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Can the abundance of tigers be assessed from their signs?

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Summary

1. Indices of abundance offer cost effective and rapid methods for estimating abundance of endangered species across large landscapes, yet their wide usage is controversial due to their potential of being biased. Here, we assess the utility of indices for the daunting task of estimating the abundance of the endangered tiger at landscape scales.

2. We use double sampling to estimate two indices of tiger abundance (encounters of pugmarks and scats per km searched) and calibrate those indices against contemporaneous estimates of tiger densities obtained using camera-trap mark–recapture (CTMR) at 21 sites (5185 km^2) in Central and North India. We use simple and multiple weighted regressions to evaluate relationships between tiger density and indices. A model for estimating tiger density from indices was validated by Jackknife analysis and precision was assessed by correlating predicted tiger density with CTMR density. We conduct power analysis to estimate the ability of CTMR and of indices to detect changes in tiger density.

3. Tiger densities ranged between 0·25 and 19 tigers 100 km^{-2} were estimated with an average coefficient of variation of 13·2(SE 2·5)%. Tiger pugmark encounter rates explained 84% of the observed variability in tiger densities. After removal of an outlier (Corbett), square root transformed scat encounter rates explained 82% of the variation in tiger densities.

4. A model including pugmark and scat encounters explained 95% of the variation in tiger densities with good predictive ability (PRESS $R^2 = 0{\cdot}99$). Overall, CTMR could detect tiger density changes of $>12\%$ with 80% power at $\alpha = 0{\cdot}3$, while the index based model had 50% to 85% power to detect $>30\%$ declines. The power of indices to detect declines increased at high tiger densities.

5. *Synthesis and applications*. Indices of tiger abundance obtained from across varied habitats and a range of tiger densities could reliably estimate tiger abundance. Financial and temporal costs of estimating indices were 7% and 34% respectively, of those for CTMR. The models and methods presented herein have application in evaluation of the abundance of cryptic carnivores at landscape scales and form part of the protocol used by the Indian Government for evaluating the status of tigers.

Key-words: camera trap, double sampling, indices of abundance, mark–recapture, *Panthera tigris*, power analysis, regression models

Introduction

Information on abundance and change in abundance is important for the effective management of endangered species (Gibbs, Snell & Causton 1999). Assessing the abundance of low density, wide ranging and cryptic species is extremely demanding in terms of time and resources (Garshelis 1992). In the absence of abundance information, conservation management decisions are often based on crude estimates, expert opinion or educated guesses, which may result in erroneous decisions that can be counterproductive for conservation (Blake & Hedges 2004). Predictive models based on indices of abundance offer an economical, practical and timely solution to this problem (Hutto & Young 2003; Conn, Bailey & Saeur 2004; Johnson 2008). An index of abundance is defined as any measurable correlative of density (Caughley 1977) typically estimated without a measure of detection rate (Conroy & Carroll 2009). Use of indices as surrogates of abundance has been

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criticized as most indices are rarely calibrated with density (Pollock *et al.* 2002; Williams, Nichols & Conroy 2002; Skalski, Ryding & Millspaugh 2005), or tested for precision in detecting population change (MacKenzie & Kendall 2002; Conn, Bailey & Saeur 2004). This latter aspect of population estimates, i.e. ability to detect change in abundance is vital for monitoring trends, essential information for adaptive management and for evaluating success of conservation programmes (Williams, Nichols & Conroy 2002; Barlow *et al.* 2008). The key in making an index useful is to link the observed numbers in the index to true abundance or density (Conroy & Carroll 2009). Probably the best and most cost effective approach is to use double sampling (Cochran 1977) where a subgroup of the sample sites is subject to both the index and quantitative estimator and then the relationship between them determined. The added advantage of double sampling is that it can directly address the issue of incomplete detection in an index (a potentially biased estimator) since it is calibrated against an unbiased accurate estimate of abundance (Conroy & Carroll 2009).

The world is witnessing the highest concern society has ever shown towards conservation of large carnivores and their ecosystems (Mech 1996). Yet, the numbers and range of most large carnivores continue to decline (Check 2006; Dinerstein *et al.* 2007). Due to the resource intensive nature of the techniques used for estimating large carnivore abundances, those techniques are rarely applied to large landscapes (but see Hayward *et al.* 2002; Barlow *et al.* 2008). In the case of the tiger *Panthera tigris* (Linnaeus 1758) that occupies wide inaccessible landscapes, obtaining reliable abundance estimates over much of its range is a daunting task (Karanth *et al.* 2003; Sanderson *et al.* 2006). Examples of tiger density estimates obtained using resource intensive camera trap mark–recapture (CTMR) in tiger occupied landscapes of India, Nepal, Bhutan and South East Asia include Karanth & Nichols (1998); O'Brien, Wibisono & Kinnaird (2003); Karanth *et al.* (2004); Kawanishi & Sunquist (2004); Wegge, Pokheral & Jnawali (2004); Karanth *et al.* (2006); Linkie *et al.* (2006); Jhala, Gopal & Qureshi (2008); Wang & Macdonald (2009); and Lynam *et al.* (2009). Most camera trapped areas were 'small' subsets of larger tiger occupied landscapes and often cameras were placed in areas that have relatively high tiger density within this landscape (e.g. Karanth *et al.* 2004; Jhala, Gopal & Qureshi 2008). Therefore, density estimates obtained from camera trapped areas cannot be extrapolated to occupied landscapes (Garshelis 1992; but see Linkie *et al.* 2006), and have limited application in estimating population size or evaluating the status of tigers at landscape, state or country scale. Occurrence of tigers in a forest patch can be ascertained by detection of their sign in the form of pugmark trails, scat, rake marks, scrape marks and vocalization (Karanth & Nichols 2002; Jhala, Qureshi & Gopal 2005a). Quanta of signs in an area are likely to be related to abundance (Smallwood & Fitzhugh 1995; Stander 1998). An attempt to quantify relationships between tiger densities and abundance of tiger signs is needed for developing models that would help in evaluating the status of tigers and conservation potential of large landscapes from indices in a timely and cost effective manner (Lynam *et al.* 2009).

The country wide total count of tigers using experts to individually identify each individual from their pugmark impressions has been severely criticized (Karanth *et al.* 2003). The grave status of tigers in India gained global attention when the official census continued to report *good* numbers even when the species became locally extinct from Sariska Tiger Reserve in 2004 and later in Panna Tiger Reserve (2009) due to poaching (Check 2006; Rajesh *et al.* 2010). Subsequently, the Prime Minister established a Tiger Task Force in 2005 to investigate and resolve the tiger crisis in the country. The Tiger Task Force identified, amongst others, the lack of a credible status assessment system as a major problem (Narain *et al.* 2005).

In this article we evaluate relationships between indices of tiger abundance and tiger density using a double sampling approach (Cochran 1977; Eberhardt & Simmons 1987). We estimate absolute tiger densities by camera trap-based mark–recapture simultaneously with estimates of quanta of tiger sign from 21 different sites (5185 km^2) from amongst 53 787 km^2 of tiger occupied forests in Central and North India (Jhala, Gopal & Qureshi 2008).

We conduct a power analysis to determine the ability of CTMR and our index-based models to detect change in tiger abundance. The methods and concept presented herein form an important component of a country-wide tiger status evaluation protocol that was assessed and recommended by the Tiger Task Force (Jhala, Qureshi & Gopal 2005b).

Materials and methods

STUDY AREAS

We sampled 18 tiger populations in central and north India (Jhala, Gopal & Qureshi 2008) with 21 independent sampling units. Sampled sites were located in the states of Uttarakhand, Uttar Pradesh, Bihar, Rajasthan, Madhya Pradesh, Orissa, Andhra Pradesh and Maharashtra (Fig. 1) and were sampled between 2006 and 2007. Based on a priori knowledge and pilot surveys we stratified potential sampling areas into high, medium, low and very low tiger abundance categories. Based on the conservation importance of the tiger populations and logistical constraints we sampled five units with high, seven units with medium, six units with low and three units with very low tiger abundance. Sampled areas ranged between 125 and 300 km^2. At a few sites (e.g. Dhaulkhand) the size of tiger occupied forest patches were small thereby restricting the area coverage of our samples. In Corbett the sample coverage was large (545 km^2) due to availability of additional resources and contiguous tiger occurrence over a large area. All sampled areas were larger than the average home-range of tigers in these habitats (Smith, McDougal & Sunquist 1987; Chundawat, Gogate & Johnsingh 1999; Sharma *et al.* 2009). Sampled sites covered all types of tiger habitats found in Central and North India ranging from the *Terai* grasslands and moist Sal *Shorea robusta* forests of Corbett, Dudhwa, Similipal and Valmiki; arid thorn and *Aneogeissus* forests of Ranthambore and Kuno; dry deciduous mixed forests of Panna; mesic Sal forests of Kanha and Bandhavgarh; teak *Tectona grandis* dominated forests in Pench, Tadoba and Melghat and deciduous forests of the Eastern Ghats in Sri Sailam Tiger Reserve (Fig. 1). The topography and rainfall also varied greatly between the study sites.

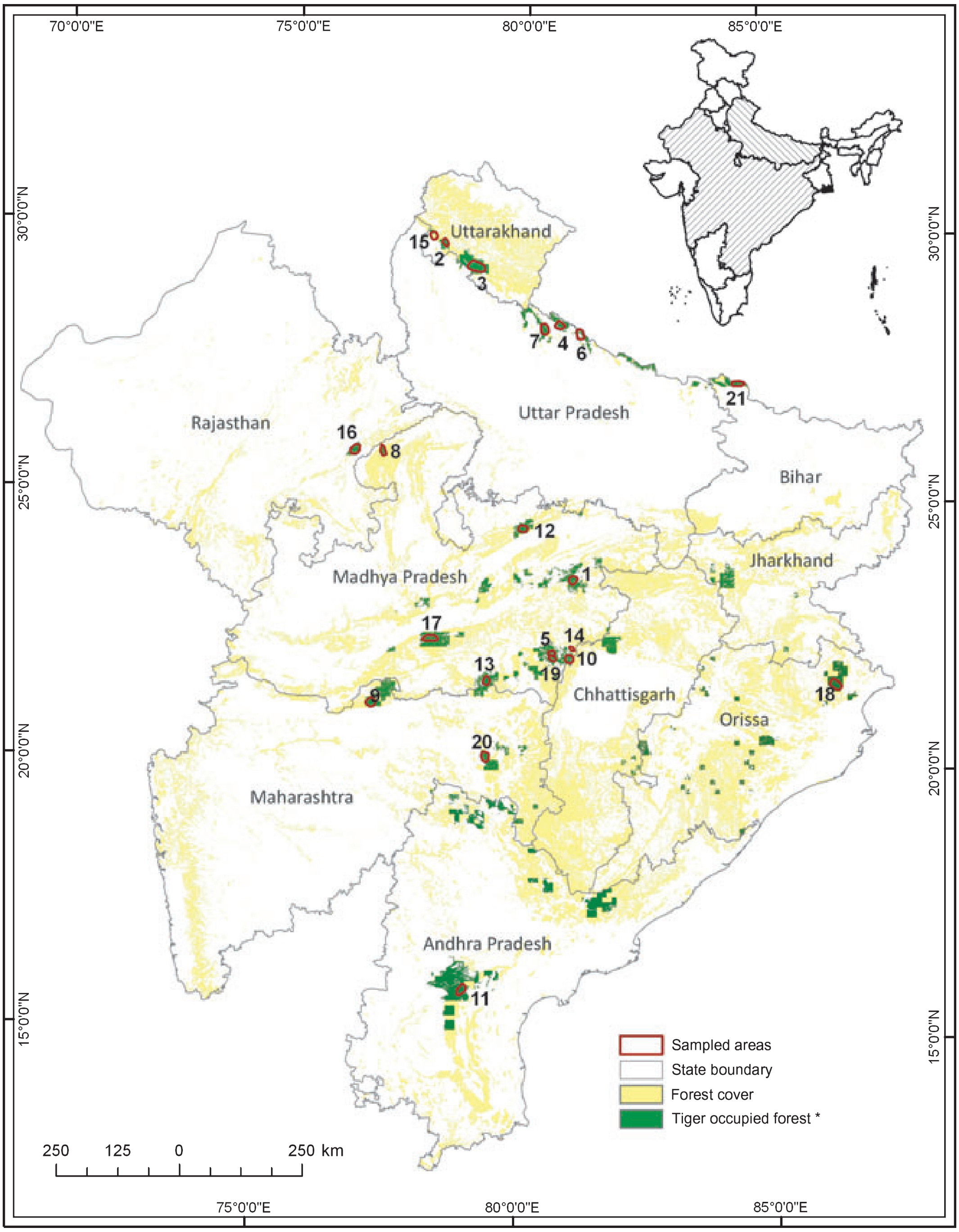

Fig. 1. Study sites for estimating tiger density overlaid on the forest cover map of India showing tiger occupied forests. Site codes are referenced in Table 1.

ESTIMATING TIGER DENSITY

Absolute tiger densities were estimated by closed capture–recapture models (Pollock *et al.* 1990) using camera traps (Karanth & Nichols 1998). We placed one double-sided remote camera unit (Trailmaster™ and/or DeerCam™) in each 2 × 2 km grid cell overlaid on the study area at each site. Within each grid cell a team of wildlife biologists with the assistance of local forest guards searched for the best location to deploy the camera unit to maximize photo-capture of tigers. This approach ensured that no gaps were left and that there was a reasonable density of camera trap units within the range of all tigers (Sharma *et al.* 2009).

Sampling durations lasted from 20 to 96 days with 20 to 120 double-sided camera units deployed at each site. Cameras were deployed simultaneously to cover the entire study area of a site, except in Corbett where we sampled the area in two blocks with equal sessions (days) in each block (Karanth *et al.* 2004). Individual tigers were identified from their unique stripe patterns and a capture matrix "X" generated for each site (Karanth & Nichols 1998). Despite substantial camera trap effort we could not photo capture tigers at two sites (Kuno and Phen) and captured less than five individuals at three sites (Table 1).

Table 1. Abundance, density and sign encounter rates of tigers from 21 sites in Central and Northern India using photographic mark–recapture and search paths. Numbers are estimates with standard errors in parenthesis

Location (site codes)	Effectively sampled area (km^2)	Camera trap nights	No of tigers photo-captured	Best site model	Closure test *P* value	Tiger numbers site estimate (SE)	Tiger numbers pooled estimate (Mh Two Mixture Model) (SE)	Capture probability Mh Mixture Model (SE)	Tiger density 100 km^{-2} (SE)	Model predicted tiger density (SE) §	Sign survey effort (km)	Pugmark Track set encounters km^{-1} (SE)	Scat encounters km^{-1} (SE)
Bandhavgarh (1)	210	680	22	Mh	0·3	26 (4·2)	29 (3·2)	0·92 (0·08)	13·6 (1·7)	12·8 (1·15)	213·0	1·31 (0·24)	4·15 (1·90)
Chilla† (2)	196	450	5	Mo	0·45	5 (0·5)	NA	NA	2·54 (0·70)	1·15 (0·47)	75·2	0·23 (0·11)	0·03 (0·02)
Corbett (3)	545	11495	102	Mth	0·43	127 (9·4)	104 (1·6)	0·90 (0·03)	19 (0·54)	12·8 (5·9)	214·7	4·24 (0·47)	0·52 (0·15)
Dudhwa (4)	221	1643	13	Mh	0·07	14 (1·5)	14 (1·2)	0·64 (0·15)	6·15 (0·87)	4·91 (0·31)	138·5	0·65 (0·10)	0·47 (0·13)
Kanha‡ (5)	108	462	12	Mh	0·22	13 (1·8)	13 (2·1)	0·22 (0·05)	12·00 (2·0)	12·23 (1·13)	90·0	1·10 (0·22)	4·13 (0·53)
Katarniaghat (6)	243	2840	12	Mo	0·5	14 (2·73)	12 (1·0)	0·91 (0·09)	5·01 (0·52)	4·31 (0·32)	87·1	0·56 (0·15)	0·37 (0·11)
Kishenpur (7)	280	1080	17	Mh	0·47	18 (4·2)	17 (1·3)	0·23 (0·19)	6·23 (0·76)	4·97 (0·32)	91·3	0·60 (0·16)	0·56 (0·29)
Kuno* (8)	400	750	NA	NA	NA	1	1	NA	0·25 (0·10)	0·05 (0·51)	151·0	0·01 (0·00)	0·01 (0·00)
Melghat (9)	267	960	11	Mh	0·96	11 (1·0)	11 (0·01)	0·18 (0·12)	4·12 (0·15)	2·5 (0·38)	197·0	0·46 (0·06)	0·11 (0·03)
Mukki (10)	125	825	8	Mb	0·14	8 (0·1)	10 (1·8)	0·77 (0·16)	7·25 (1·57)	4·1 (0·33)	144·0	0·37 (0·07)	0·55 (0·10)
Nagarjun Sagar (11)	272	1290	3	NA	NA	NA	3 (0·003)	0·51 (0·36)	1·49 (0·05)	3·87 (0·29)	101·4	0·50 (0·80)	0·24 (0·05)
Panna (12)	185	800	7	Mh	0·36	9 (1·7)	9 (1·7)	0·09 (0·2)	4·9 (1·5)	2·3 (0·35)	169·0	0·16 (0·04)	0·25 (0·07)
Pench (13)	152	1000	13	Mh	0·82	17 (2·6)	15 (1·1)	0·72 (0·12)	9·5 (0·84)	12·9 (0·77)	101·0	1·48 (0·10)	2·83 (0·10)
Phen* (14)	400	750	NA	NA	NA	2	2	NA	0·50 (0·10)	1·45 (0·39)	145·0	0·02 (0·00)	0·17 (0·06)
Dhaulkhand (15)	75	1860	1	NA	NA	NA	1 (0·001)	1·00 (0)	0·55 (0·02)	1·32 (0·54)	111·0	0·24 (0·09)	0·02 (0·01)
Ranthambore (16)	275	1716	26	Mb	0·003	28 (2·8)	27 (1·35)	0·42 (0·11)	9·81 (0·75)	7·19 (0·63)	113·0	0·60 (0·09)	1·95 (0·41)
Satpura (17)	136	600	4	NA	NA	NA	5 (1·55)	0·76 (0·23)	1·64 (0·55)	0·79 (0·45)	221·0	0·08 (0·02)	0·04 (0·02)
Simlipal (18)	323	2146	5	Mth	0·09	7 (1·1)	5 (0·01)	0·64 (0·23)	1·87 (0·06)	2·2 (0·39)	159·9	0·10 (0·03)	0·28 (0·07)
Suphkar (19)	227	1080	5	Mh	0·98	6 (2·0)	5 (0·02)	0·79 (0·19)	2·59 (0·95)	2·36 (0·38)	261·0	0·13 (0·10)	0·29 (0·17)
Tadoba (20)	250	1600	10	Mh	0·99	10 (0·3)	10 (0·1)	0·27 (0·15)	4·00 (0·21)	5·06 (0·36)	188·0	0·51 (0·10)	0·67 (0·11)
Valmiki (21)	215	1140	3	NA	NA	NA	3 (1·1)	1·00 (0)	1·49 (0·52)	2·18 (0·41)	112·5	0·36 (0·08)	0·07 (0·03)

*Tiger densities not obtained by camera trap mark–recapture.
†Tiger density estimate from Harihar, Pandav & Goyal (2009).
‡Tiger density estimate from Sharma *et al.* (2010), all other estimates obtained as part of this study.
§Tiger densities were predicted by Jackknife procedure using the best multiple regression model that had tiger pugmark and scat encounter rates as the independent variables, see text for details. Site codes in parenthesis (#) denote the location of the site in Fig. 1.

Due to the small number of tiger captures at these sites, it was not possible to obtain reliable estimates of population size, evaluate model selection or test for population closure using standard mark–recapture analysis (Kendall 1999; Stanley & Burnham 1999; Karanth & Nichols 2002). We therefore, used two separate approaches for obtaining density estimates. For sites where five or more individual tigers were captured, population size was estimated using program CAPTURE (Rexstad & Burnham 1991), whilst demographic and geographic closure population was tested using CloseTest (Stanley & Burnham 1999). For comparability with earlier estimates (Karanth *et al.* 2004), density estimates were obtained following Karanth & Nichols (1998, 2002); this method required that a buffer strip of half the mean maximum distance moved (1/2 MMDM) by recaptured tigers was added to the camera trap area to determine the effectively trapped area.

To obtain abundance estimates for the low-sample size populations, we carried out a combined analysis of the data sets where models were fitted to the pooled encounter histories from all populations (MacKenzie *et al.* 2005). Thus, information on capture probability parameters was combined across populations. The combined analysis used program MARK (White & Burnham 1999) and model Mh (with a two-point finite mixture). Since population estimates did not differ between the two analyses (individual site capture matrix and pooled matrix for all sites), the more precise population estimates obtained by the combined site analysis were used for computing tiger densities and developing our models.

The average cost of obtaining absolute density of tigers at each site considering wages of biologists, and field personnel, vehicle rental, discounted equipment and material costs, was estimated to be Rs. 850 000 (about US$ 17 000); the process took, on average, 720 man-days to accomplish.

ESTIMATING TIGER SIGN

Though this article focuses on small areas within large tiger occupied landscapes where CTMR and sign-based indices of abundance were simultaneously estimated, the methodology for sign survey was developed for application throughout all potential forested areas likely to have tigers (Jhala, Qureshi & Gopal 2005a; b). Thus, sampling for tiger sign needed to be systematically distributed throughout the forested areas of the landscape. Grid designs are statistically well suited to distribute sampling units; however, locating a grid in a large forested landscape is not an easy task for field sampling. Most of India's forests are delineated into hierarchical administrative units of forest divisions, ranges, beats and compartments. Boundaries of beats and compartments are based on natural features like ridges, waterways and dirt tracks. Each division is administered by Divisional forest officer; a Range is administered by a Range Forest Officer and a Beat by a Beat Guard who has intimate knowledge of these areas. The Beat Guard participated as a team member for sign surveys conducted in his beat. The average beat size in our study areas was 16·5 (SE 4·16) km^2. We estimated the length of the search path that had to be sampled to minimize the effect of habitat and substrate on encounter rates of tiger sign (Hayward *et al.* 2002). During a pilot study conducted in 2002–2004 in *c.* 50 000 km^2 of the Satpura-Maikal landscape we incrementally increased the length of the search path by 1 km, from 1 to 12 km and estimated encounter rates of tiger sign, we found that encounter rates of pugmark and scats stabilized after a 4 to 5 km search (Jhala & Qureshi, unpubl. data). Subsequently for this study, each survey consisted of a 5 km search for tiger signs. Surveys were not random, but instead conducted along features that were likely to have tiger sign (e.g. dirt roads, dry water courses and animal trails). Three spatially different surveys were conducted within each beat; this served to distribute our survey efforts throughout the study area. A team of 30 biologists was trained for a period of 15 days in identifying and searching, and for consistency in classification of tiger sign between observers. This team was then deployed at various study sites and each search path was walked by two observers. All encounters of tiger pugmark track sets and scats were recorded. These were distinguished from those of other carnivores based on criteria described by Jhala, Qureshi & Gopal (2005b) and Karanth & Nichols (2002), and by field training. An accurate measure of each search path was recorded using a hand held GPS unit (Garmin 72^{TM}). Encounter rates of each sign category were computed as the number of signs per km of search path. The cost of obtaining data on tiger sign indices was on average Rs. 62 000 (about US$ 1240) for each sampled site, which consisted of 22 beats (SE 2·44) on average. The time taken to sample each site for tiger signs was, on average, 220 man-days.

CALIBRATING TIGER SIGN INDICES WITH TIGER DENSITIES

Pearson's correlation coefficients were computed from 21 values obtained from the sampled sites between tiger densities and encounter rates of tiger pugmark trails, and tiger scats per km. Scatter plots of pugmark encounters and scat encounters versus tiger density were examined (see Appendix S1, Figs S1 and S2, Supporting information). A square root transformation of tiger scat encounters linearized relationship with tiger density (Sokal & Rohlf 1995). Simple and multiple linear regressions were used to investigate relationships and calibrate quanta of tiger sign with tiger density (Draper & Smith 1981; Eberhardt & Simmons 1987). Ideally, tiger densities should be known with certainty for developing relationships with indices (Engeman 2003). As this is practically impossible to achieve in free ranging populations, we used estimates of tiger densities obtained by mark–recapture methods (Pollock *et al.* 1990). To account for variability in precision of tiger density estimates we used a weighted regression approach for all the models (Sokal & Rohlf 1995). Each tiger density estimate was weighed by the reciprocal of the coefficient of variation of tiger density (CV [$\hat{D}$]) divided by the median tiger density (Wiewel, Clark & Sovada 2007). Thus, precise density estimates (smaller CV [$\hat{D}$]) made a greater contribution to the regression model.

Since one objective was to develop predictive models to estimate tiger densities from tiger abundance indices, we used least squares regression to assess the relationship between (i) pugmark trail encounter rates and tiger density, (ii) square root transformed encounter rates of tiger scat and tiger densities and (iii) multiple regression analysis with pugmark trail encounters and square root transformed scat encounters as independent variables and tiger densities as the dependent variable (Draper & Smith 1981). We assessed model fit and performance by coefficient of determination (R^2), root mean square error (RMS) and Akaike Information Criteria (Draper & Smith 1981; Sokal & Rohlf 1995; Burnham & Anderson 2002). The ability of the indices to predict tiger density was assessed using a Jackknife analysis wherein we dropped each site, re-computed the best regression model, and used it to predict the tiger density of the excluded site (Krebs 1989). The predictive performance was summarized by the predicted sum of squares R^2 (PRESS R^2), and correlation of Jackknife model estimated tiger density with CTMR tiger density (Draper & Smith 1981).

No photographic captures of tigers were obtained after over 750 trap nights in the best potential tiger habitat of 150 km^2 of Phen Sanctuary and Kuno Sanctuary. However, we obtained reliable evidence of tiger occurrence through sign when a larger area of about 400 km^2 was searched in and around each camera trap site. Based on pugmark track sets (Sharma, Jhala & Sawarkar 2005) and tiger scat obtained during the extensive search within the landscape, we conservatively estimated that two tigers operated in and around Phen Sanctuary and one tiger occurred in the Kuno landscape. Conservative Tiger densities estimated for these two sites were 0·25 and 0·5 tigers per 100 km^2 for Kuno and Phen, respectively. Since tiger densities for these two sites were not estimated by mark–recapture, we construct regression models with, as well as without, data from these two sites.

POWER OF INDICES TO DETECT CHANGE IN TIGER DENSITIES

We carried out analyses to evaluate the power of CTMR estimates of tiger density, indices, and our models based on indices to detect changes of various magnitudes at fixed type I error rates (α levels) of 0·3. Since the type I error is strictly a value judgment, and the consequence of rejecting a true null hypothesis of 'no change' is of lesser importance (to the management objective of conserving the endangered tiger) than failing to detect population declines (Beier & Cunningham 1996) we use a 'larger than usual' type I error rate. Tiger populations show natural fluctuations of substantial magnitude as a consequence of recruitment, dispersal and immigration (Karanth *et al.* 2006; Barlow *et al.* 2009). Yet, it is pertinent for wildlife managers to be able to detect changes of at least 30% size effect (especially declines), to react in a timely manner with appropriate actions. Thus, we set minimum management standards of achieving 80% power to detect 30% changes between two subsequent survey efforts (Hayward *et al.* 2002; Barlow *et al.* 2008).

We used program MONITOR (Gibbs & Eduard Ene 2010) to conduct Monte Carlo simulations at a desired power of 0·8 for evaluating the precision of CTMR, pugmark and scat encounter rates in detecting changes between two subsequent surveys. We follow Barlow *et al.* (2008) and Hayward *et al.* (2002) and use exponential response and lognormal measures to model changes in CTMR tiger density and indices of tiger abundance. Other options selected in the software were paired plot comparisons, which compare the same sites between two sampling intervals and test the hypothesis that the difference between the first and second survey averaged across all sites is greater or less than zero (two tailed tests).

To evaluate the power of using observed changes in sign indices to detect tiger population declines we fitted linear regression models in which the indices (i) were treated as the dependent variable, and CTMR tiger density (D) as the independent variable. We account for imperfect tiger density estimates by fitting a measurement error model using the estimated variance of density estimates as the measurement error variance for each observation. In the context of our problem, the null hypothesis is of the form: H0: $D_{(t+1)} - D_{(t)} = 0$ and we reject based on the difference in observed index values $i_{(t+1)} - i_{(t)}$ based on an index i. That is, we reject the hypothesis of 'no change in density' if the observed change in index values is large. The power of this test is the probability that the hypothesis is rejected given a certain prescribed change in density. For a fixed type I error rate (α) this is a standard power calculation (Casella & Berger 1990). Combining both indices into the calculation of power assumed that the indices are independent, conditional on tiger density. Further details of the power analysis are provided in Appendix S2 (Supporting Information).

All statistical analyses was done using SPSS 11 (SPSS 2001), NCSS (Hintze 2006) and R Development Core Team (2004) software packages.

Results

TIGER DENSITY

The highest tiger densities were estimated for Corbett Tiger Reserve at 19 tigers per 100 km^2 where we photographed 102 individual tigers. The lowest estimate obtained by CTMR was for Rajaji Dhaulkhand, where a single tigress was photographed twice, and density was estimated at 0·55 tigers per 100 km^2 (Table 1). Due to very low tiger densities we could not obtain camera trap photographs of tigers at Kuno and Phen. The best model selected by CAPTURE for most sites with more than five tiger captures had some form of heterogeneity in capture probabilities. CloseTest supported population closure for all sites except for Ranthambore (Table 1). Model Mh [two-point finite mixture model, where p1 = 0·038 (SE 0·002), p2 = 0·177 (SE 0·008)], using the pooled capture matrix for all sites provided more precise estimates of tiger numbers than site specific analyses in CAPTURE (Table 1).

TIGER ABUNDANCE INDICES

On average 147 (SE 12, range 75–221) km of search effort was invested at each site. The maximum number of tiger pugmark sets was recorded in Corbett and the minimum number in Kuno (Table 1). The maximum number of tiger scats was obtained from Bandhavgarh and the minimum number from Kuno (Table 1).

CALIBRATING TIGER SIGNS WITH TIGER DENSITY

Tiger pugmark set encounters had the best linear correlation with tiger densities ($R = 0{\cdot}92$, $P < 0{\cdot}0001$, $n = 21$) across all sites. Tiger scat encounter rates had a quadratic relationship with tiger densities probably due to greater persistence of scats than pugmarks within the environment. Thus, at equilibrium (where scat deposition equals decomposition), scat density would be disproportionately higher for high tiger density probably resulting in a curvilinear relationship (see Fig. S2, Supporting information). Scat encounters were found to be low in Corbett in comparison to tiger density. Transformed tiger scat encounter rates, after excluding Corbett, had a high linear correlation with tiger density ($R = 0{\cdot}91$, $P < 0{\cdot}0001$, $n = 20$).

Tiger pugmark and scat encounter rates explained 84% and 30%, respectively, of the observed variation in tiger densities (Table 2). Tiger pugmarks and tiger scats together explained 94% of the variation in tiger densities. All the three models had good predictive ability for tiger densities (PRESS $R^2 = 0{\cdot}997$, Table 2). The multiple regression model with pugmarks and tiger scats had the lowest AIC and RMS values and was therefore selected as the best model (Table 2). Jackknife predicted tiger densities correlated well with mark–recapture-based estimates of tiger densities ($R = 0{\cdot}91$, $P = 0{\cdot}0001$, Table 1). The regression coefficients presented in Table 2 were developed using data from 21 sites including the two sites where we could

Table 2. Least square regression models for estimating tiger densities from tiger sign indices ($n = 21$ sites)

Model	Independent variables	Slope	Slope P value	Intercept	Intercept P value	R^2	Adj. R^2	PRESS R^2	RMS	AIC
1	Pug mark	4·24 (0·42)	< 0·0001	2·02 (0·61)	< 0·004	0·84	0·834	0·989	17·23	105·95
2	SqRt (Scat)	6·69 (2·32)	0·0097	1·107 (1·84)	0·55	*0·303	*0·267	0·99	36·2	137·1
3	Pug mark	3·84(0·26)	< 0·0001	−0·31(0·53)	0·57	0·947	0·94	0·997	10·29	85·12
	SqRt (Scat)	4·07(0·69)	< 0·0001							

R^2 – coefficient of determination, Adj. R^2 – R^2 adjusted for degrees of freedom, PRESS R^2 – R^2 value computed from prediction sum of squares, RMS – root mean square error, AIC – Akaike information criteria.
*R^2 and Adj R^2 values after removal of outlier Corbett data were 0·824 and 0·814 respectively.

Table 3. Least square regression models for estimating tiger densities from tiger sign indices, two of the sites where tiger densities were not estimated by camera trap mark–recapture models have been omitted ($n = 19$ sites)

Model	Independent variables	Slope	Slope P value	Intercept	Intercept P value	R^2	Adj. R^2	PRESS R^2	RMS
1	Pugmark	4·21 (0·44)	0·0001	2·09 (0·64)	0·005	0·88	0·83	0·989	18·1
2	SqRt(Scat)	6·58 (2·45)	0·016	1·25 (1·98)	0·53	0·3	0·25	0·99	38·1
3	Pugmark	3·83 (0·28)	0·0001	0·28 (0·57)	0·63	0·94	0·94	0·997	10·8
	SqRt(Scat)	4·06 (0·73)	0·0001						

R^2 – coefficient of determination, Adj. R^2 – R^2 adjusted for degrees of freedom, PRESS R^2 – R^2 value computed from prediction sum of squares, RMS – root mean square error.

not photo-capture tigers. By excluding these two sites from our regression models the regression coefficients, fit, or performance were not altered (Table 3). We therefore retain the two sites in our final analysis, to have a wide range of tiger density coverage (0·25 to 19 tigers per 100 km^2).

POWER TO DETECT CHANGE IN TIGER DENSITY

Considering all sites, CTMR could detect 12% change in tiger density with a power of 0·8 between two subsequent surveys. At the desired power of 0·8, pugmark encounter rates could detect a decline of 25% and an increase of 23% over all sites, while scat encounter rates could only detect declines of 35% and increases of 37%. The desired power of 0·8 to detect minimum density declines of 30% at each site by subsequent surveys could be achieved only if the CTMR density estimate had a coefficient of variation less than 20%. The power of the best index-based model to detect a 30% decline in tiger density ranged between 50% and 85% at a type 1 error rate of 0·3. The power to detect a decline in tiger density was higher for pugmark encounter rates in comparison to scat encounter rates. The power of the models increased at higher tiger densities (Fig. 2 and Appendix S2, Supporting information).

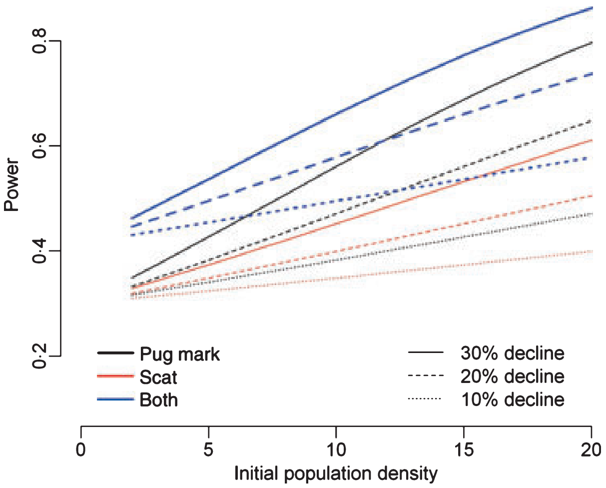

Fig. 2. The power of index based models to detect tiger density declines of various magnitudes at a type 1 error rate of 0·3.

Discussion

ESTIMATING TIGER DENSITIES

Tiger densities estimated by camera trap data in a mark–recapture framework ranged between 0·55 and 19 tigers per 100 km^2, and were estimated with an average precision of 13 (SE 3·2)% CV (Table 1). In the cases of Phen and Kuno, tiger density was so low that population estimation through CTMR was impractical and would have required much greater effort than we invested (Kawanishi & Sunquist 2004). Such low density areas rarely harbour breeding populations of tigers in Indian forests and, thus, contribute little to tiger abundance (Jhala, Gopal & Qureshi 2008). However, their importance to serve as dispersal corridor habitats or their potential to harbour breeding populations in the future should not be disregarded. The duration of sampling lasted for a maximum of 96 days (for Corbett) while all others were less than 60 days. Most of our study areas abutted hard boundaries on some sides. Considering the longevity of tigers and by considering tigers > 1·5 years for population estimation, we believe that we were justified in assuming demographic closure. The statistical test for closure (Stanley & Burnham 1999) supported population closure in the majority of our sampled sites for which the number of tiger captures was sufficient to perform a meaningful test (Kendall 1999). Population closure was not supported for Ranthambore (Table 1). However, from our additional intensive and extensive camera trapping efforts and ongoing telemetry study of tigers, we were reasonably certain that the Ranthambore population was geographically and demographically closed during our sampling period.

INDICES OF ABUNDANCE

Use of indices for evaluating abundance and population trends of endangered species has been a matter of serious debate (Ellington & Lukacs 2003; Hutto & Young 2003; Conn, Bailey & Sauer 2004; Jhonson 2008). Most proponents of indices advocate the practicality of using indices as surrogates for abundance (Hutto & Young 2003). It would be extremely difficult and resource intensive to attempt to estimate populations of tigers throughout their range using robust approaches like CTMR (Lynam *et al.* 2009). Simple indices of tiger sign offer a cost effective alternative to the evaluation of tiger status over larger landscapes (Pollock *et al.* 2002; Linkie *et al.* 2006). The cost and time required for estimating indices of tiger abundance was only 7% and 33% respectively of the cost and time required to estimate tiger abundance with camera traps. The main arguments against the use of indices are that they are rarely calibrated with absolute abundance estimates (Williams, Nichols & Conroy 2002; Conroy & Carroll 2009). Herein, we address this concern using the double sampling approach (Cochran 1977; Pollock *et al.* 2002) and collect index and density data from the same areas simultaneously (Skalski, Ryding & Millspaugh 2005; Conroy & Carroll 2009).

Amongst the 19 sites sampled successfully with camera trap, tiger densities ranged from 0·55 to 19 tigers per hundred km^2 (Table 1), giving a wide spectrum of density for calibrating indices. Skalski, Ryding & Millspaugh (2005) recommend using a double sampling approach with a minimum data set of $n = 5$ when correlations between sign and abundance are above 0·85. Our data adequately satisfy these recommendations.

The regression model included both tiger pugmark and scat as independent variables was selected as the best model by AIC (Table 2). This model had exceptionally good predictive ability (PRESS $R^2 = 0{\cdot}99$) across a wide spectrum of naturally occurring tiger densities (0·25 to 19 tigers per 100 km^2) and did not suffer from problems of collinearity (variance inflation factor < 1·1, tolerance = 0·97, condition number < 14). The high significance level of both predictor variables ($P < 0{\cdot}0001$), and substantial increment in the predictive power of the model by inclusion of scat encounter rates, justifies the use of a full, two predictor model for estimating tiger densities (Whittingham *et al.* 2006). The model should be used to estimate tiger densities when tiger sign data are collected in the manner described here to generate similar observational data within the data range used to develop the models.

POWER TO DETECT TIGER DENSITY DECLINES

It is important for population estimates to be able to detect changes in abundance (Gibbs, Snell & Causton 1999), especially declines in the case of the endangered tigers (Beier & Cunningham 1996). The average precision (CV) of our tiger densities using individual site population estimates was 23(SE 3)% and 13·2 (SE 2·5)% using the combined site analysis approach. This level of precision seems to be typical for CTMR density estimates for tigers, as the average CV observed from 29 tiger density estimates was 28·8 (SE 4·1)%. To detect a 30% decline at each site by two consecutive surveys the required precision was < 20% CV. Our CTMR site estimates met this criterion in 68% of cases. The low power of the index-based models to detect declines in tiger abundance between two consecutive surveys was expected (Fig. 2), given that our power analysis took into account variability of CTMR density, pugmark encounter rates and scat encounter rates. Type I error (or the probability of rejecting a true null hypothesis i.e. no change in tiger density) was set quite high at 0·3 in comparison to traditional statistical norms. This error does not have serious consequences with regard to tiger conservation, in comparison to our inability to detect a decline in tiger density. With $\alpha = 0{\cdot}3$, the index-based model could detect 30% of declines in tiger density with power ranging between 50% and 85%. The management threshold of 80% power to detect 30% of declines between two subsequent surveys was achieved for sites with a tiger density > 10 tigers per 100 km^2 (Fig. 2). The current estimate of power and effect size is computed for two subsequent samples. The power for detecting tiger density declines could be increased by improving the precision of CTMR density through use of likelihood based spatially explicit estimator models (Efford, Brochers & Byrom 2009; Royle *et al.* 2009), improving precision of indices by increasing sampling effort (Eberhardt & Simmons1987), and by using time series data for trend analysis in place of two sample comparisons (Gibbs, Snell & Causton 1999).

The relationships between indices of tiger abundance and tiger density developed here are applicable across Central and North India encompassing about 300 000 km^2 of forested habitat (Fig. 1). Similar relationships could be investigated for other regions and species. The initial costs and effort of double sampling vast landscapes are a major deterrent to this effort, but once undertaken, they lead to rapid and cost effective assessments of the status of the target species. The precision of model predictions will increase as more double sampling data accumulate with further time and effort (Eberhardt & Simmons 1987; Pollock *et al.* 2002).

Tiger populations in India are characterized by source–sink dynamics (Pulliam 1988). Most reserves harbouring a breeding population of tigers (currently about 13 000 km^2) serve as sources to populate and maintain tiger occupancy of sink habitats (currently about another 80 000 km^2) (Jhala, Gopal & Qureshi 2008). Source populations across the tiger's range are under threat from commercial poaching (Check 2006). Poaching can deplete a source and cause extinctions within a short period of time (Chapron *et al.* 2008; Rajesh *et al.* 2010). Due to the small size of most source populations in India (Jhala, Gopal & Qureshi 2008), habitat linkages between sources that permit exchange of individuals are important elements for long-term survival of tigers (Wikramanayaka *et al.* 2004; Dinerstein *et al.* 2007). Tiger habitats throughout their range are threatened by development projects and human pressures (Sanderson *et al.* 2006). Considering the precarious status of tigers (Sanderson *et al.* 2006), it is essential that wildlife managers and policy makers are able to protect tiger populations effectively wherever they are declining, by timely deployment of remedial measures (Gibbs, Snell & Causton 1999). Source populations of tigers are of paramount importance and should be monitored annually by resource intensive CTMR. Population estimates made using CMTR can detect population changes over short time periods and provide additional information on population dynamics (e.g. survival rates and recruitment, see Karanth *et al.* 2006). In addition, all areas occupied by tigers should be surveyed every 2 years to provide up-to-date indices of abundance. Index-based surveys can provide assessments of spatial occupancy, population extent and the viability of connecting corridor habitats (Linkie *et al.* 2006). Now, with the calibration of tiger sign indices, they can also provide reliable estimates of tiger abundance. Implementation of a continuous monitoring programme (CTMR and index surveys) will substantially increase our ability to detect trends in tiger density.

As with all large carnivores, the conservation of tigers is dependent on the appropriate management of large areas of landscape (Woodroffe & Ginsberg 1998; Wikramanayaka *et al.* 2004). Vast areas of tiger habitat are rapidly vanishing (Dinerstein *et al.* 2007) and major investment is required to monitor, manage and safeguard these habitats to ensure their long-term survival. The approach and models developed herein permit rapid and cost effective assessments of abundance to monitor the status of tigers at landscape scales. This information is vital for conservation investment, habitat management, planning development projects, formulation of policy and for law enforcement.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Scatter plots of indices of tiger abundance versus Camera Trap Mark–Recapture Tiger Density.

Appendix S2. Power analysis from Abundance Index Data.

Fig. S1. Tiger pugmark sets encountered per kilometre walk plotted against tiger density (tigers 100 km^{-2}) estimates obtained by camera traps using mark–recapture closed population estimators.

Fig. S2. Tiger scats encountered per kilometre walk plotted against tiger density (tigers 100 km^{-2}) estimates obtained by camera trap mark–recapture.

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