSNP, are usually more reliable than models generated with large PAO estimates (MacKenzie et al. 2002).

The SEHM is analogous to resource selection function (RSF) models, as both yield values within resource units that are proportional to the probability of use. However, RSF models are usually estimated from presence–absence or presence (used)/available data. Our SEHM approach has overcome the three main problems associated with RSF models by: (i) accounting for false absences by incorporating a detection probability through repeat surveys; (ii) statistically testing for spatial auto-correlation (Lennon 1999); and (iii) not arbitrarily defining suitable habitat as RSF > 0·5 (Boyce & MacDonald 1999) but instead linking this to occupancy through the PAO estimate.

From the KS region, absolute tiger abundance was determined from densities derived from different forest types. However, the SEHM identified that forest proximity to roads influenced relative tiger abundance. A retrospective approach might therefore develop a SEHM and use the significant landscape factors to determine camera trapping sites. We partially controlled for the effect of roads on tiger density because camera traps extended from the forest edge nearest to roads, towards the forest interior furthest from roads. However, this was not possible for montane forest as none existed at the forest edge. Overall, tiger density still showed a relationship

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*Journal of Applied
Ecology*, **43**,
576–586

with forest type. Furthermore, tiger densities might have been estimated in each habitat type in each core area. However, this would have taken more than 5 years, making the assessment process less useful.

### PVA MODEL VALIDATION

Difficulties associated with PVA modelling frequently arise because the requisite data are lacking. In order to minimize such difficulties, we evaluated relative, rather than absolute, extinction risk, with projections over a short time period, and with stochasticity modelled by true probability sampling, rather than by truncating numbers (Burgman & Possingham 2000). Recognizing concerns over the application of PVA, our PVA predictions comprised only part of a decision-support tool, as opposed to a decision-making tool, which has greater advocacy (Starfield 1997).

In KSNP, the smaller subpopulations in cores 1 and 3, whilst more prone to extinction through stochastic processes (Kenney *et al*. 1995), were shown to be viable as long as poaching was minimized. Similarly, Karanth & Stith (1999) found that isolated tiger populations containing only six breeding females could be demographically viable. This contrasts with the findings of Reed *et al*. (2003), that a minimum population of between 280 and 2275 tigers may actually be necessary to ensure long-term demographic and genetic viability (Reed *et al*. 2003). While importantly focusing attention on the vulnerability of wild tiger populations, Reed *et al*.'s (2003) estimates were derived from a non-tiger-specific PVA model, which did not model tiger demographic patterns at the fine scale used in our study. Furthermore, Reed *et al*. (2003) modelled genetic stochasticity, for which data on the number of lethal equivalents are scarce in most carnivore populations. Therefore, we found it more useful to concentrate on measurable demographic parameters (Beissinger & Westphal 1998; Wiegand *et al*. 1998). Our PVA highlighted the fragility of tigers in core 4, especially if subjected to regular poaching. However, tigers still persist in core 4, which suggests that the physical barrier presented by the non-asphalt road that divides cores 4 and 2 does not prevent their movement. If future camera trapping on either side of the road confirms connectivity between cores 4 and 2, then future modelling could consider their viability as a single combined core. Finally, our PVA might be advanced by collecting and incorporating breeding site data for modelling source–sink metapopulations (Wikramanayake *et al*. 2004).

For KSNP, the PVA models emphasized the merits of concentrating anti-poaching effort on the smallest subpopulations and maintaining habitat connectivity between core 2 and both cores 1 and 4. The conversion of forest to farmland has completely isolated cores 1 and 3. This stresses the importance of focusing anti-poaching efforts on core 3, which is the strategy that the PVA predicted to provide the greatest benefits for this core. However, these conservation strategies are dependent

on future poaching and deforestation patterns in and around each core area (Pressey & Taffs 2001). If a new road bisected core 2, making it more vulnerable than the other core areas, it would warrant greater protection measures at core 2. Thus, within each core area, separate detection–non-detection surveys should be conducted on a yearly basis to determine the change in tiger population trends (i.e. PAO estimates) so that the success of tiger conservation strategies in KSNP can be evaluated.

### THE EFFECT OF ROADS

The construction of a road through high-quality tiger habitat in Russia was found to reduce a source population to a sink population that no longer provided supplementary tigers to neighbouring areas (Kerley *et al*. 2002). Roads detrimentally affect other large carnivores, such as Iberian lynxes *Felis pardini*, Eurasian lynxes *Lynx lynx* and pumas *Puma concolor*, by increasing unnatural mortality rates through road kills (Ferreras *et al*. 1992; Maehr 1997; Kramer-Schadt *et al*. 2004), and grizzly bears *Ursus arctos* and wolves *Canis lupus* by restricting movements across their ranges (Mace *et al*. 1996; Whittington, St Clair & Mercer 2004). The other insidious effect of roads is that they provide access to more remote habitat that contains greater amounts of bushmeat for poachers (Bennett & Robinson 2000) and better quality land for farmers (Linkie, Smith & Leader-Williams 2004).

### CONSERVATION OF LARGE CARNIVORES

The approach developed in this study has wide application to the conservation of cryptic species living at low densities over large areas, such as many large carnivores. The detection–non-detection survey method can be used to monitor population trends through changes in PAO estimates. The combined SEHM and PVA model can be used to determine which strategies are most likely to be successful and cost-effective at protecting different subpopulations. As carnivores must be managed in both physical and political landscapes (Treves & Karanth 2003), this approach can also be used to show stakeholders what is likely to happen without appropriate conservation intervention.

## Acknowledgements

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