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Demography of a high-density tiger population and its implications for tiger recovery

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Abstract

1. Prioritizing conservation of source populations within landscapes is proposed as a strategy for recovering tigers globally. We studied population dynamics of tigers in Corbett National Park (CNP) in Indian *Terai*, which harbours the largest and highest density tiger population in any protected area of the world. Through population viability models, we demonstrate the importance of CNP in tiger recovery within western *Terai*.

2. We camera trapped 521 km^2 of CNP using open population capture–mark–recapture framework between 2010 and 2015 to estimate annual abundance, spatially explicit density, survival, recruitment, temporary movements, sex ratio and proportion of females breeding. We model metapopulation persistence with and without Corbett as a source within western *Terai* landscape at different levels of poaching and habitat connectivity.

3. In 6 years, we recorded 6,202 photo-captures of 307 individual tigers. Annual tiger abundance and density were stable at 120 (*SE* 19) and 14 (*SE* 3) per 100 km^2 respectively. Detection probability of tigers was 0.18 (*SE* 0.03) and detection-corrected male:female sex ratio was female biased (0.80 *SE* 0.13). Apparent annual survival probability was 0.79 (*SE* 0.05) for females and 0.60 (*SE* 0.04) for males. Survival of tigers in CNP (0.68 *SE* 0.12) was lower than that reported for other populations. CNP tigers showed high reproduction with 54.8 (*SE* 5.1)% females breeding and with addition of 35 (*SE* 8)% as new recruits to the population each year. Small tiger populations in western *Terai* with moderate poaching could only persist through dispersal from CNP.

4. *Synthesis and applications.* Corbett tiger population was characterized by a stable high density, high reproductive rate and low survival, resulting in high turnover rates (32%–48%) between successive years. Such source populations could sustain low-level poaching and with habitat connectivity, recover tiger populations across the landscape. This study establishes potential thresholds that can likely be achieved by tiger populations under optimal natural conditions and highlights the importance of prioritizing conservation of source populations within tiger landscapes. This information can be used to plan and implement realistic tiger recovery programmes globally.

1 | INTRODUCTION

Tigers (*Panthera tigris*), the flagship species of Asian forested eco-systems, have lost over 40% of their range in the last two decades primarily due to demand-driven poaching, loss of habitat and its prey (Dinerstein et al., 2007). In densely populated Asia, space allocation for tiger conservation is one of the most limiting factors. The situation becomes even more challenging since protected areas (PA) by themselves are often too small to sustain viable tiger population in the long term (Wikramanayake et al., 1998). The average size of a PA in India, which is home to about 70% of the world's wild tigers (Jhala, Qureshi, & Gopal, 2015), is 393 km^2 (http://www.wiienvis.nic.in/Database/ProtectedArea854.aspx). However, due to high prey densities, some of these PAs have the potential to support high tiger density and if they lie embedded in a contiguous forested landscape, they can help maintain viable tiger population in that landscape. Therefore, tiger conservation strategy in India aims to preserve such small areas within larger connected landscapes as metapopulations (Qureshi et al., 2014). High-density tiger population in core areas of tiger reserves is achieved by making them free of human settle-ment and their impacts through incentivized voluntary relocation (Wildlife Protection Act, 1972; amendment 2005 http://www.india environmentportal.org.in/files/THE-20WILD-20LIFE.pdf) and habi-tat management for enhancing prey density. These activities require high investments, and the National Tiger Conservation Authority spent 7–20 million USD annually on incentivized voluntary human resettlement from within core areas of Tiger Reserves between 2010 and 2015 (https://projecttiger.nic.in/content/144_6_Villa geRelocation11thPlan.aspx and https://projecttiger.nic.in/conte nt/148_6_VillageRelocation12thPlan.aspx). This strategy is in con-sonance with Walston et al. (2010) who recommended protecting source tiger populations as a priority since these areas encompass only 6% of the current tiger distribution but harbour nearly 70% of wild tigers. This tenet has been debated widely with opponents pro-posing that landscape scale conservation should be the priority for a wide-ranging carnivore like the tiger (Wikramanayake et al., 2011). Metapopulation models parameterized with realistic tiger demo-graphic data that evaluate tiger population persistence at landscape scales along with real-life data on tiger recovery would help resolve this debate.

Information on tiger vital rates is sparse and pioneering work of Sunquist (1981) and Smith (1993) that used radiotelemetry on ti-gers in Nepal *Terai* still remains the best source of information on the subject. Subsequently, Kenny, Smith, Starfield, and McDougal (1995), Kerley et al. (2003), Karanth, Nichols, Kumar, and Hines (2006), Duangchantrasiri et al. (2016), Majumder, Qureshi, Sankar, and Kumar (2017) and Sadhu et al. (2017) used camera trap-based capture–mark–recapture (CMR) and known fate models to estimate survival and movement parameters of tigers. Studying wildlife de-mography through telemetry provides information on survival, dis-persal and helps tease apart temporary movement from permanent ones. However, such studies are constrained by the number of ani-mals that can be radio-tagged due to the limitation of resources and permission for capture. Alternatively, camera trap-based CMR has proved to be a useful approach to study vital rates of large carnivore populations (Duangchantrasiri et al., 2016; Harmsen et al., 2017; Karanth et al., 2006; Majumder et al., 2017; Sharma et al., 2014). Although camera trap-based CMR approach addresses the limited sample size of telemetry studies, the vital rates obtained by CMR cannot distinguish between mortality and permanent emigration (Pollock, 1982). However, information generated by well-designed camera trap study is useful in understanding many aspects of de-mography that include vital rates such as apparent survival, re-cruitment, movement, time-specific detection-corrected sex ratio and percentage of breeding females in the population. Recent ap-proach using spatially explicit open capture (SECR) CMR models has attempted to distinguish between emigration and mortality (Ergon & Gardner, 2014; Gardner, Sollmann, Kumar, Jathanna, & Karanth, 2018). However, these approaches are still under development (Efford, 2019) and require a very large-scale camera trapping to cap-ture dispersal events of large carnivores, making them impractical for application (Ergon & Gardner, 2014).

The *Terai* landscape is renowned for its productivity, high con-centration of ungulates and therefore, ability to sustain some of the highest density of tigers in the world (Dinerstein, 1980; Sunquist, 1981; Smith, 1993). Long-term work on tigers in the Nepal *Terai* has provided information on tiger demography through telemetry (Smith, 1987, 1993; Sunquist, 1981) and camera trapping (Barlow et al., 2009). Most of our knowledge on population dynamics and vital rates of tigers in India is from central India (Majumder et al., 2017; Panwar, 1979; Sadhu et al., 2017; Schaller, 1967) and from the Western Ghats (Karanth et al., 2006). While Corbett on the Indian side of *Terai* harbours the single largest tiger population in a single protected area in the world, estimated at 169–261 tigers, with a density of 16 ± 1.60 tigers per 100 km^2 (Bisht et al., 2015; Contractor, 2007), this population remains data deficient in our un-derstanding of tiger demography and ecology. Corbett provides a unique opportunity to study a system that has been able to sustain one of the highest tiger densities in the world. The mechanisms behind this are of importance in current times of limited space and vanishing large mammals. The demographic parameter estimates from a high-density tiger population at/or approaching carrying capacity can be used for model-based predictions (Karanth & Stith, 1999) so as to gain an understanding of long-term population

dynamics as well as form a basis for management interventions. This information will also help set realistic targets for achievable tiger numbers, enabling work towards reaching the set objective of 'TX2 commitment' by Tiger range countries (https://www.wwf. de/fileadmin/fm-wwf/Publikationen-PDF/Global-Tiger-Recovery-Program-Nov-4.pdf, Global Tiger Initiative, Global tiger recovery program 2010–2022).

We sampled Corbett National Park (CNP) from 2010 to 2015 using camera trap-based open CMR framework. Apart from abundance, we estimate sex-specific survival rates, sex ratio, reproductive and turnover rates in this high-density tiger population. We subsequently use these parameters to model the metapopulation of tigers in western *Terai* and evaluate the importance of the source value of Corbett tiger population in sustaining long-term tiger persistence within the landscape. We compare our model results with observed recovery of tigers in the western *Terai* Landscape (Jhala, Qureshi, & Gopal, 2008; Jhala, Qureshi, Gopal, & Sinha, 2011; Jhala et al., 2015).

Most tiger populations are plagued with low density, low reproductive rates and high mortality rates. Tigers of Corbett are a contradiction of sorts, as they occur at high density with a reasonably large population and have high reproductive rates. Our study provides insights in the demographic processes that operate in high-density populations like Corbett. It spells hope for tiger conservation efforts and shows that establishing source tiger populations similar to that of Corbett within each tiger landscape is the first step towards global tiger recovery.

2 | MATERIALS AND METHODS

2.1 | Study area

Terai Arc Landscape in India can be divided into two parts, Western *Terai* between the Yamuna and Sharda rivers and Eastern *Terai*, the area east of the Sharda river (Harihar & Pandav, 2012). The study was conducted in 521 km^2 of CNP situated in the Western *Terai* (Figure 1), comprising the foothills of the Himalayas, the Shivalik range and the *doon* valley. Corbett Tiger Reserve forms the major source population of tigers in Western *Terai*, while Chitwan National Park in Nepal is the major source in Eastern *Terai*. Most striking feature of this landscape is the perennial water streams called *sots* that act as water sources for wildlife throughout the year. The rich alluvial system and perennial water source support a thriving ungulate population (64 [*SE* 8.6] Chital [*Axis axis*] per km^2 and 9 [*SE* 1.1] Sambar
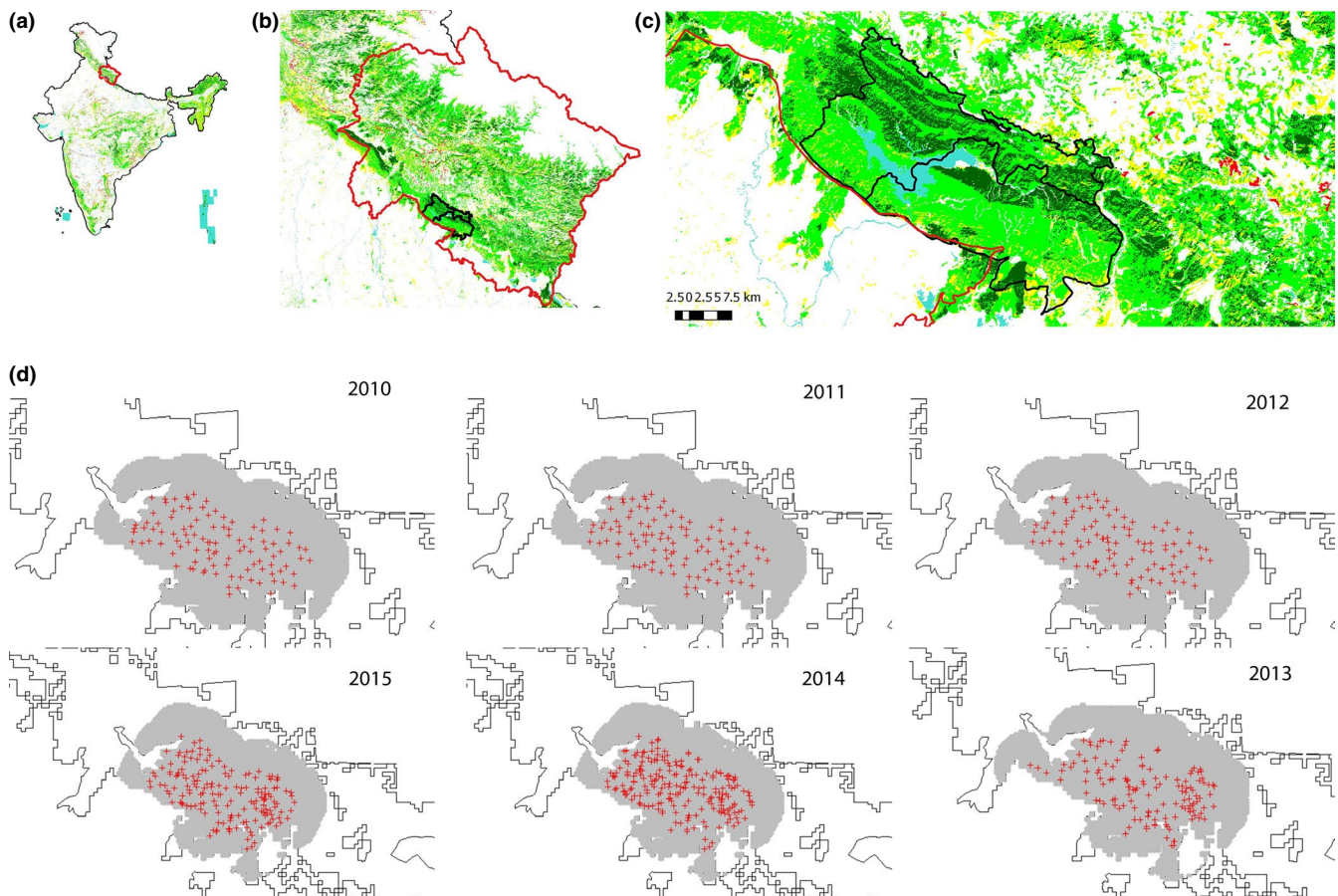

FIGURE 1 Map showing position of study area (Corbett National Park) overlaid on forest cover (green colour) map in (a) India and (b) state of Uttarakhand, (c) Corbett Tiger Reserve and (d) Camera trap locations (+) with a buffer of 8 km overlaid on tiger habitat mask for years 2010–2015 (clockwise)

TABLE 1 Tiger density (per 100 km^2) and major prey density (per km^2) from some important tiger conservation sites in India

Sites	Tiger	SE	Chital	SE	Sambar	SE	Source
Kanha	6.1	0.7	30.1	4.34	15.34	3.34	Awasthi et al. (2016), Kumar et al. (2015)
Ranthambhore	6.4	1	33.8	6.52	25.67	4.56	Sadhu et al. (2015)
Sunderbans	5.8	1.2	5.24	1.23	NA	NA	Roy et al. (2016)
Pench (Maharashtra)	3	0.6	15.69	7.14	6.6	2.9	Bhagat, Reddy, Joshi, Pariwakam, and Bansod (2015)
Rajaji	2.9	0.9	16.2	5.79	12.06	3.75	Pandav et al. (2015)
Nagarhole	11	0.9	29.85	4.36	3.56	0.57	Karanth, Kumar, Parameshwaran, Srivastha, and Sharma (2015)
Corbett	14	3	64	8.6	9	1.1	Bisht et al. (2015)

[*Rusa unicolor*] per km^2, Jhala et al., 2015) in the park as compared to some of the other Tiger Reserves in the country (Table 1).

Champion and Seth (1968) classified forests of CNP into three major types, namely Northern moist deciduous (3C), Northern tropical dry deciduous (5B) and Himalayan subtropical pine forest (9). Other than the Tiger, the park supports felids like Leopard *Panthera pardus*, Leopard cat *Prionailurus bengalensis* and Jungle cat *Felis chaus*. Other carnivores include Golden jackal *Canis aureus*, Sloth bear *Melursus ursinus*, Himalayan black bear *Ursus thibetanus*, Yellow-throated Marten *Martes flavigula*, Indian grey mongoose *Herpestes edwardsii*, Palm civet *Paradoxurus hermaphroditus*, Large Indian civet *Viverra zibetha*, Small Indian civet *Viverricula indica* and Smooth-coated otter *Lutrogale perspicillata*. Herbivores include Elephants *Elephas maximus*, Sambar, Chital, Barking deer *Muntiacus vaginalis*, Wild pig *Sus scrofa*, Hog deer *Axis porcinus*, Nilgai *Boselaphus tragocamelus*, Serow *Capricornis thar* and Goral *Naemorhedus goral*. The avifauna of CNP is also very rich with 554 species of resident and migratory birds of which 21 species are globally threatened (https://avibase.bsc-eoc.org).

2.2 | Data collection

We used CMR in a robust design framework (Pollock, 1982) by camera trapping 521 km^2 area of CNP consistently between 2010 and 2015. We deployed camera trap units that function on activity and passive infrared triggering mechanism to photograph tigers. Camera traps were deployed in pairs at each station, on either side of trails, so as to photo-capture both flanks simultaneously of each passing animal (Karanth & Nichols, 1998). Distance between camera trap stations was maintained between 1 and 1.5 km so as to ensure no 'holes' in the sampled area. This high camera density (Figure 1) ensured that all tigers in the study area had a good chance of photo-capture with no tiger having zero probability of photo-capture (Pollock, Nichols, Brownie, & Hines, 1990). Camera trap stations were selected based on reconnaissance sign surveys as well as expert knowledge of local field assistants. Potential camera trap point locations were recorded on the ground using a handheld GPS (Etrex 30 and Garmin 72); these locations were then plotted on Google Earth to select points for camera deployment to

adhere to above-mentioned camera distance and correct for any sampling holes.

Due to logistic constraints (limited number of camera traps and field biologists) during the initial years (2010–2012), we sampled the study area in two blocks of ~250 km^2 area each. These two blocks were sampled 120–150 days apart. With increased availability of camera traps and trained field staff, we camera trapped the entire study area (521 km^2) simultaneously in 2013–2015 (see Table S1).

2.3 | Data analysis

Photographic captures and subsequent identification of tiger individuals through program EXTRACTCOMPARE (Hiby et al., 2009) yielded capture histories of individuals in the standard X-matrix format (Otis, Burnham, White, & Anderson, 1978). All CMR analyses excluded cubs (<1 year old) because of their low photo-capture probability and high mortality (Karanth et al., 2006). We grouped remaining >1-year-old tigers into a single age class because of difficulty in differentiating between adults and subadults from camera trap photos alone (Sadhu et al., 2017). Owing to a large sample size (*n* = 307) and ability to sex most individuals, we were able to obtain gender-specific parameter estimates.

2.4 | Population dynamics

We analysed capture data under the Robust design initially proposed by Pollock (1982) and subsequently modified by Kendall, Pollock, and Brownie (1995), Kendall, Nichols, and Hines (1997). Pollock's (1982) robust design was a two-stage analysis where abundance was estimated using closed population models for each primary period, while transition parameters were estimated between primary periods. All analyses were done in program MARK 8.x version 2017 (White & Burnham, 1999). Our study consisted of 6 years (2010–2015) of data with each year as a 'primary period' (Kendall et al., 1995, 1997; Pollock, 1982; Williams, Nichols, & Conroy, 2002). The tiger population was expected to be open to gains and losses between these primary periods while closed within the duration of sampling (42 days secondary periods) within each year. Kendall et al. (1995, 1997) developed a full likelihood approach that combined

Pollock's (1982) two step analysis into a single analysis. The full likelihood approach allows an animal to be unavailable for capture at any given time (or a temporary emigrant). The probability of availability is modelled to be (a) completely random or depends on whether the animal was (b) available for capture in the previous primary period or (c) actually captured in the previous primary period (Kendall et al., 1997). We first modelled capture probability (*detection models*) and subsequently, conditioning on the best selected detection model, we modelled state and transition parameters of interest (i.e. abundance, survival and movement) that were in consonance with tiger ecology.

Each of our primary period consisted of 42 camera trap nights (secondary periods). Between 2010 and 2012, sampling was carried out in two blocks (see Table S1). Between 2012 and 2013, due to the shift from two block sampling to a single block, tigers from the second block were exposed to an interval of 6 months between primary periods instead of 12 months. We explicitly account for this single shorter primary period by estimating separate survival rate for this 6-month period in MARK (Cooch & White, 2011) and subsequently converting it to annual survival for estimating average survival across years. By merging the blocks for analysis, we could likely violate the population closure assumption required for abundance estimation. Tigers are long-lived in comparison to our sampling interval (Mazak, 1981). We therefore tested if model selection and abundance estimates differed when (a) the two blocks were analysed separately (see Table S2a,b) and (b) data from the two blocks were merged for a single analysis (see Table S2c–f). Total population abundance for each year for this block analysis was estimated using a more parsimonious model (see Table S2c) in MARK that did not account for sex-based heterogeneity in detection and considered transition parameters to be constant. This approach was preferred for estimating total population size as a simpler model provided better precision on total abundance estimates. Since results from separate analyses of the two blocks and the combined analysis yielded abundance estimates that were not different from each other (see Table S2f,g), we subsequently report results from the combined dataset analyses as this increased sample size allowed us to estimate gender-specific parameters.

2.5 | Detection models

Here, we model individual detection probability based on the frequency of recaptures within a primary period, using maximum likelihood approach. We modelled individual detection probability (capture probability (p) and recapture (c)) by addressing the following sources of variability:

1. We hypothesized that the detection of tigers was likely to differ between sexes since territory size and movement rates differ between male and female tigers (Smith, 1993; Sunquist, 1981) and as also observed in jaguars (Sollmann et al., 2011). We modelled this potential source of variability in capture probabilities by incorporating sex as a covariate in the detection model.

2. Camera trap density was relatively low at 1 per 5 km^2 for the years 2010–2012 compared to a relatively high camera trap density of 2 per 5 km^2 for 2013–2015. We expect that detection probability of tigers would be higher during years (2013–2015) with higher camera trap density. We, therefore, modelled detection with two time period effects; period (a) 2010–2012 with low camera trap density and period (b) 2013–2015 with high camera trap density.

The full detection model (P) was (P~$p_{(m(ct), f(ct), u(ct))}$; $c_{(m(ct), f(ct), u(ct))}$) where capture (p) and recapture (c) were different for male (m), female (f) and unsexed tigers (u) for the two time periods (ct) that differed in camera density.

By accounting for heterogeneity caused by gender, effect of camera trap density along with traditional behaviour response (p≠c) (Otis et al., 1978; Williams et al., 2002), we address the specific conditions in our study that could potentially account for variation in detection probability of tigers. Even though we had a 'large' sample (n = 307) of photo-captured tigers, this sample size was too small for more complex detection models like heterogeneity within gender groups, as these models did not converge.

2.6 | State and transition models

We modelled transition parameters such as survival and temporary movement rates using maximum likelihood approach on detection/non-detection of individuals across primary periods after accounting for detection probability within a primary period. Hence, using the best detection model(s), we subsequently model the state and transition. For these parameters, we evaluate the following hypotheses:

2.7 | Survival

There was no reason to suggest that habitat, prey or poaching differed in CTR between study years that could affect survival rates. Hence, we did not expect survival rates to differ between years. However, males and females have differential life-history traits (Smith, 1993) and should have different survival probabilities. We expected males to have lower survival compared to females as observed in most mammalian species (Krebs, 1972). We therefore modelled survival as constant (null model $S_{(.)}$) or differing between sexes ($S_{(g)}$).

2.8 | Movement

We did not expect movement parameters to change between years for the same reason as mentioned above. Males are the dispersing sex in tigers while females are more philopatric (Smith, 1993; Sunquist, 1981); we therefore expected movement in and out of the study area to differ between sexes. Corbett has one of the highest tiger densities in the world (Bisht et al., 2015; Contractor, 2007) and therefore competition for resources (food and mates) would also likely be high. If we found movement estimates to be very small (e.g. <0.1%) for either gender, we considered them to be negligible, and

in our subsequent models, we fixed them at zero for parsimony and ease of computation.

Two movement parameters (Kendall et al., 1997), that is, temporary emigration (G″) and temporary immigration (1-G′) as defined below, were modelled.

1. Temporary emigration (G″) is the probability of going out of study area in a primary period if the animal was present in the previous primary period but remaining within the super population, and
2. Probability of staying away (G′) from the study area in a primary period given that the animal was part of the super-population in the previous primary period.

We fitted 16 models for the entire robust design analysis. We used sample size-corrected Akiake's information criteria (AIC_c) (Akaike, 2011) to select models which best explained our data from candidate competing models. To account for uncertainty associated with model selection, we used model averaging by AIC_c weights to average model parameters (Akaike, 2011).

2.9 | Abundance and spatially explicit density

The open CMR models (mentioned above) provide estimates of annual abundance ($\hat{N}$) as derived parameters in program MARK 8.x (White & Burnham, 1999). Density ($\hat{D}$) was estimated through likelihood-based spatially explicit capture recapture of tigers (Borchers & Efford, 2008; Efford, 2004) using package *secr ver.* 3.0.1 (Efford, 2017) in program R *ver* 3.4.1 (R Core Team, 2013). In SECR, we tested models where spatial scale of detection (σ) and capture probability of activity centres (g_0) were gender specific or similar between sexes.

2.10 | Sex ratio and reproductive rate

We estimated detection-corrected number of males and females from our best model to arrive at sex ratio. We examined each photo-capture event of females and termed them as 'breeding' if they were pregnant or lactating (Sadhu et al., 2017). Full udders and prominent nipples in a breeding female are visible about 7–10 days before parturition and till the cubs are weaned by 165 days (Gittleman, 1986; Smith & McDougal, 1991). From our long-term ad libitum observations in the study area, we found that one of the female's lactation period lasted for 155 days, which was similar to the lactation period mentioned in Gittleman (1986) and Smith and McDougal (1991). We sampled the study area for 42 days in a year; therefore, all females that delivered cubs ≤5 months before our sampling period would comprise the pool of breeding females available for sampling each year.

We estimated the actual number of breeding females (B_f) during the primary sampling by correcting the number of breeding females photo-captured by the detection probability of breeding females. $B_f = n_L/p_{bf}$, where n_L = number of breeding females detected in each primary sampling period, p_{bf} = probability of detecting a breeding female.

Since birth seasonality is not profound in tigers (Sunquist, 1981), we consider tigers to breed throughout the year for our computation. Breeding females (B_{fy}) in a year would be:

$$B_{fy} = B_f \times (\text{Days in a year} \div \text{Sampling Days})$$
$$\times (\text{Days Detected as Breeding} \div \text{Sampling Days})$$

$$B_{fy} = B_f \times (365 \div 42) \times (165 \div 42)$$

Since we could potentially have 8.69 intervals of 42-day sampling in a year and pregnancy/lactation was detectable for 165 days, a single breeding female could potentially be detected in 3.93 sampling intervals in 1 year.

2.11 | Recruitment and population trend

Recruitment is the number of new individuals added to the population in time *t* per individual at time *t* − 1. Recruitment in case of a camera trap study is the product of fecundity and survival from cub to >1-year-old tigers as well as immigrants from neighbouring areas. We estimated number of recruits (B_t) in time *t* as;

$$B_t = \hat{N}_{t+1} - \hat{N}_t \times S$$

where $\hat{N}_{t+1}$ = abundance estimate at time *t* + 1, $\hat{N}_t$ = abundance estimate at time *t*, S = survival probability (Skalski, Kristin, & Millspaugh, 2010).

Another important parameter for population dynamics is the population trend. We regressed natural log of tiger density against years (2010–2015). The slope of the regression provides an estimate of the instantaneous growth rate (*r*) (Caughley, 1977; Skalski et al., 2010). A significant positive slope implies an increasing population and a negative slope implies population decline, while a slope of zero implies a stationary population (Caughley, 1977). For a population near its carrying capacity, we expect the growth rate not to be significantly different from zero. With high potential for reproduction in tigers (Mazak, 1981), we hypothesize that, at carrying capacity, the recruits from CNP would disperse into the larger landscape so as to maintain a stationary population (growth rate near zero).

2.12 | Metapopulation viability analysis

In early 2006, the western *Terai* tiger population consisted of separate populations constituted by (a) Rajaji NP, (b) Corbett tiger reserve, (c) Ramnagar forest division and (d) Nandhore forest division. These populations though distinct, probably exchanged individuals occasionally through forested corridors constituted by the Shivalik hill forests and some remnant forests in valley habitats. Distances between these populations ranged between 1 and 146 km with varying magnitude of resistance to tiger movement in the intervening corridor habitats. Corbett NP harboured the largest tiger population numbering close to 108 ± 4.5 (Contractor, 2007). We evaluate the importance and role of Corbett tigers in sustaining and promoting

tiger occupancy and abundance within the Western *Terai* landscape by modelling a Population Viability Analysis in Vortex ver. 9.9 (Lacy, 1993) using published tiger demography and parameters estimated by us in Corbett (Kenny et al., 1995; Sadhu et al., 2017; Smith, 1987, 1993; Smith & McDougal, 1991). We varied cub survival in our models to be between 0.65 and 0.55 to capture observed empirical estimates (Smith & McDougal, 1991) as well as reduced survival rates of juveniles and subadults to capture the lower limits of population persistence. We modelled realistic scenarios (see Table S3) wherein we evaluate persistence of single isolated populations of varied sizes (20, 50 and 100 tigers) exposed to various levels of poaching and catastrophic events. Subsequently, we model a metapopulation depicting the western *Terai* scenario with four populations and their initial tiger numbers as estimated in 2006 (initiation of the country-wide tiger estimation, Jhala et al., 2008). We model the metapopulation with Corbett population being small ~20 tigers and with its observed population size (≥200) to understand its role in sustaining long-term tiger persistence within the landscape. We also model a scenario wherein the landscape was depleted of tiger populations with only the source (Corbett) remaining. These scenarios address the specific case of prioritizing source population at the cost of smaller populations, answering whether such a strategy would permit long-term tiger persistence in the landscape. Movement rates between the four populations were based on our field observations from camera trap data (Jhala et al., 2008, 2011, 2015) and reducing these to half, so as to depict a higher resistance to movement in the landscape (loss of corridors). With the above models we test, Walston et al.'s 6% solution hypothesis wherein the authors propose to prioritize conserving source population within landscapes. We elucidate our model results by comparing them with observed increase in tiger occupancy and abundance within western *Terai* landscape.

3 | RESULTS

A total sampling effort of 35,784 camera trap-nights yielded 6,202 photographic captures of 307 individual tigers during our 6-year study (2010–2015) (Table 2). Of the 307 individuals, 130 were females, 118 males and 59 individuals whose gender could not be ascertained. Individuals in the unidentified gender group had 1–2 captures in a given primary period and were not photo-captured in succeeding years. Across all years, males on an average were photo-captured 11 (*SE* 1.2 range 1–72; median 6) times, while females had average photo-captures of 11.6 (*SE* 1.1 range 1–62; median 7).

3.1 | Open-CMR-robust design-based vital rates of tigers

3.1.1 | Detection probability

Tiger detection probability was best explained by the model that accounted for (a) gender-based differences (b) behavioural response of tigers and (c) the camera density. The closest competing model differed by a Delta AIC_c of 2.64 (Table 3). Detection probability for all years was high at 0.86 (*SE* 0.04) for all tigers with no difference between males (0.86, *SE* 0.01) and females (0.87, *SE* 0.01). The overall capture probability was 0.8 (*SE* 0.04) during years with low camera trap density and 0.92 (*SE* 0.05) for high-density camera trap years.

Using the best detection model, the state and transition model that had the lowest AIC_c (Table 3) accounted for gender differences in survival had no temporary movement for males and unidentified gender class while accounting for random temporary movements in females. Model estimates of survival and movement parameters differed between males (0.6 *SE* 0.04) and females (0.79 *SE* 0.05) with females having higher survival and temporary movements (Table 4).

3.1.2 | Abundance, density and recruitment

Tiger numbers ranged from 109 to 139 over the 6 years of study (Table 5). Estimates of detection probability (g_0) at the activity centre for males (0.08 *SE* 0.02) and females (0.12 *SE* 0.05) were similar. While the spatial scale of detection, σ, which is a measure of activity range radius for males (2.11 *SE* 0.24 km), was almost

TABLE 2 Details of sampling effort, detections and number of individual tigers photo-captured within 521 km^2 of consistently camera trapped area of Corbett National Park, 2010–2015

Primary period	CT density	Trap-nights	No. photo-captures	M_{t+1}	Cumulative no. of tigers	#M	#F	No. breeding females
2010	Low	4,326	466	89	89	36	43	11
2011		4,410	461	98	129	34	37	10
2012		4,410	925	93	162	30	33	8
2013	High	6,300	1,183	109	201	31	39	8
2014		9,324	1,135	118	251	34	62	7
2015		7,014	2,032	115	307	50	62	16

Abbreviations: CT density, Camera trap density; Low, one per 5 km^2; High, two per 5 km^2; M_{t+1}, unique individuals photo-captured; #M, Number of male tigers; #F, Number of female tigers.

TABLE 3 Model selection statistics for detection and transition models using the robust design analysis on tiger photo-capture data from Corbett National Park, 2010–2015

S. no	Model	AIC_c	Delta AIC_c	AIC_c weights	Model Likelihood	Num. par	Deviance
Detection models							
1	$S_{(.)}G'_{(.)}G''_{(.)} p_{(M(ct), F(ct), U(.))}c_{(M(ct), F(ct), U(.))}$	17,408.82	0.00	0.82	1.00	14	17,217.96
2	$S_{(.)}G'_{(.)}G''_{(.)}p_{(g,ct)}c_{(g,ct)}$	17,412.53	3.71	0.13	0.16	16	17,217.63
3	$S_{(.)}G'_{(.)}G''_{(.)}p_{(g)}c_{(g)}$	17,521.81	112.98	0.00	0.00	9	17,341.03
4	$S_{(.)}G'_{(.)}G''_{(.)}p_{(ct)}c_{(ct)}$	17,743.04	334.22	0.00	0.00	7	17,566.29
5	$S_{(.)}G'_{(.)}G''_{(.)}p_{(.)}c_{(.)}$	17,898.81	489.99	0.00	0.00	5	17,726.07
6	$S_{(.)}G'_{(.)}G''_{(.)}p=c_{(g)}$	17,917.80	508.98	0.00	0.00	6	17,743.06
7	$S_{(.)}G'_{(.)}G''_{(.)}p=c_{(t)}$	18,148.45	739.63	0.00	0.00	5	17,975.72
8	$S_{(.)}G'_{(.)}G''_{(.)}p=c_{(.)}$	18,306.76	897.94	0.00	0.00	4	18,136.03
Transition models							
1	$S_{(g)}G'_{(F,M=U=0)}G''_{(F,M=U=0)}p_{(M(ct), F(ct), U(.))}c_{(M(ct), F(ct), U(.))}$	17,404.70	0.00	0.60	1.00	17	17,207.77
2	$S_{(g)}G'_{(.)}G''_{(.)} p_{(M(ct), F(ct), U(.))}c_{(M(ct), F(ct), U(.))}$	17,407.34	2.64	0.16	0.27	17	17,210.41
3	$S_{(g)}G'_{=}G''_{(.)} p_{(M(t), F(ct), U(.))}c_{(M(ct), F(ct), U(.))}$	17,408.41	3.71	0.09	0.16	16	17,213.50
4	$S_{(.)}G'_{(.)}G''_{(.)} p_{(M(ct), F(ct), U(.))}c_{(M(ct), F(ct), U(.))}$	17,408.82	4.13	0.08	0.13	14	17,217.96
5	$S_{(.)}G'_{=}G''_{(.)} p_{(M(ct), F(ct), U(.))}c_{(M(ct), F(ct), U(.))}$	17,410.14	5.44	0.04	0.07	13	17,221.30
6	$S_{(.)}G'_{=}G''_{(g)} p_{(M(ct), F(ct), U(.))}c_{(M(ct), F(ct), U(.))}$	17,411.06	6.37	0.02	0.04	14	17,220.20
7	$S_{(g)}G'_{(g)}G''_{(g)}p_{(g,ct)}c_{(g,ct)}$	17,414.18	9.48	0.01	0.01	22	17,207.11

Abbreviations: S, survival; G'', temporary emigration; G', probability of staying away; p, capture probability; c, recapture probability; g, gender; M, males; F, females; U, unidentified gender; ct, are the two time periods differing in camera trap density; (.), parameter kept constant.

TABLE 4 Model averaged estimates of capture (p),recapture (c) probability, survival (S) and temporary movement (G''& G') for female and male tigers in Corbett National Park, 2010–2015

Gender	Camera trap density	Detection parameters	Estimate (SE)	Survival (SE)	Gamma' (SE)	Gamma'' (SE)
Female (n = 130)	Low	p	0.05 (0.007)	0.79 (0.05)	0.58 (0.24)	0.22 (0.06)
		c	0.12 (0.005)			
	High	p	0.07 (0.007)			
		c	0.18 (0.005)			
Male (n = 118)	Low	p	0.06 (0.007)	0.60 (0.04)	0	0
		c	0.14 (0.006)			
	High	p	0.06 (0.007)			
		c	0.20 (0.007)			

Abbreviations: G'', temporary emigration; G', probability of staying away.

double than that of females (1.1 SE 0.75 km). Overall tiger density was stable at 14 (SE 3) per 100 km^2 from 2010 to 2015 (Table 5). Detection-corrected sex ratio (male:female) was 0.80 (SE 0.13, Table 5).

3.1.3 | Reproductive rate

During each sampling period, 32%–39% of photo-captured females were found to be breeding (Table 2) and the proportion of females actually breeding was estimated to be 54.8 (SE 5.1)%, amounting to an average of 28 (SE 3.2) females breeding each year within the study area.

3.1.4 | Population trend

The slope (r) of the regression of ln (D) versus years was not different from zero (r = 0.003 ± 0.03, p = 0.93, R^2 = 0.002) suggestive of a stationary tiger population (Figure 2).

3.1.5 | Metapopulation viability

Small tiger populations <20 were liable to go extinct by themselves in the next 100 years (Table 7); such populations were extremely sensitive to poaching with extinction probability increasing to almost 100% even with one tiger being poached annually (Table 7). Medium

TABLE 5 Abundance, spatially explicit density, sex ratio, movement parameter (σ) and detection probability (g_0) at activity centres of tigers in Corbett National Park, 2010–2015

|	Abundance estimates from MARK				Density estimates from SECR					
Yr	$\hat{N}_F$ (SE)	$\hat{N}_M$ (SE)	$\hat{N}$ (SE)	M:F	ESA (km²)	$\hat{D}$ (SE)	σ F (SE) (km)	σ M (SE) (km)	g_0 F (SE)	g_0 M (SE)
2010	50 (4.10)	43 (3.39)	124 (8.92)	0.84	586	16 (1.6)	1.43 (0.06)	2.12 (0.09)	0.03 (0)	0.03 (0.003)
2011	43 (3.67)	40 (3.37)	117 (8.57)	0.92	601	14 (1.6)	1.06 (0.03)	2.01 (0.08)	0.12 (0.01)	0.05 (0.004)
2012	39 (3.38)	36 (3.01)	109 (8.15)	0.91	635	14 (1.6)	0.8 (0.02)	2 (0.05)	0.05 (0)	0.2 (0.002)
2013	46 (3.81)	37 (3.08)	109 (8.15)	0.79	590	12 (1.2)	1.3 (0.05)	2.56 (0.1)	0.01 (0)	0.08 (0.009)
2014	68 (3.22)	37 (2.36)	124 (6.25)	0.55	735	17 (1.5)	1.04 (0.7)	1.8 (0.6)	0.3 (0.02)	0.09 (0.006)
2015	68 (3.22)	56 (3.03)	139 (6.74)	0.81	790	15 (1.4)	1 (0.07)	2.18 (0.02)	0.2 (0)	0.04 (0.003)

Abbreviations: $\hat{N}_F$, population estimate of females; $\hat{N}_M$, population estimate of males; $\hat{N}$, overall population estimate (including unsexed tigers); M:F, detection corrected male to female ratio; $\hat{D}$, spatially explicit density; σ, sigma, the movement parameter; g_0, detection probability; ESA, effective sampling area; Yr, year.

(>50) to large populations (>100) had high persistence probability and large populations could also buffer low levels of poaching-related mortality (2M and 1F annually). The simulated landscape of western *Terai* had very high persistence for the next 100 years in the absence of poaching and could also accommodate moderate tiger offtake/poaching from each of the four populations before the survival of the metapopulation was at risk (Table 7). However, in the absence of Corbett as a source population thereby reducing immigration, individual populations showed extinctions (Table 7, Scenario 16 &17).

In the scenarios when all tiger populations (except Corbett) were extirpated, dispersal from Corbett re-established these populations in the landscape. Reducing permeability of corridors connecting these populations by half impacted recolonization and increased extinction risks (Table 7, Scenario 13).

4 | DISCUSSION

Tiger density (12–17 per 100 km²) within CNP is one of the highest recorded in the world and leads to a quiver of questions about how large carnivore populations might behave when crowded to this extent. In
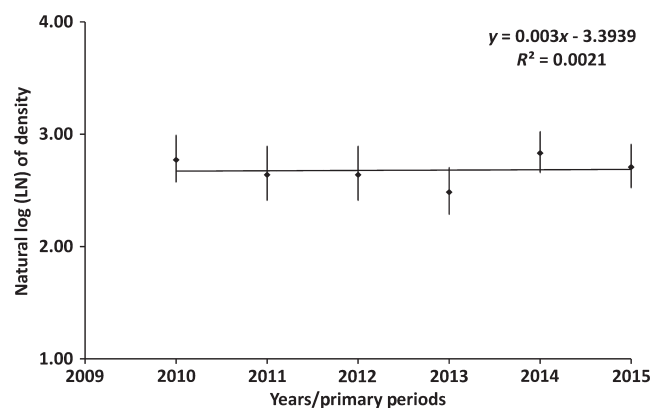
FIGURE 2 Natural log of tiger density (with 95% confidence intervals) plotted against years for 2010–2015 in Corbett National Park

the first ever long-term monitoring of tigers in the Indian *Terai*, we attempt to characterize this population and provide useful and novel insights into this important source population. This study constitutes one of the largest camera trap dataset obtained for any large carnivore in the world, enabling us to model complex combinations of parameters (Gerber, Ivan, & Burnham, 2014) and for the first time estimate gender-specific survival and other vital parameters for tigers.

For the robust design, population closure is a prerequisite for abundance estimation within secondary periods, while the population is open between primary periods for estimates of survival and movement parameters. Therefore, our block approach in sampling (2010–2012) could adversely affect population estimates due to violation of population closure assumption within the primary periods but would not have any influence on other parameter estimates like survival which were addressed with appropriate analysis. However, independent and pooled estimates of abundance of the blocks did not differ (see Table S2g). Since both adjacent blocks had high tiger density, movement between them was restricted, and we found only 4–5 individual tigers common between the two adjacent blocks (amounting to 4% of the population). Therefore, combining the data of the two blocks for the first 3 years did not alter our inferences on annual population abundances.

4.1 | Detection probability

Larger movement of males, that is, larger home range leads to a greater σ in SECR compared to females. Tigers in our study had high capture probabilities. Increase in camera trap density resulted in increased capture probability by 12%, mainly due to better detection of the proportion of the population that inherently had low detectability (unsexed tigers). While for sexed individuals (males and females), the capture probability increased by about 4%.

4.2 | Survival

Survival estimated in CMR studies is apparent survival which includes death and permanent emigration. Survival probability

TABLE 6 Comparative review of camera trap-based open capture–mark–recapture studies carried out on tigers from across their range

Parameters	Nagarhole[a]	Huai Kha Khaeng[b]	Pench[c]	Corbett[d]
Survival	0.77 (SE 0.05)	0.80–0.96	0.66 (SE 0.04)	0.68 (SE 0.02)
Temporary emigration	0.10 (SE 0.07)	Not reported	Not reported	0.2 (SE 0.08)[e]
Mean maximum distance moved (km)	3.74 (SE 0.56)	4.37 (SE 1.05)	5.33 (SE 0.91)	4.6 (SE 0.96)M 2.8 (SE 0.77)F
Density/100 km^2	9.7 (SE 1.8)	1.68 (SE 0.69)	3.70 (SE 0.8)	14 (SE 3.0)
Growth rate (%)	3 (SE 0.2)	5 (SE 0.3)	15 (SE 0.11)	0.3 (SE 3.0)

Note: Mean Maximum Distance Moved-For all individual tigers with recaptures the maximum distance between camera traps with captures was recorded and averaged. For Corbett, we have separate estimates for males (M) and females (F).

[a]Karanth and Sunquist (1995), Karanth et al. (2006), Karanth and Sunquist (2000).
[b]Duangchantrasiri et al. (2016).
[c]Majumder et al. (2017).
[d]Current study.
[e]Temporary emigration estimate for the females, males in the study did not show temporary movements.

varied between genders, where apparent annual survival probability of males (0.60) was much lower than that of females (0.79). Of 130 females photo-captured during the study period (2010–2015), we identified 61 (~50%) to be residents since they were photo-captured in two or more primary periods compared to 38% males who were residents. Females are philopatric and this is reflected in their survival rates, while low survival rate of males is characteristic of large carnivores, which are exposed to higher risks and are the dispersing gender in tigers (Smith, 1993). None of the published studies on population dynamics of tigers from open CMR have estimated gender-specific survival because of relatively small datasets (Karanth et al., 2006, *n* = 78; Majumder et al., 2017, *n* = 66 and Duangchantrasiri et al., 2016, *n* = 90) (Table 6). Hence, lack of gender-specific estimates from India and across the tiger's range limits our comparison of estimates. The overall estimate of annual apparent survival of adult tigers (0.68) in Corbett was lower than that reported for tigers in South India (0.77, Karanth et al., 2006) and in Thailand (0.82, Duangchantrasiri et al., 2016). High density likely leads to intense competition which is reflected as depressed apparent survival rates. A telemetry study on Corbett tigers and/or large-scale (>2,000 km^2) long-term camera trapping (Ergon & Gardner, 2014) is required to further tease apart emigration from mortality as well as provide insights into dispersal and territoriality.

4.3 | Recruitment and source population

Corbett tiger population is a paradox of sorts as it maintains a stable high-density population yet has low apparent survival rates. With over 54.8 (SE 5.1)% females found breeding each year with a high level of recruitment (35 [SE 8]%), this likely results in high emigration and turnover rates in the population. The number of breeding females within CNP exceeds the number recommended for long-term viable tiger source populations (20–25, Chapron et al., 2008; Gopal, Sinha, Mathur, Jhala, & Qureshi, 2007 and PVA results Table 7). Tiger population in Nagarhole and Russian Far East were observed to increase at 3%–6% (Karanth, Nichols, Kumar, Link, & Hines, 2004 and Miquelle, Smirnov, Zaumyslova,

Soutyrina, & Johnson, 2015). CNP tiger population remained stable across years. The population fluctuated between 109 and 139 tigers within the study area of ~500 km^2 and was likely to be at carrying capacity where recruitment replaces deaths and emigration. Considering the mortality rate of Corbett tigers to be similar to tigers in Ranthambhore (10%–16%, Sadhu et al., 2017) which was also at high density, the apparent mortality of 32% can then be partitioned into actual mortality (10%–16%) and 16%–22% to emigration. This suggests that 19–26 tigers disperse annually out of CNP, highlighting the importance of CNP as good source population (Pulliam, 1988) for the landscape.

4.4 | Movement

Competition renders temporary movements inefficient as individuals are unlikely to regain territories once lost. We found different temporary movement rates between females and males in Corbett. Males showed little to no temporary movement. This suggests that males either moved permanently out of the study area or died. This is in consonance with tiger ecology (Smith, 1993) where males are the dispersing sex and permanently disperse out of the natal area to minimize inbreeding (Pusey, 1987).

Industrial development, mining, palm plantations, highways and other linear structures are fragmenting prime wildlife habitat across Asia. Large carnivore conservation is limited by shrinking space as forested areas are converted into smaller islands. This problem is amplified in India which is a hub for development. Tiger occupancy within India's tiger landscapes is maintained by protecting at least one significant source population within each landscape. Our simulation results show the importance of a large source in a landscape, as also proposed by Walston et al. (2010). In the absence of such a source connected to other populations, tiger persistence within smaller populations in a landscape was prone to extinction events and could not tolerate even moderate offtake by poachers. Small isolated tiger populations were extremely vulnerable to extinction especially in the face of poaching as also shown by Chapron et al. (2008). Due to the current illegal demand for tiger body parts, it would practically be impossible to stop poaching entirely. Although efforts to minimize

TABLE 7 Single and metapopulation viability analysis results for the western Terai landscape from 17 scenarios (Table S3a–c) in Vortex 9.9. All the results are from models run with parameters reported in Table S3b and the models with reduced parameters are reported in Table S5

Scenario	PopName	N_0	K	Dispersal	Harvest	S-r (SD)	PE	N-ext (SD)	N-all (SD)	Me.TE
1	SmallPop	15	20	NA		0.04 (0.17)	0.24	16.4 (3.84)	12.48 (7.71)	54
2	MedPop	30	50	NA		0.05 (0.11)	0	45.22 (5.12)	45.09 (5.68)	65
3	MedPop	30	50	NA	1M+1F	−0.01 (0.15)	0.71	37.03 (11.18)	10.94 (17.95)	39
4	LargePop	75	100	NA		0.05 (0.09)	0	92.47 (7.91)	92.47 (7.91)	0
5	LargePop	75	100	NA	2M+1F	0.03 (0.09)	0	88.88 (8.69)	88.79 (9.13)	61
6	LargePop	75	100	NA	2M+2F	0.03 (0.11)	0.1	89.16 (9.91)	79.92 (28.71)	44
7	Rajaji	15	50	Normal		0.06 (0.13)	0	42.24 (7.45)	42.24 (7.45)	0
	Corbett	120	200			0.02 (0.08)	0	175.68 (15.89)	175.68 (15.89)	0
	Ramnagar	35	50			0.06 (0.13)	0	42.02 (7.72)	42.02 (7.72)	0
	Nandhore	10	30			0.08 (0.15)	0	25.24 (4.98)	25.19 (5.08)	43
	Metapop	180	330			0.04 (0.06)	0	285.12 (22.18)	285.12 (22.18)	0
8	Rajaji	15	50	Normal	1M	0.06 (0.15)	0.04	41.38 (9.13)	39.94 (11.47)	19
	Corbett	120	200		2M+1F	0.02 (0.08)	0.01	169.3 (18.12)	168.29 (22.31)	51
	Ramnagar	35	50		1M	0.06 (0.14)	0	41.89 (7.54)	41.82 (7.71)	68
	Nandhore	10	30		1M	0.06 (0.19)	0.11	22.53 (7.29)	20.61 (8.82)	23
	Metapop	180	330		5M+1F	0.03 (0.06)	0	270.66 (29.83)	270.66 (29.83)	0
9	Rajaji	15	50	Half		0.06 (0.13)	0	41.21 (7.69)	41.17 (7.79)	33
	Corbett	120	200			0.04 (0.07)	0	182.34 (14.26)	182.34 (14.26)	0
	Ramnagar	35	50			0.05 (0.13)	0	41.48 (7.71)	41.48 (7.71)	68
	Nandhore	10	30			0.06 (0.16)	0	24.26 (5.1)	24.21 (5.2)	46
	Metapop	180	330			0.04 (0.06)	0	289.19 (20.75)	289.19 (20.75)	0
10	Rajaji	15	50	Half	1M	0.05 (0.15)	0.22	39.57 (10.79)	31.17 (18.32)	17
	Corbett	120	200		2M+1F	0.03 (0.08)	0	178.34 (15.49)	178.34 (15.49)	0
	Ramnagar	35	50		1M	0.05 (0.14)	0	41.06 (8.4)	40.95 (8.64)	50
	Nandhore	10	30		1M	0.03 (0.22)	0.67	13.51 (10.2)	6.16 (8)	18
	Metapop	180	330		5M+1F	0.04 (0.06)	0	256.61 (27.5)	256.61 (27.5)	0
11	Rajaji	0	50	Normal		0.08 (0.15)	0	42.04 (7.79)	42.04 (7.79)	0
	Corbett	120	200			0.02 (0.08)	0	175.58 (16.13)	175.58 (16.13)	0
	Ramnagar	0	50			0.08 (0.15)	0	41.87 (7.54)	41.87 (7.54)	0
	Nandhore	0	30			0.09 (0.17)	0	25.56 (5.01)	25.56 (5.01)	0
	Metapop	120	330			0.04 (0.06)	0	285.05 (21.89)	285.05 (21.89)	0

(Continues)

TABLE 7 (Continued)

Scenario	PopName	N_0	K	Dispersal	Harvest	S-r (SD)	PE	N-ext (SD)	N-all (SD)	Me.TE
12	Rajaji	0	50	Normal	1M	0.049 (0.23)	0.32	27.9 (18.01)	20.17 (18.64)	0
	Corbett	120	200		2M+1F	0.02 (0.08)	0	169.66 (17.87)	168.98 (20.81)	43
	Ramnagar	0	50		1M	0.17 (0)	0.006	42.01 (7.89)	41.77 (8.44)	0
	Nandhore	0	30		1M	0.22 (0.22)	0.17	21.09 (8.46)	18.29 (9.95)	0
	Metapop	120	330		5M+1F	0.07 (0.004)	0.004	250.21 (30.43)	249.21 (34.23)	43
13	Rajaji	0	50	Half		0.07 (0.16)	0	41.39 (7.71)	41.39 (7.71)	0
	Corbett	120	200			0.04 (0.07)	0	181.81 (15.04)	181.81 (15.04)	0
	Ramnagar	0	50			0.07 (0.15)	0	41.19 (8.01)	41.19 (8.01)	0
	Nandhore	0	30			0.07 (0.18)	0	24.45 (5.32)	24.45 (5.32)	0
	Metapop	120	330	Half		0.05 (0.06)	0	288.84 (21.41)	288.84 (21.41)	0
14	Rajaji	0	20	Half		0.05 (0.24)	0.84	9.71 (6.11)	1.87 (4.26)	0
	Corbett	20	30			0.03 (0.15)	0.1	24.27 (5.41)	21.85 (8.86)	60
	Ramnagar	0	20			0.05 (0.24)	0.57	10.2 (5.24)	4.7 (5.89)	0
	Nandhore	0	20			0.05 (0.23)	0.78	11 (6.41)	2.74 (5.36)	0
	Metapop	20	90	Half		0.03 (0.13)	0.08	33.77 (11.35)	31.16 (14.14)	60
15	Rajaji	0	20	Reduced		0.06 (0.22)	0.95	24.69 (17.72)	1.51 (6.89)	0
	Corbett	20	30			0.04 (0.14)	0.06	25.06 (4.95)	23.6 (7.55)	59
	Ramnagar	0	20			0.06 (0.21)	0.78	25.68 (17.88)	5.85 (13.32)	0
	Nandhore	0	20			0.06 (0.23)	0.94	13.88 (10.29)	1.14 (4.28)	0
	Metapop	20	90			0.04 (0.14)	0.05	33.81 (17.17)	32.1 (18.3)	58
16	Rajaji	0	50	Half		0.13 (0.2)	0.51	41 (15.58)	20.25 (23.01)	0
	Corbett	20	30			0.10 (0.1)	0	28.47 (3.32)	28.47 (3.32)	0
	Ramnagar	0	50			0.12 (0.2)	0.12	43 (12.24)	38.02 (17.82)	0
	Nandhore	0	30			0.13 (0.2)	0.18	24.72 (7.91)	20.48 (11.62)	0
	Metapop	20	160			0.11 (0.13)	0	107.22 (34.22)	107.22 (34.22)	0
17	Rajaji	0	50	Reduced		0.04 (0.18)	0.24	16.09 (3.71)	12.23 (7.53)	49
	Corbett	20	30			0.04 (0.14)	0.03	25.48 (4.8)	24.77 (6.28)	62
	Ramnagar	0	50			0.03 (0.18)	0.18	14.57 (4.8)	12.09 (6.86)	56
	Nandhore	0	30			0.04 (0.18)	0.17	16.28 (3.98)	13.56 (7)	43
	Metapop	20	160			0.04 (0.09)	0	62.65 (15)	62.65 (15)	0

Abbreviations: S-r, Stochastic growth rate; PE, Probability of extinction; N, ext-Population size at year 100 for populations that did not go extinct; N-all, average population size for all the populations; M.TE, Median time for extinction; Me.TE, Mean time for extinction; M, adult male; F, adult female; PopName, Population name; LargePop, Large population (*n* = 75, K = 100); MedPop, Medium population (*n* = 30, K = 50); SmallPop, Small population (*n* = 15, K = 20); MetaPop, Metapopulation; N_0, Initial Population; K, Carrying capacity.
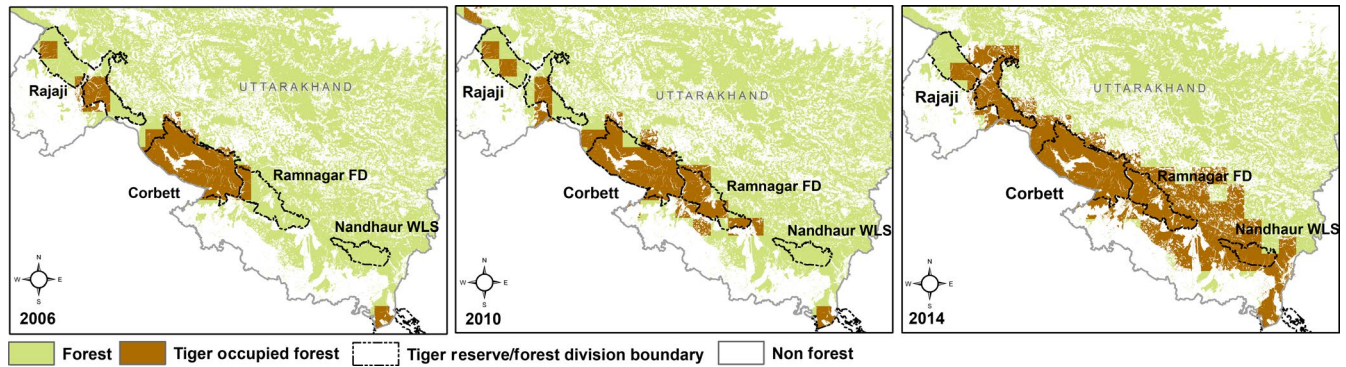
FIGURE 3 The *Terai* landscape was sampled for tiger signs by a 15 km search within each 15 km² forested patch as part of the occupancy survey for national tiger status evaluation (Jhala et al., 2008, 2011, 2015). Forest patches where tiger sign was detected are marked in brown. Expansion in tiger occupancy from Corbett Tiger Reserve across western *Terai* landscape is clearly seen from 2006 to 2014

poaching through patrolling and law enforcement are required, simultaneously, a strategy to increase recruitment by having a good source population (>100) in the landscape that buffers the offtake of poachers would ensure tiger persistence. The PVA results corroborate the prioritization of resource allocation to important source populations within landscapes (Walston et al., 2010) as without securing them first, tiger recovery within large landscapes is difficult. However, Walston et al. (2010) do not advocate conservation of only source populations but propose to prioritize them for allocating limited resources. Our results acknowledge the relevance of landscape scale conservation as tiger occupancy of the landscape can only be possible with functional dispersal corridors. Prior to 2006, tiger populations were estimated by unreliable means (Karanth et al., 2003) and the official tiger estimate for India was 3,642 tigers (Narain, Panwar, Gadgil, Thapar, & Singh, 2005). Subsequent to the local extinctions of Sariska and Panna tigers caused due to poaching in 2005 and 2009 (Check, 2006; Gopal, Qureshi, Bhardwaj, Singh, & Jhala, 2010), the first tiger status estimation based on modern scientific approach was implemented and put the population at a precariously low number of 1,411 (1,165–1,657; Jhala et al., 2008). At that time, camera trap study in CNP (2006–2007) estimated the population to be at 108 (*SE* 4.5) within the same area of 500 km² (Contractor, 2007) as the current study. This was identified as one of the few sources of tigers remaining within the country and was prioritized for conservation investment (Jhala et al., 2008). After 2006, investment in stringent protection and resettlement of human habitation were undertaken and over 300 families were rehabilitated from within the core area of Corbett TR under the new incentivized voluntary rehabilitation package (Narain et al., 2005; Wildlife Protection Act, 1972, 2006 amendment). By 2012, the entire Corbett Tiger Reserve (1,288 km²) had a tiger density comparable to that of the CNP, with Corbett Tiger Reserve being home to about 143–198 tigers (Bisht et al., 2012). This strategy of high investment in a source population has paid dividends and resulted in an increase in tiger occupancy and numbers in the larger landscape of western *Terai* between 2006 and 2014 (Figure 3), where tigers have increased from 178 (*SE* 17) individuals occupying 1,901 km² to 340 (*SE* 41) individuals occupying 6,576 km² (Jhala et al., 2008, 2011, 2015).

The high-density source population of CNP was characterized by a stable population with high proportion of females breeding, high recruitment, low apparent survival and high turnover of individuals. These characteristics permitted tigers to be produced at rapid rates to disperse and populate most available habitat within the landscape within a period of 8 years. The optimal *Terai* and foothill habitats were almost all occupied by tigers by 2014, and tigers are now dispersing to high altitude habitats as well (Bhattacharya & Habib, 2016). Our study documents potential thresholds that can be achieved by tiger populations under optimal conditions. This information and the strategy of focusing conservation efforts on source populations within each landscape can be used to plan and implement realistic tiger recovery programmes globally.

AUTHORS' CONTRIBUTIONS

Y.J. and Q.Q. conceived, designed and secured the resources for the study; Shikha and Sudip conducted the field work; Shikha and Y.J. analysed the data; Shikha and Y.J. wrote the manuscript. All authors

contributed critically to the drafts and revisions and gave final approval for publication.

DATA ACCESSIBILITY

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