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Demography of a small, isolated tiger (*Panthera tigris tigris*) population in a semi-arid region of western India

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Abstract

Background: Tiger populations have declined globally due to poaching, prey depletion, and habitat loss. The westernmost tiger population of Ranthambhore in India is typified by bottlenecks, small size, and isolation; problems that plague many large carnivore populations worldwide. Such populations are likely to have depressed demographic parameters and are vulnerable to extinction due to demographic and environmental stochasticity. We used a combination of techniques that included radio telemetry, camera traps, direct observations, and photo documentation to obtain 3492 observations on 97 individually known tigers in Ranthambhore between 2006 and 2014 to estimate demographic parameters. We estimated tiger density from systematic camera trap sampling using spatially explicit capture-recapture (SECR) framework and subsequently compared model inferred density with near actual density.

Results: SECR tiger density was same as actual density and recovered from 4.6 (SE 1.19) to 7.5 (SE 1.25) tigers/100km^2 over the years. Male: female ratio was 0.76 (SE 0.07), and cub: adult tigress ratio at 0.48 (SE 0.12). Average litter size was estimated at 2.24 (SE 0.14). Male recruitment from cub to sub-adult stage (77.8%, SE 2.2) was higher than that of females (62.5%, SE 2.4). But male recruitment rate as breeding adults from the sub-adult stage (72.6%, SE 2.0) was lower than females (86.7%, SE 1.3). Annual survival rates, estimated by known-fate models, of cubs (85.4%, $CI_{95\%}$ 80.3–90.5%) were lower than that of juvenile (97.0%, $CI_{95\%}$ 95.4–98.7%) and sub-adult (96.4%, $CI_{95\%}$ 94.0–98.9%) tigers. Adult male (84.8%, $CI_{95\%}$ 80.6–89.2%) and female (88.7%, $CI_{95\%}$ 85.3–92.2%) annual survival rates were similar. Human-caused mortality was 47% in cubs and 38% in adults. Mean dispersal age was 33.9 months (SE 0.8), males dispersed further (61 Km, SE 2) than females (12 Km, SE 1.3). Higher age of first reproduction (54.5 months, SE 3.7) with longer inter-birth intervals (29.6 months, SE 3.15) was likely to be an effect of high tiger density.

Conclusion: Demographic parameters of Ranthambhore tigers were similar to other tiger populations. With no signs of inbreeding depression there seems to be no eminent need for genetic rescue. The best long-term conservation strategy would be to establish and manage a metapopulation in the Ranthambhore landscape.

Keywords: Camera traps, Dispersal, Inter-birth interval, Known fate, Litter size, Mortality, Radio-telemetry, Ranthambhore, Spatially explicit capture-recapture, Survival

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Background

At the onset of the nineteenth century, India was home to nearly 40,000 tigers (*Panthera tigris tigris*, Linnaeus) [1], while currently there are around 2200 left [2]. The decline in tigers was primarily due to hunting, prey depletion, followed by habitat loss [3]. A timely and proactive conservation measure, in the form of Project Tiger initiated in 1973 by the Indian Government [4], initially halted the rapid decline caused by trophy hunting. But an increased demand for tiger body parts in China and Southeast Asia in the past 25 years has severely impacted wild tiger populations. Demand driven poaching resulted in the local extinction of tigers in Sariska and Panna Tiger Reserves in India [5, 6]. Most tiger populations currently are small, isolated, and highly structured [3, 7, 8]. Such populations are vulnerable to extinction events caused by environmental and demographic stochasticity [9, 10]. Ranthambhore was a famous hunting reserve for the *Maharajas* of Jaipur, and numerous *shikar* (hunting) camps were organized in pre and post-independence era [11]. Subsequent to India's independence, intensity of hunting increased since tiger *shikar* was considered a social status symbol. This unregulated hunting caused a severe decline in Ranthambhore tiger population, and before the onset of Project Tiger (1973), there were around 14 tigers left in Ranthambhore [12]. After an initial recovery in 1980's, rampant poaching in 1992 and 2005, caused Ranthambhore tiger population to decline below 15 individuals from about 40 [13, 14]. Local extinctions in the last five decades suggest that tigers of the semi-arid region of western India are most vulnerable [15]. The tiger population of Ranthambhore is the only population that survives in western India. It typifies the problems many large carnivore populations face globally i.e. small founder population and lack of connectivity with other source populations. Small isolated populations like Ranthambhore are susceptible to loss of genetic variability caused by genetic drift and inbreeding depression [16, 17]. Such populations often lose their ability to adept in response to environmental changes and some manifest deleterious effects in the form of morphological abnormalities and depressed population vigour [18, 19]. Hence, understanding demographic parameters of a potentially genetically compromised population to determine the need for genetic rescue is important for developing appropriate conservation strategies [20]. Quantifying demographic parameters needs long-term data over multiple generations and for long-lived carnivores such datasets are rare [21]. Till date most population studies conducted on tigers aim at estimating abundance [22–29], while studies on demographic parameters (like survival rates, litter size, sexual maturity, reproductive success) have been sparse (but see [30–32] for *P. t. tigris* and, [33, 34] for *P. t. altaica*).

Herein, we report demographic parameters of free ranging tigers from Ranthambhore Tiger Reserve from a nine-year study where 97 individually known tigers were monitored, and annual density estimated by spatially explicit capture-recapture using camera traps. By 2012 due to intensive monitoring, we had photo-captured almost all tigers of Ranthambhore and had developed a catalogue for individually identifying them. We use this information to compare snapshot density estimated by model-based inference with near reality. We also compare demographic parameters of Ranthambhore tigers with those of other tiger populations and conclude that though Ranthambhore tigers have undergone population bottlenecks, with limited gene flow and small population size, their demographic parameters do not seem to be compromised.

Methods

Study area

The study was conducted from 2006 to 2014 in Ranthambhore Tiger Reserve (hereafter RTR, latitudes $25^0 41'$ N to $26^0 22'$ N and longitudes $76^0 16'$ E to $77^0 14'$ E) which is situated at the junction of two ancient mountain ranges, the Aravalli and the Vindhya. RTR is part of the western Indian landscape that has Sariska Tiger Reserve in the north, Kuno Wildlife Sanctuary and Madhav National Park in the east, Ramgarh Visdhari Wildlife Sanctuary and Mukundara Hills Tiger Reserve in the south-western part (Fig. 1). The core area of RTR was composed of Ranthambhore National Park (392 km^2), Sawai Mansingh Sanctuary (290 km^2) while Kailadevi Wildlife Sanctuary (630 km^2) was designated as the buffer zone of RTR. Within this western Indian landscape, tigers were only present in Ranthambhore NP during the commencement of this study and subsequently colonised Sawai Mansingh Sanctuary in 2008–09. These together comprise the only source population of tigers in the landscape. During this study, tigers from this population were reintroduced in Sariska [35] and six tigers dispersed into northern as well as south-eastern and eastern part of the landscape (Fig. 1).

The sub-tropical dry climate of RTR experiences three distinct seasons: mostly dry winters (October–February, minimum average temperature 5 °C, relative humidity ~10%), hot summers (March–June, mean maximum temperature 45 °C, relative humidity 10–15%), and humid monsoons (July–September, average rainfall 700 mm, relative humidity >60%). RTR primarily comprises of steep hills, gentle slopes, plateaus, and narrow valleys dotted with shallow man-made perennial lakes. The area is representative of dry deciduous *Anogeissus pendula* forests in association with *Acacia*, *Butea*, *Capparis*, *Zizyphus* and *Prosopis* species (5B/C_2 - Northern Tropical Dry

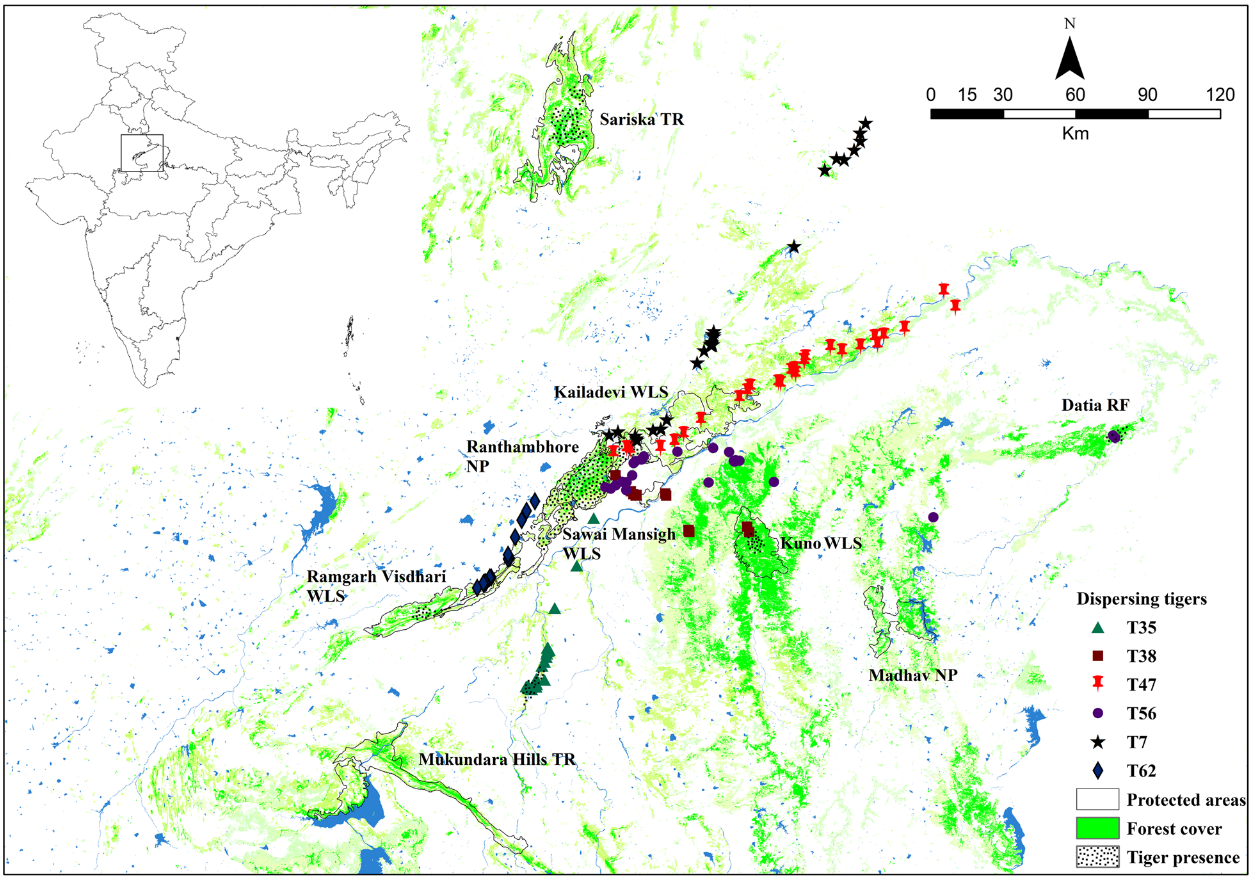

Fig. 1 Landscape of Ranthambhore showing the tiger reserve and other tiger occupied forest patches in western India. Locations of six individual tigers that dispersed out of the tiger reserve are shown. The map inset shows the location of Ranthambhore Tiger Reserve within IndiaTR - Tiger Reserve; NP - National Park; WLS- Wildlife Sanctuary; RF – Reserve Forest; Ranthambhore NP, Sawai Mansingh WLS and Kailadevi WLS together constitute the Ranthambhore Tiger Reserve

Deciduous forests. 6B/DS1 - *Zizyphus scrub*, DS1 - Dry deciduous scrub and 5/DS4 - Dry Grasslands, of Champion & Seth [36] classification). A diverse assemblage of carnivore species (17 species from 7 different families) were recorded during the course of the study, which include tiger, leopard (*Panthera pardus*, Linnaeus), sloth bear (*Melursus ursinus*, Shaw), striped hyena (*Hyaena hyaena*, Linnaeus), caracal (*Caracal caracal*, Schreber), fishing cat (*Prionailurus viverrinus*, Bennett), jungle cat (*Felis chaus*, Schreber), desert cat (*Felis silvistris*, Schreber), rusty-spotted cat (*Prionailurus rubuginosa*, I. Geoffroy Saint-Hilaire), golden jackal (*Canis aureus*, Linnaeus), Indian fox (*Vulpes bengalensis*, Shaw), honey badger (*Mellivora capensis*, Schreber), common palm civet (*Paradoxurus hermaphorditus*, Pallas), small Indian civet (*Viverricula indica*, É. Geoffroy Saint-Hilaire), Indian gray mongoose (*Herpestes edwardsii*, É. Geoffroy Saint-Hilaire), small Indian mongoose (*Herpestes auropunctatus*, Hodgson), and ruddy mongoose (*Herpestes smithi*, Gray). Tiger prey species present in the study area were chital (*Axis axis*, Erxleben), sambar (*Rusa unicolor*, Kerr), nilgai (*Boselaphus tragocamelus*, Pallas), chinkara (*Gazella bennetti*, Skyes), wild pig (*Sus scrofa*, Linnaeus), common langur (*Semnopithecus entellus*, Dufresne) and rhesus macaque (*Macaca mulata*, Zimmermann).

Field methods: Monitoring of tigers

We monitored 97 individual tigers during the study (2006 to 2014) through camera traps, radio-telemetry and routine patrolling (for direct sightings and photo-documentation) by researchers and forest staff. We developed criteria for classifying tigers into age groups by observing known-age individuals and use teeth eruption, ware, and body characteristics (see Additional file 1 for age estimation of tigers) similar to that of lions [37, 38]. We classified tigers into six age classes, namely, cubs (< 12 months), juveniles (12-24 months), sub-adults (2–3 years), young adults (4–5 years), prime adults (6–10 years) and old adults (> 10 years). Of the 97 tigers, 74 were known since cub stage, and their age was known to the exact month. Sex of the individuals was ascertained by the time cubs were 6 months old.

Camera trapping

Camera traps were used a) in a systematic grid-based design (4km^2 in 2006, 2009, 2012 and 2013, and 2km^2 in 2014) for a short duration to estimate tiger abundance, and b) to target specific areas so as to determine the presence and use of the area by particular individual tigers throughout the study period.

a) The entire tiger occupied part of RTR was sampled in a systematic manner during the study by placing a pair of camera traps at each selected location within a grid. After conducting a reconnaissance survey, camera traps were placed on dirt roads, animal trails, fire lines and dry river beds at locations that maximized the chances of photo-capturing tigers. A pair of camera traps (TrailMaster® Lenexa KS USA, Cuddeback™ Green Bay USA, MOULTRIE® Alabama USA, or Stealth Cam® LLC Grand Prairie USA), facing each other, were placed at each location to get both flank photos of tigers at the same time. Each Camera was programmed with unique trap ID, time and date stamp on each photograph. Location of each camera trap was recorded by handheld GPS unit (Garmin 72™ and Garmin Etrex® 10, Kansas, USA) and plotted on a digitized map of RTR in GIS domain to ensure no sampling holes were present. Cameras were checked every 2–3 days to ensure proper functioning and recovery of data. Each photo captured tiger was identified to individuals by comparing their stripe patterns and given a unique id (e.g. T1, T2, and so on). The entire study area was sampled simultaneously within a period of 28 to 51 days so as to adhere to the assumption of population closure [39]. The camera trapped area sampled each year as estimated by joining the outer most camera traps ranged between 139 to 492 km^2 (Table 1).

b) Besides systematic camera trapping conducted once in a year, cameras were also used in a need based manner to record photographs of specific tigers. Areas of tigers that were not seen for over 60 days were specifically targeted. These special efforts were carried out by placing multiple camera traps and conducting an intensive ground search in most probable locations of that tiger. The effort continued till the fate of that tiger was ascertained by locating it or confirming its death or dispersal. Since the landscape outside of the tiger reserve was human-dominated, the presence of dispersing tigers was quickly detected by reports of livestock kills and sighting of tigers or their signs by villagers. The research team along with forest department staff subsequently tried to locate each such tiger and ascertain its identity through sighting, camera traps or hand held photography.

Radio telemetry

Eight tigers (three adult males, one adult female, three sub-adult males and one sub-adult female) were radio-collared between April 2007 to May 2009. Tigers were anesthetized with ketamine hydrochloride in combination with medetomidine injected intramuscularly using a gas-powered projectile dart delivery system [40]. Tigers were collared with a Very High-Frequency transmitter (Telonics, Arizona, USA) and in most cases with a Global Positioning System with ground download facility

Table 1 Sampling details and parameters estimates of tiger density from camera trap based spatial capture-recapture analysis in Ranthambhore Tiger Reserve

Year	No. of camera locations	Camera trap Polygon (km^2)	Trap Nights	M_{t+1}[a]	N[b](SE)	P[e]	Known tiger population > 1 Year			D (SE)[d] /100km^2 (CI$_{95\%}$)	Known density[c] /100km^2	g0 (SE)	σ (SE) Km
							♂	♀	Cub				
2006	40	139	48	16	16 (0.73)	1.0	5[f]	15[f]	15[f]	4.62 (1.19) (2.81–7.59)	–	♀: 0.06 (0.009)	2023.0 (131.6)
												♂: 0.03 (0.007)	4162.6 (430.4)
2009	48	162	28	25	26 (1.52)	0.96	19[f]	17[f]	2[f]	8.75 (1.79) (5.88–13.02)	–	♀: 0.05 (0.009)	1547.0 (110.2)
												♂: 0.05 (0.009)	1564.4 (104.3)
2012	60	223	45	22	30 (3.9)	0.73	12	16	6	5.68 (1.22) (3.74–8.64)	5.60	♀: 0.08 (0.008)	1529.0 (81.7)
												♂: 0.08 (0.007)	2136.9 (97.2)
2013	76	464	51	37	40 (2.62)	0.92	18	20	14	7.56 (1.25) (5.47–10.44)	7.60	♀: 0.05 (0.005)	1480.7 (85.5)
												♂: 0.05 (0.005)	1948.7 (83.3)
2014	182	492	48	39	39 (1.38)	1.0	21	21	12	7.22 (1.16) (5.27–9.88)	7.63	♀: 0.05 (0.006)	1496.5 (73.3)
												♂: 0.04 (0.003)	2161.7 (78.4)

[a] M_{t+1}: Unique adult tigers photo-captured in camera traps

[b] N: Population estimates derived from spatially explicit capture recapture technique (regional population size using 'region.N');

[c] Known density: Known tiger population/ tiger occupied area ♂: Male; ♀: Female

[d] D: Density estimates (model averaged); g0: detection probability at home range center; σ: movement parameter

[e] P: Proportion of the population detected by camera trap survey

[f] Since all tigers were not photo-captured, here we have reported the minimum number of known individuals

(HABIT, British Columbia, Canada). Soon after the radio-collaring operation, Atipamezole was administered for reversing the effect of the tranquilizer [40]. Animals were left after natural reflexes and behaviour returned and subsequently monitored through telemetry. Radio-collared tigers were tracked and regularly monitored (>three times a week) from a vehicle or on foot throughout the functional period of those collars. Tigers were tracked with the help of a hand-held directional 3- element Yagi antenna and Telonics and HABIT receivers. After the battery life of the radio-collars, the surviving collared tigers were monitored through camera traps and visual sightings.

Routine patrolling

Due to intensive camera trapping over the years and photo documentation by researchers and park officers, we were reasonably certain that almost all tigers of RTR were photo-captured by 2012 and were individually known. Our claim of knowing almost all RTR tigers was substantiated by the fact that in subsequent years no unknown adult tiger was recorded either by camera traps or by any other means. All additions to RTR population from 2012 onward till date were from known cubs. A photo album was developed and shared with the staff and officers of RTR in 2012 with additions and deletions done every 6 months. Since adult tiger numbers ranged between 20 to 40 individuals, it was possible to identify each tiger on most occasions it was sighted and often photographed with digital cameras by forest department staff and researchers. When in doubt these photographs were compared with the photo-album or on the computer to ascertain the tiger's identity. A daily record on all tiger observations was maintained in a register which was subsequently transferred to a database.

Analytical methods: Estimating demographic parameters of tigers

Tiger abundance

We used likelihood based spatially explicit capture-recapture (SECR, [41, 42] in package 'secr' on R platform [43, 44] to estimate tiger density from the systematically sampled camera trap data over the years (2006, 2009, 2012, 2013, and 2014; Table 1). SECR consists of two sub-models. The distribution sub-model depicts the spatial distribution of detectors and animal captures in the landscape. The detection sub-model (g(x)) declines with increasing distance between the animal's activity centre, and this spatial scale of detection is parameterized by sigma (σ). A spatial capture history matrix, a trap layout matrix, and a habitat mask that excluded non-habitat areas from the SECR model space were prepared and used in secr. Home-range size (as indexed by σ) is often correlated with density [45]. Since the tiger population of RTR increased during our study period, we, parameterized σ and g0 (capture probability at the activity centre) separately for each year. Male and female tigers were likely to differ in their ranging patterns. Hence we used gender as a covariate to model heterogeneity in movement parameter (σ). Half-normal detection function was used to model σ. We used AIC_c (Akaike Information Criterion corrected for sample size) [46] to compare models with the null model (where g0 and σ were constant) and amongst themselves. Models with less than five delta AICc values were considered probable and the parameter estimates were obtained by AICc weighted model averages [47]. Cubs (<12 months) were excluded from density estimation since this cohort is underrepresented in camera traps and has relatively high mortality [22, 48]. Since by 2012 we were reasonably certain that almost all tigers of RTR were individually known to us, we use this information to compare estimates obtained by SECR with actual known density.

Sex ratio and female reproductive parameters

Since sex of all tigers was known, we have calculated sex ratio (adult males: Adult females) for each year (sampling without replacement) by counting the total number of males and females in the population, and an estimate of its versatility between years [49].

Before giving birth, females restricted themselves to a small area of their territory [30, 50] and were often detected through frequent photo-captures and higher intensity of use at a particular site. Births were confirmed from photo-captures or direct sighting of lactating females (Additional file 1), while most cubs were recorded (photo-captured or sighted) with their mother only after they were about 2 months old. Since litter size at birth was rarely known, our reported litter size could be an underestimate as mortality before 2 months' age was not known. The ratio of cub: adult tigress was computed. Age at first reproduction was determined by recording first birth of tigresses that were monitored since they were cubs. Inter-birth intervals were recorded from intensively monitored tigresses that littered more than once during the study period. We recorded intervals between two successive litters when all cubs of the previous litter died before reaching dispersal age (more than 2 years) and compare these with intervals between two successive litters when cubs of the previous litter survived beyond dispersal age.

Reproductive success and recruitment

We recorded reproductive success of tigresses as the number of cubs that survived to the age of independence (24 months). Individually identified tiger cubs that were monitored up to young adult stage allowed us to determine the age at which these tigers acquired territories either by displacing established tigers or in vacant habitats through dispersal. We calculated recruitment as the proportion of cubs that survived to the sub-adult stage (≥ 24 month). We also computed recruitment of sub-adults to successful breeders as the proportion of sub-adults that subsequently established territories. Territoriality was inferred when a young-adult exclusively used an area that was earlier used by other adult tigers of the same gender or dispersed to a vacant habitat and lived there for several months.

Survivorship

We estimated stage specific (cub, juvenile, sub-adult, young adult, prime adult, and old adult) survival probabilities of tigers by using known-fate model [51] in program MARK (*ver.*7, [52]). Known-fate models use Kaplan-Meier estimator [53, 54] to estimate survival which requires that fate of the individual is known with certainty during the period a particular individual is monitored. All individuals do not enter the study simultaneously but are added in a staggered manner known as the staggered entry design [54]. Radio-telemetered individuals provide the best data for such analyses [51]. However, in our case, besides the eight collared tigers that were located several times a week, each known individual tiger was observed (camera trap photo-captured, directly observed or photographed from hand-held cameras) at least once every month, and its fate recorded (see Additional file 2). In rare cases when an individual was not observed during an interval the known-fate model allows its observation to be 'censored' from the analysis [51]. Data on survival/death of tigers was compiled on a monthly basis. We subsequently pooled this data for a three-month period to have a good number of observations on each tiger as well as to have an interval that was meaningful for survivorship analysis of tigers that are reasonably long-lived. Live-dead encounter history matrix for tigers was made by pooling encounter histories of 3 months into one interval where *10* represented survival of the individual throughout the interval, *11* represented mortality of the individual during the interval, and *00* represented censoring the individual when that individual was not observed during the three-month interval. Only 59 observations on seven tigers out of 3492 observations from 97 tigers were censored during the study (see Additional file 2), forming a very small proportion (1.6%) of observation where fate could not be ascertained for that interval. All of these seven tigers were observed in subsequent periods, but by censoring them for intervals they were not recorded, we add to the uncertainty in our estimates [51]. Seven tigers (two juveniles, one sub-adult male, one young adult male, and three old adult females) out of 97 that we monitored went 'missing' during the study period. We considered two extreme scenarios for these individuals in our survival analysis: a) a highly likely conservative scenario, that these tigers were poached, and b) a more optimistic but less likely scenario that these tigers dispersed and we were unable to trace them. In case of scenario 'a', we modelled these tigers as dead, and in case of scenario 'b', we censored them from our analysis. The resultant estimates of survival would encompass the true estimate. For our analysis, the matrix was right censored for all the surviving tigers at the end of December 2014. Tigers that survived and were monitored from cub to adulthood were included in subsequent stages with the assumption that survival rates were independent for different stages. As part of tiger reintroduction program, seven tigers were translocated from RTR to Sariska Tiger Reserve during the study period [55]. These individuals were censored in our survival analysis at the time of their translocation since these tigers would be exposed to a different set of environmental factors in Sariska that determine their survival probability. We formulated and run different candidate models which were ecologically plausible and compare them using AICc values. Model averaged survival estimates were obtained for models with less than five delta AICc values [47].

Mortality events were confirmed when carcasses were recovered, and causes of mortality were recorded on the basis of post-mortem report compiled by experienced veterinary personnel and/or by questioning eyewitnesses (if any). Cub mortalities were confirmed when found dead. However, not all cub carcasses could be recovered. A cub was considered dead if it was not detected (not photo-captured or sighted) with its mother for more than a month [34]. There were no incidents where a cub that was not recorded for over a month (considered dead) was ever seen again. We considered seven tiger cubs (ranging from 2 to 10 months) that were provisioned by park managers after the death of their mother, as dead since they were unlikely to have survived in the wild on their own.

The small and isolated nature of RTR made it possible for us to follow and ascertain dispersal events of tigers. Tigers that left the National Park had to traverse human-dominated areas where their presence was detected readily by local communities who were always on a high vigil for large carnivores. The presence of tigers was detected from signs and examination of livestock kills (which were compensated by the Government). Our research team and park managers ascertained the identity of these tigers by targeted effort of camera trapping and visual sighting. Due to the high profile nature of RTR as well as the small tiger population that was vulnerable to poaching, the park management along with the research team made a concentrated effort to locate each tiger individually to ascertain its wellbeing. Mortality events were categorized into natural mortality (death of the mother, infanticide, old age, disease, intra-specific strife), human-caused mortality (poaching, poisoning, accidents due to human causes), and unknown.

Dispersal age and distances

We considered tigers to have reached dispersal age once they became ≥24 month old (considering the lowest age of dispersal). At this age most tigers no longer moved with their mothers and were capable of hunting on their own. Dispersals from the natal area were confirmed through telemetry, camera trap photographs, direct observations and hand-held photography of tigers. Dispersal distances (Euclidean distance) of these tigers were measured from the centre of their natal area to the most extreme location of that tiger.

Results

Tiger abundance

On the average an effort of 3715 (SE 1324) camera trap nights were invested each year (Table 1). In most years the model having g0 as constant (.) and movement parameter (σ) having sex-specific responses was selected as the best-fit model. In year 2009 the null model (g0(.), σ(.)) was selected as the best model (Additional file 3: Table S1). Annual model averaged density estimates varied from 4.6 to 8.7 tigers per 100 km^2 (Table 1). The movement parameter (σ) was consistently larger for males compard to females and was found to decline asymptotically with an increase in density for males (Fig. 2). The density estimate obtained from SECR did not differ from near actual density (Table 1).

Sex ratio and female reproductive parameters

Adult sex ratio (male: female) in the initial years (2006–07) was female biased (0.38, SE 0.04) and became marginally female biased (0.91, SE 0.04, 2008–14) in subsequent years. Overall male: female ratio was 0.76 (SE 0.07) during the study period. The total number of breeding females in RTR ranged between 12 to 15 (see Additional file 4: Figure S1). We recorded litter size from 33 litters of 18 females, and the mean litter size was 2.24 (SE 0.14; range = 1–4 cubs). Most of the litters were of two (50%) or three (31%) cubs (Fig. 3). Overall cub: adult female ratio (n = 9 years) was 0.48 (0.12 SE). We could ascertain the age at first reproduction for 11 tigresses that were monitored since they were cubs as 54.5 months (3.7 SE; range 33–68 months). Eight out of these 11 tigresses produced their first litter after 4 years of age, while only two tigresses gave birth before 3 years (see Additional file 5: Figure S2). The average interval between two successive litters (inter-birth interval) was 29.6 months (SE 3.15; range = 7–51 months, n = 14 intervals from 8 tigresses). Intervals were shorter when all cubs of previous litter died before reaching independence (24 months, 15.0, SE 4.04 months, n = 3) than when cubs of previous litters survived till independence (33.64, SE 2.83 months, n = 11, see Additional file 6: Figure S3).

Reproductive success and recruitment

More than 50% of the intensively monitored breeding females (n = 18) successfully raised all their litters to independence, while around 10% of the females failed to raise any of their cubs during the study period (Fig. 4). Data on 51 individuals indicated that male recruitment rate from cub to the sub-adult stage was higher (77.8%, SE 2.2) than females (62.5%, SE 2.4). But male recruitment rate as breeding adults in the population from the

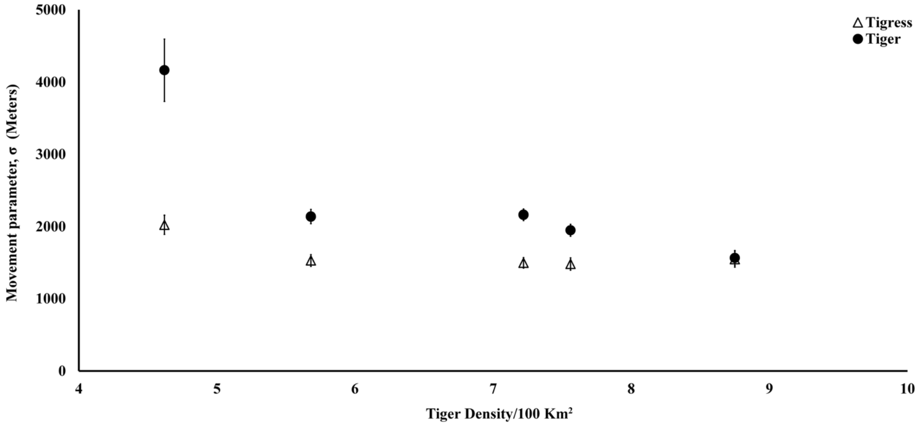

Fig. 2 The relationship between the movement parameter σ estimated using likelihood based spatially explicit capture recapture models and tiger density. Movement parameter σ for tigers declined asymptotically with increasing density while σ for tigresses remained relatively constant with increasing density

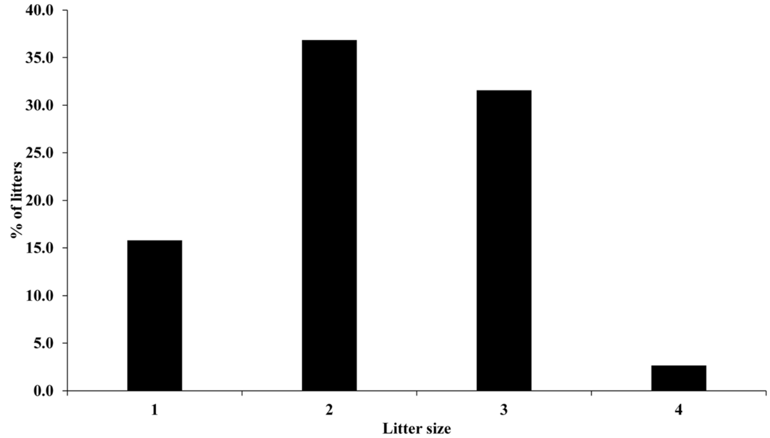

Fig. 3 Percent frequency of different sized litters (*n* = 33) of tigresses observed in Ranthambhore Tiger Reserve

sub-adult stage was lower (72.6%, SE 2.0) than females (86.7%, SE 1.3, Table 2).

Survivorship

The average annual survival rate of cubs (85.4%) were comparatively lower than that of other age classes (Table 3). Annual survival rate increased after cub stage, remained constant till prime adult stage after which it declined (Table 3). Survival rates for males and females were similar for younger stages while females had marginally higher survival in older stages (Table 3). The survival estimates with our conservative approach of considering seven missing tigers as dead did not statistically differ from survival estimates when these tigers were censored from the analysis (Additional file 7: Table S2).

We recorded 25 mortality events (17cubs and juveniles, and 8 adults) during our study. Amongst all cub and juvenile mortality, 41% were natural (infanticide and death of mother due to natural causes), 47% were human caused (mother poached, accidents due to human causes and poisoning) and 12% of these could not be ascertained (Fig. 5). Amongst all adult mortality, 50% were natural (old age, disease, and intra-specific strife), and 38% were human-caused (poisoning and poaching, Fig. 5), the cause of 12% adult mortality could not be determined.

Dispersal age and distances

We recorded dispersal of 29 tigers, of these six were long distance dispersal out of RTR (Fig. 1). Mean dispersal age of tigers in RTR was 33.9 months (SE 0.8, range = 24–42 months). Mean male dispersal distances (60.6, SE 2.1 Km) were larger than that of females (12.1, SE 1.3 Km, Fig. 6). Most of the females established their territory near their natal area while the majority of the males dispersed further from their natal areas. Five out of 16 males and one out of 13 females dispersed outside RTR and settled in forest patches within the larger landscape. These long distance dispersal movements ranged from 56 to 220 km Euclidean distance from their natal areas.

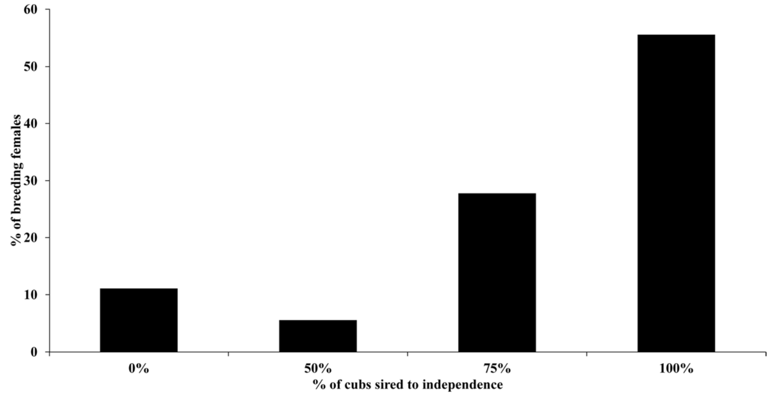

Fig. 4 Reproductive success of breeding females in Ranthambhore Tiger Reserve measured as a percentage of cubs that survived to recruitment age (24 months) (*n* = 74 cubs from 33 litters of 18 females)

Table 2 Recruitment of tigers with known fate (from ~2 months of age to age of independence >2 years and as territorial adults >3 years) in Ranthambhore Tiger Reserve

Classes	No. of cubs	Recruitment to adult stage (%)	Recruitment as territorial adults (%)
Male	27	21 (77.8%, $CI_{95\%}$: 73.5–82.0%)	16 (76.2%, $CI_{95\%}$: 72.4–80.0%)
Female	24	15 (62.5%, $CI_{95\%}$: 57.8–67.1%)	13 (86.7%, $CI_{95\%}$: 84.1–89.2%)
All	51	36 (70.6%, $CI_{95\%}$: 64.2–76.9%)	25 (69.4%, $CI_{95\%}$: 64.0–74.8%)

Discussion

Tigers are conservation dependent species and require substantial investments in terms of management and protection for their long-term persistence [56]. Information on survival, recruitment, litter size, reproductive parameters, dispersal, sex ratio and density that we provide in this paper are the basis of estimating population viability and planning management interventions.

We mostly use standard methodology, but adept some and develop a few approaches required for procuring data from endangered carnivores. The subsequent analyses of these data do not violate any underlying assumptions of the analytical procedures. We believe that we were justified in using Known-Fate model for estimating survival due to the high frequency (every month) of observations of 97 individually known tigers for determining their fate (see Additional file 2). As explained in our methods, we 'censored' surviving individuals when the study was completed and for the few occasions in-between when we could not determine the fate of individuals [51]. Open population capture-mark-recapture models cannot distinguish between emigration and mortality, and are confounded by the nuisance parameter of imperfect detection [51, 57]. Therefore, known-fate models though being data intensive, provide more precise and more informative parameter estimates.

Table 3 Survival rates of tigers (n = 97) in Ranthambhore between 2006 to 2014

Age class	Gender	Sample size	Average annual survival rate[a] ($CI_{95\%}$)
Cubs (< 12 months)	Male	39	85.35 (80.3–90.4) %
	Female	35	85.40 (80.3–90.5) %
Juveniles (1–2 years)	Male	33	97.05 (95.4–98.7) %
	Female	26	97.06 (95.4–98.7) %
Sub adults (2–3 years)	Male	28	96.46 (94.0–98.9) %
	Female	19	96.49 (94.1–98.9) %
Young adults (3–5 years)	Male	20	93.87 (88.0–99.8) %
	Female	18	94.26 (89.0–99.6) %
Prime adults (5–10 years)	Male	15	82.53 (74.6–90.4) %
	Female	20	86.43 (80.7–92.1) %
Old adults (> 10 years)	Male	3	82.78 (76.9–88.7) %
	Female	12	84.52 (79.1–90.0) %
Adults (> 3 years)	Male	38	84.88 (80.6–89.2) %
	Female	50	88.74 (85.3–92.2) %
All adults (> 3 years)	Male and Female	88	86.99 (84.3–89.7) %

[a] Conservative estimates, where we have considered seven 'missing' tigers as dead; a more likely scenario

During the initial phase of the study (i.e. 2006) tiger density in RTR was low (Table 1) as the population was recovering from a recent decline caused by poaching. In subsequent years, density increased with good protection and fluctuated between 5.6 to 8.7 tigers/ 100km^2 with a mean density of 7.5 (SE 2.7) tigers/ 100km^2 (Table 1). This fluctuation in tiger density was likely due to synchrony in breeding by several females and recruitment of a large cohort of sub-adults that became available for camera trap sampling at an approximate interval of 2 years. As tiger density increases within a limited area, we would expect home-range to either decrease and/or show an increase in overlap. The movement parameter σ is an index of home-range radius over short time duration [42]. Efford et al. [45] show an asymptotic decline in σ with increase in tiger density from data across India. Herein, we demonstrate a similar relationship between σ and tiger density within a single population which we believe is ecologically more meaningful (Fig. 2). The asymptotic nature of σ for males and a relatively constant σ for females suggests that male tigers' home range decline to some extent with increase in tiger density, while home range size in females, which is based primarily on food availability [31], does not change with density. This could be interpreted to suggest that either tigresses do not invest energy in acquiring a home range larger than required to rear cubs or that Ranthambhore National Park was already near carrying capacity density with little scope of reduction in home-range sizes for tigresses. The increase in tiger numbers in RTR was accompanied with an increase in tiger occupancy while the number of breeding females remained relatively constant (12 to 15) during our study period (see Additional file 4: Figure S1). Camera trap data suggests that the entire core area of RTR (Ranthambhore National Park and Sawai Mansingh Sanctuary) was occupied by tigers by 2014. We also witnessed intense competition between mothers and daughters for breeding territories. This was another indication that tiger density was at or near carrying capacity within the core of RTR. For high density populations near carrying capacity regulatory mechanisms may include delayed age of first reproduction, increased inter-birth intervals, smaller litter sizes and depressed survival [58]. Delayed female age of first reproduction and longer intervals between two

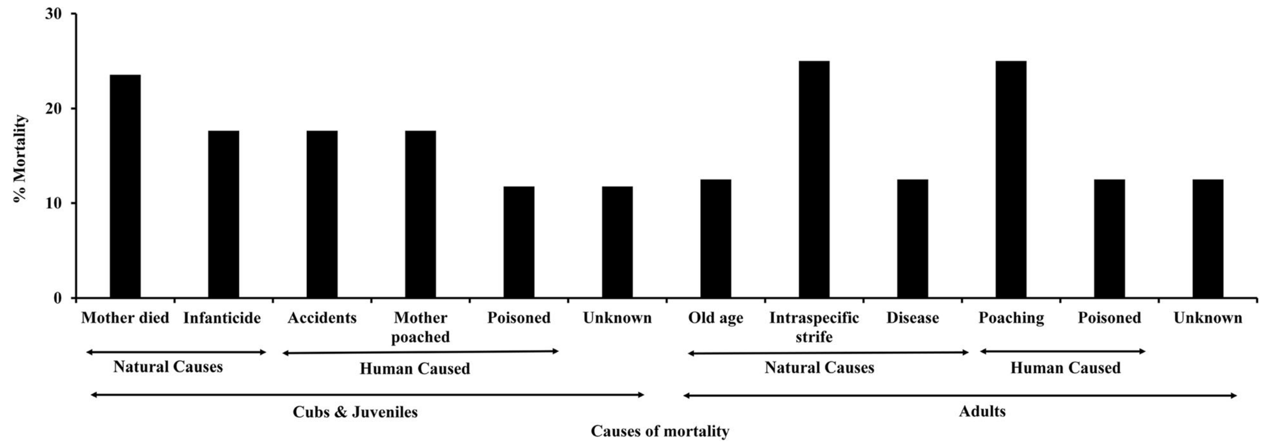

Fig. 5 Cause-specific mortality of cubs and juveniles ($n = 17$) and adult tigers ($n = 8$) in Ranthambhore Tiger Reserve between 2006 to 2014

successive litters observed in RTR tigers were likely an effect of high tiger density at or nearing carrying capacity inside the core of RTR. Parameters that could potentially be depressed by inbreeding depression like litter size, cub survival, and disease caused mortality were either similar or better in comparison to other tiger populations (Table 4).

In highly inbred populations morphological abnormalities are often observed and resistance to disease is often compromised [18, 59]. During our study we did not encounter cubs with abnormalities or skeletal defects and mortality of tigers attributed to disease was only one. The morphometric measurement of RTR tigers captured for radio-collaring were among those of the largest recorded for tigers in India (YV Jhala, unpublished data). These observations along with comparable demographic parameters to other tiger populations, suggest that there were no deleterious effects that had as yet manifested among RTR tigers due to population bottlenecks, small size and isolation [18]. This seems likely, since, till recent times the semiarid zone tiger population of central India was large and well connected [15] and the population bottlenecks that RTR tigers passed through did not remain very small for long periods of time (less than one generation time) [60]. However, we lack data on early infant mortality and foetal loss during pregnancy, which are some of the parameters that would be influenced by inbreeding depression. Reddy et al. [61] conclude that RTR tigers had reasonable genetic diversity comparable to other central Indian tiger populations. Studies that link genetic variability with population size, connectivity, and ultimately with demography are required for conservation management of large carnivores.

Females that had lost cubs before their recruitment age gave birth within a smaller time interval as also reported in tigers [62] and in Asiatic lions [38]. Due to a high level of protection, poaching was rare inside RTR during the study period. Therefore, long and stable tenures of territorial males were recorded (mean 5.6 years, range 4 to 11 years, $n = 13$). Only three cases of infanticide were observed during this study; this contrasts with studies on tigers in Chitwan National Park in Nepal [30] and Asiatic lions in Gir [38], where infanticide was a major cause of cub mortality. Mean dispersal age of RTR tigers (~33 months) was higher than reported for Chitwan (~23 months) [30], and Amur tigers (~19 months, Kerley et al. 2003). Young tigers were not compelled to leave their natal territories due to new male takeovers [30]. This stability in territorial male tenures allowed young tigers, especially males, to continue to live longer within their natal area enhancing their survival and achieving rapid growth to breeding body size. On four occasions we observed sub-adult male tigers occupy small ranges in peripheral areas of resident male territories. Once such tigers become sufficiently

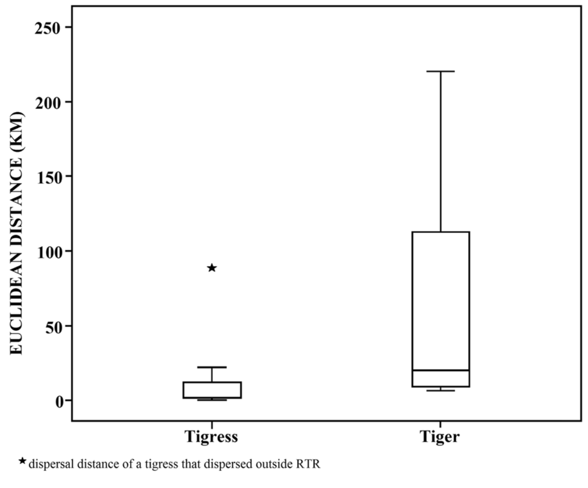

Fig. 6 Dispersal distances of tigresses ($n = 13$) and tigers ($n = 16$) from their natal area in Ranthambhore landscape

Table 4 Comparison of demographic parameters of tigers from Ranthambhore Tiger Reserve with demographic parameters from published studies

Sources	Area (sub-species)	Litter size	Female age at 1st reproduction (years)	Inter-birth intervals (months)	Cub survival probability	Adult survival	
						Male	Female
Sankhala 1978 [67]	Zoo, India (*Panthera tigris tigris*)	2.9 (*n* = 49)	3–6 years	24–36	NA	NA	
Smith & McDougal 1991 [30]	Wild, Nepal (*P. T. tigris*)	2.98 (n = 49)	3.4 years (n = 7)	21.6 (n = 7)	0.65	NA	
Chundawat et al. 2002 [68]	Wild, India (*P. t. tigris*)	2.3 (*n* = 12)	NA	21.6 (n = 14)	NA	NA	
Kerley et al. 2003 [33], Goodrich et al. 2008 [34]	Wild, Russia (*P. T. altaica*)	2.4 (± 0.6) (n = 16)	4 (± 0.4) years (*n* = 4)	21.4 (± 4.4) (*n* = 7)	0.53–0.59	0.63 (±0.2)	0.81 (±0.1)
Singh et al. 2013 [32]	Wild, India (*P. t. tigris*)	2.9 (± 0.2) (n = 18)	NA	25.2 (± 1.8) (n = 9)	NA	NA	
Singh et al. 2013 [32]	Wild, India (*P. t. tigris*)	2.3 (±0.1) 2(*n* = 22)	NA	33.4 (± 3.7) (n = 7)	NA	NA	
Present study	Wild, India (*P. t. tigris*)	2.24 (±0.14) (n = 33)	4.54 (± 0.3) years (n = 11)	29.6 (± 3.1) (*n* = 14)	0.85 (±0.02)	0.84 (±0.02)	0.88 (±0.01)

NA not available

large so as to challenge resident males, they expand their range into that of the residential males' territory. By following this strategy relatively smaller and inexperienced sub-adult males avoid lethal encounters with larger and experienced males during their initial dispersal stage [31].

Ten out of 13 sub-adult females established territories near their natal areas, two females established their territory inside RTR but ~20 km away from their natal area, and one female dispersed outside the reserve (~90 km). We observed that females either established their territory beside their mothers (*n* = 3) or occupied a part of their mother's territory and gradually pushed their mother off (*n* = 5). One female that initially occupied her mother's territory by displacing her mother produced her first litter in this territory, but subsequently shifted her territory with her 12-month-old cubs (of her second litter) ~10 km away from her natal territory. This shift coincided with the takeover of her natal territory by a new male tiger. Her natal territory was subsequently occupied by her daughter from her first litter.

The dispersing sex in tigers is known to be males [31]. Amongst RTR tigers, males did disperse larger distances than females, but opportunities to disperse were restricted in this landscape. Large dispersal distances travelled by tigers (once out of RTR), and older age of dispersal reflects the difficulty a tiger faces in locating appropriate vacant habitat to settle. The small reserve size combined with very little and disjunct tiger habitat available outside the reserve system within a hostile human-dominated habitat matrix restricted dispersal. Males that managed to disperse and locate habitat patches tried to settle there, but due to lack of female tigers in these patches, were unable to breed. If areas of Kailadevi Wildlife Sanctuary (part of RTR buffer), Kuno Wildlife Sanctuary, Ramgarh Visdhari Wildlife Sanctuary and Mukundara Hills Tiger Reserve (Fig. 1) are made free of human settlements through incentivised voluntary relocation scheme (WPA 1972; 2006 amendment), these areas could harbour breeding population of tigers. Simultaneously dispersal corridors between these tiger habitats and with core of RTR need to be secured and restored to promote a metapopulation in this landscape. Initially, once these areas have been appropriately restored and have sufficient prey base, this tiger dispersal could be aided by translocating tigers. Establishing and managing the tiger population in the larger Ranthambhore landscape as a metapopulation [63] would be desirable for long-term conservation.

Park authorities often intervene by treating injured tigers in-situ or supplementing food resources for orphan/sick cubs. These activities, although well intentioned, hinder the natural process of selection and the social dynamics of the species [38, 64]. Such interventions also reduce the genetic fitness of the population over time by ensuring the survival of unfit individuals especially if sick animals are treated, saved and allowed to breed [18]. Interfering with the natural process may be necessary for highly endangered populations where every living individual counts. However, RTR is now a high tiger density area [65], and therefore, management interference of health care should be extremely selective, if any.

Conclusion

Our study did not find any evidence of detrimental effects resulting from a small population that could potentially be inbred and there seems to be no current need for genetic rescue [20] of RTR tigers. Currently RTR has about 15 breeding units and adult female survival of about 88%, these are bare minimal requirements to ensure long-term persistence [66]. Managing the Ranthambhore landscape by restoring habitat patches and connectivity with RTR so as to promote a metapopulation of tigers would enhance the potential of long-term persistence of this last remaining semi-arid tiger population in western India.

Additional files

Additional file 1: Field Guide for Aging Tigers. (PDF 8068 kb)

Additional file 2: Individual tiger monitoring data used for "Known Fate" survival analysis. (PDF 98 kb)

Additional file 3: Table S1. Sampling details and parameters estimates of annual tiger density from camera trap based spatial capture-recapture analysis in Ranthambhore Tiger Reserve. (PDF 84 kb)

Additional file 4: Figure S1. Number of breeding tigresses in each year observed in Ranthambhore Tiger Reserve during the study period. (TIFF 258 kb)

Additional file 5: Figure S2. Age at first reproduction of tigresses ($n = 11$) observed in Ranthambhore Tiger Reserve. (TIFF 515 kb)

Additional file 6: Figure S3. Inter-birth intervals of tigresses in Ranthambhore Tiger Reserve when all cubs of previous litter died before reaching independence ($n = 3$ litters) and when cubs of previous litters survived beyond 24 months (n = 11). (TIFF 344 kb)

Additional file 7: Table S2. Survival rates of tigers ($n = 97$) estimated in an optimistic (where we have censored seven 'missing' tigers) as well as a conservative (a more likely scenario where we have considered seven 'missing' tigers as dead) approach in Ranthambhore between 2006 to 2014. (PDF 8 kb)

Abbreviations

AIC_c: Akaike Information Criterion, corrected for sample size; $CI_{95\%}$: 95% Confidence Interval; g0: Capture probability at activity centre; n: Sample size; NP: National Park; RTR: Ranthambhore Tiger Reserve; SE: Standard Error; SECR: Spatially Explicit Capture Recapture; TR: Tiger Reserve; σ: Sigma, movement parameter

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Availability of data and materials

All data are either reported in tables in the text or in the supplementary material online.

Authors' contributions

YVJ and QQ conceived the study, and raised funds, YVJ & QQ supervised the study, AS and PPC, YVJ conducted the field work, YVJ did the radio-collaring, QQ, RSS and SS coordinated the field work, assisted in radio-collaring, RSS and SS provided logistic support, assisted in monitoring tigers and locating dispersing tigers, AS and YVJ analysed the data and wrote the manuscript. All authors have read, provided inputs, and given their consent to publish the final manuscript.

Ethics approval

Permissions for capture and collaring tigers were obtained under the Wildlife (Protection) Act 1972 from the Ministry of Environment and Forests, Government of India and the Chief Wildlife Warden, Government of Rajasthan. The technical committee of the National Tiger Conservation Authority which also considers the well-being of animals and ethics of research approved the research project. Tigers were anesthetized using standard drugs under supervision by qualified veterinarians. All tigers were observed from a safe distance till they fully recovered from the anaesthesia and walked away into the forest.

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

Publisher's Note

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