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RESEARCH

Effects of a reintroduced tiger population on large carnivores in Panna Tiger Reserve, central India

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Abstract
Large carnivores shape ecosystem structure through trophic cascades and resource facilitation, yet multi year, multi-species density studies remain scarce limiting effective conservation management. This study aimed to address this gap by investigating population dynamics of three sympatric large carnivores (tigers: *Panthera tigris*, leopards: *Panthera pardus*, and hyena: *Hyaena hyaena*) residing in Panna Tiger Reserve, central India, using individual-level capture-recapture data (2017-2021). We applied maximum likelihood (ML-SECR) and Bayesian (B-SECR) spatially explicit capture-recapture methods to estimate density, abundance and the spatial scale of detection (σ). Tiger density increased from 3.77 ± 0.79 to 6.69 ± 1.06 per 100 km² (ML-SECR) and 2.1 ± 0.14 to 4.23 ± 0.31 per 100 km² (B-SECR), with a female-biased population structure. Leopard density, the highest reported across Indian tiger reserves, ranged from 23.87 ± 2.21 and 30.07 ± 2.31 per 100 km² (ML-SECR) and 19.70 ± 1.39 to 22.87 ± 1.34 per 100 km² (B-SECR), exhibiting a marginal declining trend. Hyena density remained stable (13.76 ± 1.49 to 16.58 ± 1.64 per 100 km² ML-SECR; 8.22 ± 0.35 to 9.25 ± 0.55 per 100 km², B-SECR), reflecting adaptive responses to resource competition. The spatial scale parameter (σ) was highest in tigers, followed by hyenas and leopards, with males exhibiting larger ranges than females. Spatial analysis revealed that leopard density was higher in areas of low tiger density, with pronounced seasonal segregation during summer. The recovering tiger population did not supress leopard density, instead, intense intra-specific competition emerged as the primary driver of leopard population dynamics. Declining σ with increasing carnivore density indicates density-dependent home-range compression across all three species.

Keywords Bayesian analysis · Capture-recapture · Density · Large carnivore · Population

Introduction

Large carnivores significantly impact mammal community structure through resource facilitation and trophic cascades, despite exhibiting cryptic behaviour, high mobility, and low population densities (Karanth 1995; Ripple et al. 2014). In the Anthropocene, habitat loss, fragmentation, poaching and prey depletion pose major challenges to the long-term survival of large carnivores (Seidensticker et al. 1999). These challenges have led to a sharp decline in the tiger (*Panthera tigris*) population, which has decreased by ~93% from its global historical range (Goodrich et al. 2015). Similar declines are observed in other large carnivores, including lions (*Panthera leo*, 94%), cheetahs (*Acinonyx jubatus*, 92%), leopards (*Panthera pardus*, 79%), and striped hyenas (*Hyaena hyaena*, 15%; Wolf and Ripple 2017). Consequently, large carnivores have experienced local extinctions in various regions worldwide (Michalski and Peres 2005; Brugière et al. 2015; Louys 2014; Mahmood et al. 2021). For instance, tigers were locally extirpated from Sariska and Panna Tiger Reserves (PTR) in the central Indian tiger landscape in 2005 and 2009 respectively (Sankar et al. 2010; Wildlife Institute of India 2009) due to the poaching.

Protected areas have played a crucial role in supporting the persistence and recovery of numerous large mammal species (Margules and Pressey 2000; Brooks et al. 2009).

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After reintroduction of initial three founder individual (two females and a male) in 2009, PTR is one such protected area, holding a recovered tiger population (Ramesh et al. 2013), along with viable co-predator populations of leopards and hyenas (Jhala et al. 2021). The tiger, an endangered flagship species, requires effective conservation management based on its population size, abundance, and existing threats (Krebs et al. 2010).

Tigers and leopards, the two largest sympatric felids in the central Indian landscape, coexist as obligate carnivores and solitary hunters (Kumar et al. 2019; Rather et al. 2021). The striped hyena, characterized by its large body size and solitary, nocturnal behaviour, is widely distributed in the arid and semi-arid landscapes of India (Califf et al. 2020). It primarily functions as a facultative scavenger, feeding on carcasses of domestic and wild ungulates (Singh et al. 2010). Intra-guild competition among large carnivores, leading to the displacement of individuals of subordinate species by dominant ones, is well documented (Holt and Polis 1997; Linnell and Strand 2000). Notably, such competitive interactions often classify the tiger as the dominant and the leopard as the subordinate species (Odden et al. 2010; Harihar et al. 2011). Therefore, assessing the effects of apex predators on the density dynamics of other carnivores is crucial for understanding carnivore coexistence.

The development of camera trap-based classical capture-recapture (CR) methods (Otis et al. 1978; Karanth and Nichols 1998) has become the preferred approach for estimating the abundance of uniquely identifiable individuals of a species with high certainty. This approach combines CR and conventional distance sampling (Burnham et al. 1980; which is known as Spatially Explicit Capture-Recapture (SECR) methods. This method has been effectively used for tigers (Jhala et al. 2020), leopards (Kalle et al. 2011), and hyenas (Gupta et al. 2009). However, despite their ecological significance, there are limited studies on the long-term population trends of these species (Durant et al. 2011). Most studies on tiger population trends utilize either classical non-spatial closed capture-recapture models (Karanth et al. 2006; Harihar et al. 2009) or statistically less rigorous track counts (Miquelle et al. 2015).

Large carnivores have been the focal species of numerous density estimation studies, such as tigers (Jhala et al. 2020; Qureshi et al. 2023), leopards (Edgaonkar 2008; Kalle et al. 2011; Mondal et al. 2012), and hyenas (Gupta et al. 2009; Panda et al. 2022; Alam et al. 2015). A more limited studies have examined these species together such as tiger-leopard (Lamichhane et al. 2019; Rather et al. 2021) or leopard-hyena (Mandal et al. 2017) pairs. However, no study has focused all these three species concurrently, so as a result, the impact of two large carnivores on mammalian scavengers such as hyena is not known. Here, we investigate the population dynamics of these three sympatric large carnivores (two obligate predators and one facultative scavenger), with specific focus on: (a) estimating their density and population size, (b) assessing whether temporal variation in the density of the reintroduced tiger population was associated with corresponding variation in leopard and striped hyena densities; and (c) examining changes in home range size (the spatial scale parameter, σ) with change in density. Based on evidence of interference competition between tigers and leopards and the potential facilitation of scavengers through carrion provisioning, we hypothesized that tiger density would be negatively associated with leopard density (Harihar et al. 2011) and positively associated with striped hyena density (Prugh and Sivy 2020). We further hypothesized that the spatial scale parameter (σ), used as an index of home-range size, would decline with increasing conspecific density, consistent with density-dependent space use (Mattisson et al. 2013; Efford et al. 2016). This study represents the first-ever attempt to investigate the density and abundance of multiple large carnivores over substantial timescale in a dry deciduous forest ecosystem.

Methods

Study area

PTR is situated in the Vindhyan hill range of the Central Indian highlands, encompassing the districts of Panna, Chhatarpur, and Damoh in Madhya Pradesh (Fig. 1). PTR is administratively divided into a core zone of 542 km² and a buffer zone of 1032 km², which includes the Gangau Wildlife Sanctuary. The distinctive plateau of the Vindhyan hill range features unique topographical elements such as gorges, rocky escarpments, and caves (Dutta et al. 2024). Elevations within PTR range from 164 to 555 mASL. The Ken River, the only perennial river in the region, traverses the lower basin. The vegetation within PTR is characterized by tropical dry-deciduous forests (Champion and Seth 1968; Meher-Homjio 2001). Dominant tree species include teak (*Tectona grandis*), tendu (*Diospyros melanoxylon*), and kardhai (*Anogeissus pendula*). The reserve also contains mixed forests, exclusive bamboo patches, grasslands (particularly in areas of relocated villages), and riparian forests. The climate is sub-tropical dry with three distinct seasons: a hot, dry summer (March-June) with maximum temperatures of 45 °C and relative humidity of 15-20%; a humid monsoon season (July-October) with average precipitation of 1100 mm; and a cool, dry winter (November-February) with minimum temperatures of 5 °C and relative humidity around 15%. The apex predator in this ecosystem is the tiger (*Panthera tigris*), with the leopard (*Panthera pardus*)

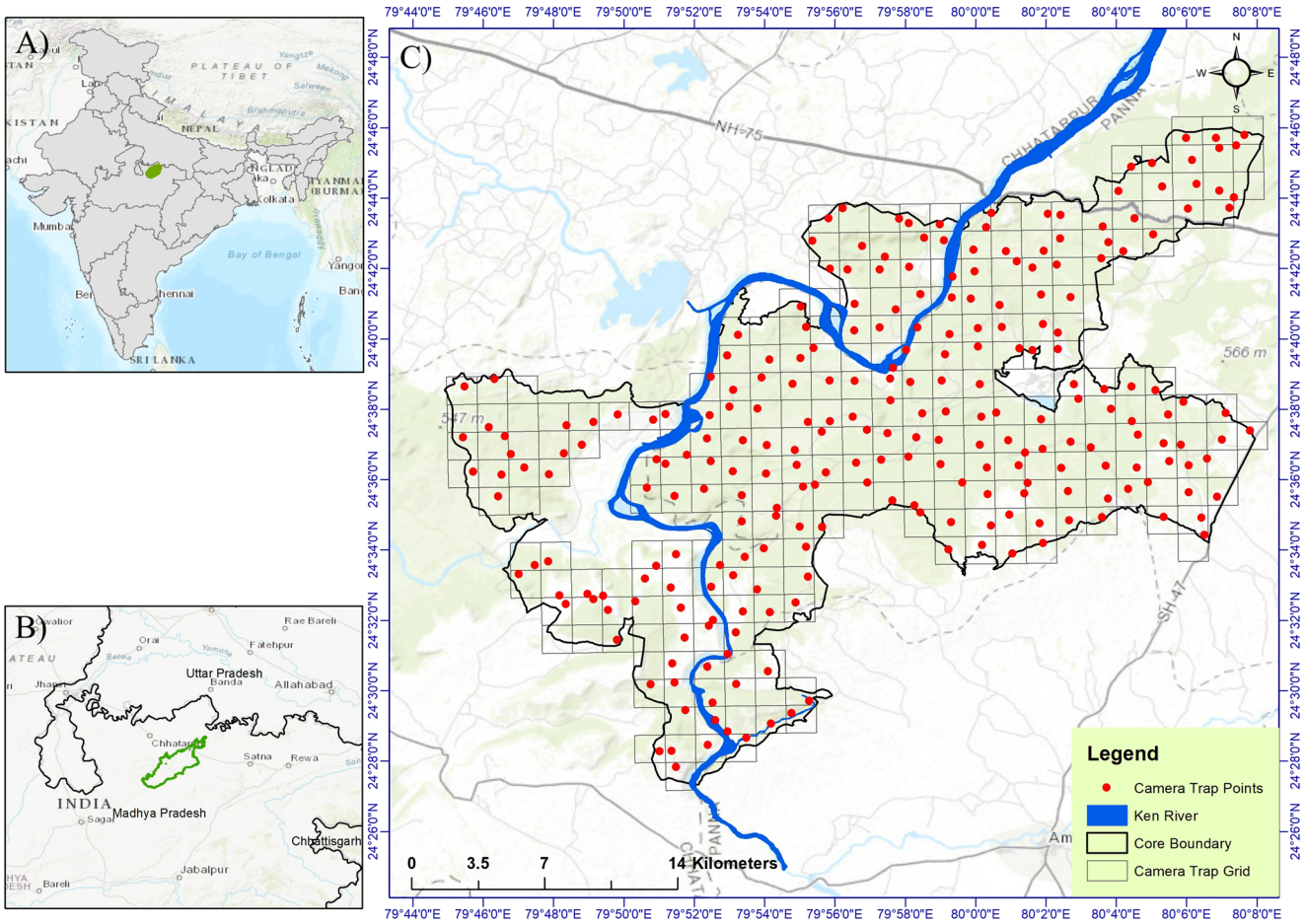

Fig. 1 Map showing the position of the study area. Map (**A**) India, (**B**) state of Madhya Pradesh, **C**) camera tarp locations within the core area of Panna Tiger Reserve

serving as the second most dominant predator. The ecosystem supports a variety of other carnivores, including the Indian wolf (*Canis lupus*), golden jackal (*Canis aureus*), striped hyena (*Hyaena hyaena*), sloth bear (*Melursus ursinus*), Asiatic wild dog (*Cuon alpinus*), Indian fox (*Vulpes bengalensis*), and smaller carnivores such as the honey badger (*Mellivora capensis*), jungle cat (*Felis chaus*), Asiatic wildcat (*Felis silvestris*), and rusty-spotted cat (*Prionailurus rubiginosus*). Major prey species in PTR include chital (*Axis axis*), sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelus*), chinkara (*Gazella bennettii*), chousingha (*Tetracerus quadricornis*), and wild pig (*Sus scrofa*). The buffer zone of PTR is home to approximately 30,000 people residing in 63 settlements, along with a livestock population of roughly 6,300.

Data collection

Field methods

We conducted a camera trap survey from 2017 to 2021 during the winter and summer seasons. Camera traps were deployed (stations: 243–254) during January-February for winter sampling and May-June for summer sampling (mean duration: 32: 29-35 days, Table S1). Pairs of automated motion-triggered digital camera traps (Cuddeback C1; www.cuddeback.com) were deployed within a 2 km² grid cell framework following the All India Tiger Estimation guidelines (Jhala et al. 2020). The average distance between two adjacent camera trap stations was 1.05 ± 0.28 km (± SD), ensuring intensive sampling coverage. Camera traps were installed on either side (facing each other) of animal trails, forest roads, riverbeds, and mid-slopes at 30-40 cm above ground level to optimize the capture of large carnivores (Chen et al. 2009; Johnson et al. 2009; Evans et al. 2019). All camera traps operated 24 h a day during the sampling period and were programmed to take one photograph

per trigger with a 5-second delay interval. Camera trap data were checked at 15-day intervals. This research was conducted under permit number Technical/4301, dated 09/06/2015, issued by the Principal Chief Conservator of Forest (Wildlife Division), Madhya Pradesh, India.

Analytical methods

Images retrieved from the camera traps were identified to the species and individual-level identification of tigers, leopards, and hyenas based on their pelage patterns using the Program Hotspotter (Crall et al. 2013). The photos were also manually cross-checked. Capture-recapture (CR) matrices for each species were prepared. Genders for tigers and leopards were identified based on genitalia and secondary sexual characteristics (e.g. nipples) from images.

Density

Maximum likelihood framework

We applied maximum likelihood (ML) based spatially explicit capture-recapture (SECR) approach (ML-SECR; Efford et al. 2004) to estimate the densities of three carnivore species. This approach incorporates fundamental parameters, including the detection probability at the home-range center (g_0) and the spatial scale of detection (σ). It assumes that animals are independently distributed in space and occupy distinct home ranges (Borchers and Efford 2008). The model utilizes the spatial coordinates of captures to assess detection probability (g_0) as a function decreasing with increasing distance (σ) from the animal's activity center (Efford et al. 2004). Data analysis was performed using the 'secr' package (Efford 2024) in R 4.3.2 (R Core Team 2023). The model space was delineated with an eight km buffer around the outermost trap locations, excluding non-habitat areas to define the final region for model integration, forming the habitat mask for density estimation (Efford 2024). We fitted null models (D ~ 1, lambda0 ~ 1, sigma ~ 1) along with eight distinct model combinations to predict carnivore density. Akaike Information Criterion (AIC) values were computed for each model to identify the optimal fit. To address variations in home-range sizes between males and females, which affect capture and movement probabilities (Sunquist and Sunquist 2002), we conducted separate density estimations for each gender.

Bayesian framework

In addition to ML-SECR, we estimated the density and abundance of tigers, leopards, and hyenas using Bayesian SECR (B-SECR) models implemented in the 'SPACECAP' package (Gopalaswamy et al. 2012) in R 4.3.2 (R Core Team 2023). The Bayesian framework is considered more robust than ML (Beerli 2006). We created an eight km buffer from the peripheral camera trap locations and generated equally spaced points (580 m apart, grid size of 0.336 km²; Gopalaswamy et al. 2012; Lamichhane et al. 2019) to represent hypothetical home-range centers. Each analysis was conducted with 50,000 Monte Carlo Markov Chain (MCMC) iterations, including a burn-in of 10,000 iterations and a thinning interval set to 10. The burn-in parameter designates the initial steps of the MCMC run to be discarded, while the thinning parameter specifies the steps to be omitted to mitigate serial autocorrelation. We configured the model definitions to 'trap response present,' which implements a 'trap-specific' behavioural response where the probability of capture at a specific trap increases (or decreases) after the initial capture. The 'Spatial Capture-Recapture' option runs a spatially explicit capture-recapture analysis. Convergence of the MCMC chain was assessed using Geweke statistics (Geweke 1992). The augmentation value was assigned based on the upper limit of the predicted population size obtained from ML-SECR. We generated a pixelated map of the densities of the three carnivore species at the home-range center size (0.336 km²). Similar to ML-SECR, here λ denotes the detection probability at the home-range center, and σ represents the spatial scale of detection.

Both ML-SECR and SPACECAP packages account for camera trap failures by considering the effort (active vs. non-active camera traps) over number of occasions (i.e., trapping nights) and calculating the detection probability based on the specified effort. Additionally, the movement parameter σ, often used as a surrogate for home range size, was shown to be density-dependent, declining exponentially with increasing animal density (Efford et al. 2016). We tested this index with the density of three carnivores by performing a generalized linear model (GLM) using the density of carnivores as independent variables.

Results

During the study period (2017–2021), we processed a total of 3,462 tiger photos, 5,414 leopard photos, and 11,371 hyena photos, with a cumulative trap effort of 47,641 trap nights (Table S1). We identified 55 individual tigers, including 24 males and 31 females, and 264 individual leopards, including 121 males and 143 females. Additionally, we identified 162 different hyenas during the study tenure, however, sex could not be reliably determined from the camera-trap photographs and was therefore not included in the analysis.

Table 1 Session-wise density of tigers (*Panthera tigris*) in two different methods (ML-SECR and B-SECR) within the Panna Tiger Reserve. Here M(t+1) indicates the total number of unique individuals identified in each session. 'N' is denoting the estimated abundance along with projected range of population size (Figure S1, Table S3A-F)

Session	CT	M(t+1)	M	F	SECR			SPACECAP		
					Density/100 km^2	*N*	Range	Density/100 km^2	*N*	Range
W18	244	23	9	14	3.77±0.79	23±0.72	23–27	2.1±0.14	26±1.71	23–29
W19	248	32	14	18	5.16±0.91	32±0.71	32–35	3.01±0.20	37±2.42	32–41
S19	254	33	13	20	5.24±0.92	33±1	33–39	3.23±0.29	42±3.76	35–49
W20	245	39	14	25	6.4±1.03	39±0.96	39–45	3.69±0.22	45±2.74	40–50
S20	243	40	17	23	6.69±1.06	40±1.06	40–46	4.23±0.31	52±3.73	45–58
W21	249	35	14	21	5.61±0.95	35±0.72	35–39	3.45±0.24	42±2.94	36–47

Table 2 Session-wise density of leopards (*Panthera pardus*) in different methods within the Panna Tiger Reserve. Here M(t+1) indicates the total number of unique individuals identified in each session. 'N' is denoting the estimated abundance along with projected range of population size (Figure S2, Table S5A-F)

Session	CT	M(t+1)	M	F	SECR			SPACECAP		
					Density/100 km^2	*N*	Range	Density/100 km^2	*N*	Range
W18	244	172	82	90	30.07±2.31	183±3.94	178–194	22.20±1.17	271±14.32	242–299
W19	248	161	76	85	27.81±2.20	170±3.70	166–181	22.39±1.23	273±15.03	244–302
S19	254	151	74	77	25.66±2.10	162±3.87	157–172	22.87±1.34	279±16.36	248–309
W20	245	175	85	90	28.91±2.19	177±1.69	176–183	21.25±0.99	259±12.02	237–281
S20	243	126	60	66	23.87±2.21	145±6	136–161	19.70±1.39	240±16.91	209–270
W21	249	149	75	74	25.12±2.09	159±3.62	154–167	21.39±1.19	261±14.49	235–290

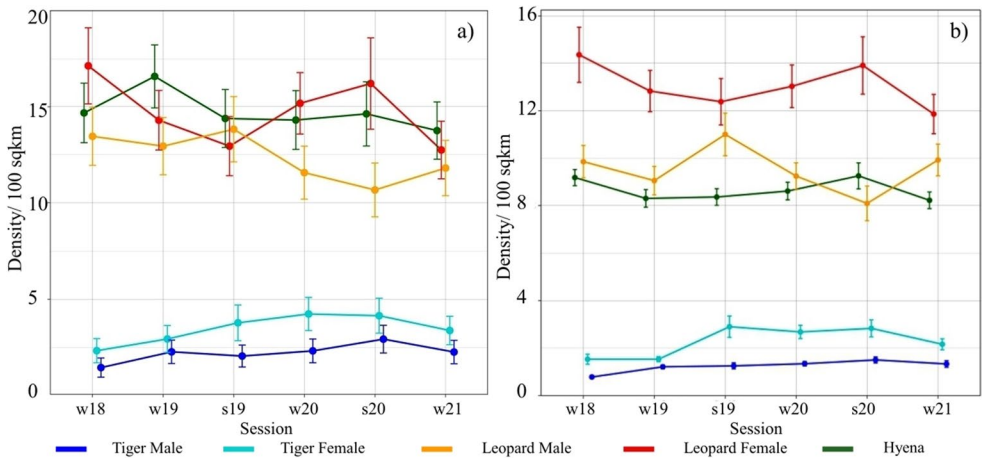

Fig. 2 Graph showing the session wise density of tigers (*Panthera tigris;* male-female), leopards (*Panthera pardus;* male-female) and hyenas (*Hyaena hyaena*), using two different methodologies (**a**) ML-SECR and (**b**) B-SECR

Density

Our estimates revealed a notably high density of tigers within the core area of PTR as reflected by ML-SECR and B-SECR models. We observed an increasing trend in tiger density, varying from 3.77±0.79 to 6.69±1.06 per 100 km² (ML-SECR, Table 1, Table S2A) and 2.10±0.14 to 4.23±0.31 per 100 km² (B-SECR, Table 1, Table S2B) from winter 2018 to summer 2020 with a slight decline during the winter 2021 session. The tiger population was female-biased and showed a high degree of heterogeneity. The maximum estimated tiger population sizes were 46 (ML-SECR) and 58 (B-SECR) individuals including within the eight km buffer from the camera trap array during the camera trap session summer 2020.

Leopard density, which did not have any sex bias, was 5–6 times higher than tiger density, with estimates ranging from 23.87±2.21 to 30.07±2.31 per 100 km² in ML-SECR (Table S4A) and 19.70±1.39 to 22.87±1.34 per 100 km² in B-SECR (Table 2, Table S4B). Contrary to tiger density, leopard density showed marginally decreasing trend since 2018, For winter 2021, ML-SECR estimated 159±3.62 leopards, with an estimated range of 154–167, whereas B-SECR estimated 261±14.49 individuals, with a range of 235–290.

In terms of gender-based density analyses, male tiger population densities ranged from 1.44±0.5 to 2.92±0.72 per 100 km², while female densities varied from 2.32±0.63 to 4.23±0.86 per 100 km² (Fig. 2a, Table S6A-C) according to the ML-SECR method. The B-SECR method showed

Table 3 Session-wise density of hyenas (*Hyaena hyaena*) in different methods within the Panna Tiger Reserve. Here M(t+1) indicates the total number of unique individuals identified in each session. 'N' is denoting the estimated abundance along with projected range of population size (Figure S3, Table S11A-F)

Session	CT	M(t+1)	SECR			SPACECAP		
			Density/100 km^2	*N*	Range	Density/100 km^2	*N*	Range
W18	244	95	14.68±1.55	95±0.71	95–98	9.18±0.34	112±4.17	105–120
W19	248	86	16.58±1.64	86±0.91	86–92	8.30±0.37	101±4.48	92–109
S19	254	87	14.39±1.51	88±1.07	87–93	8.36±0.35	102±4.28	93–109
W20	245	88	14.31±1.53	88±0.87	88–94	8.61±0.37	105±4.53	96–114
S20	243	82	14.63±1.67	89±3.75	85–100	9.25±0.55	113±6.7	99–124
W21	249	85	13.76±1.49	86±1.12	85–91	8.22±0.35	100±4.29	91–108

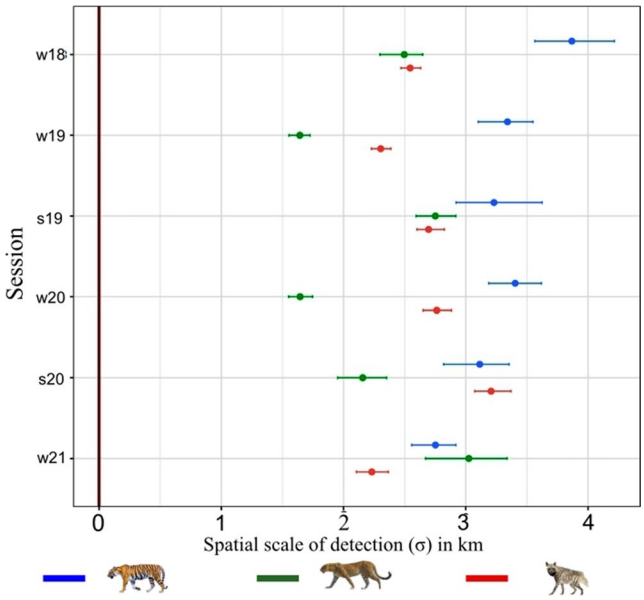

Fig. 3 Plot showing session-wise changes of the spatial scale of detection (σ) of three different carnivores

male tiger population densities ranging from 0.78±0.06 to 1.49±0.13 per 100 km², while female tiger densities ranged from 1.53±0.11 to 2.89±0.44 per 100 km² (Fig. 2b, Table S7A-C). Similarly, leopard density also varied between females and males. Male leopard density ranged from 10.67±1.4 to 13.83±1.7, while female density ranged from 12.75±1.5 to 17.13±1.98 based on the ML-SECR method (Fig. 2a, Table S8A-C). B-SECR showed similar patterns, with male leopard density varying from 8.09±0.73 to 11±0.9, and female leopard density recorded as high as 14.36±1.16 and as low as 11.86±0.83 (Fig. 2b, Table S9A-C).

We recorded comparatively stable hyena population the four years of monitoring. Using the ML-SECR method, density ranging from 13.76±1.49 to 16.58±1.64 per 100 km^2 (Table S10A), and the highest population abundance was 100 in summer 2020. Whereas, B-SECR estimated the density ranging from 8.22±0.35 to 9.25±0.55 per 100 km^2 with the maximum abundance of 124 individuals (Table 3, S10B).

The sigma (σ) value, representing the spatial scale of detection and an index of home range size, varied widely among all three carnivores on a yearly and seasonal basis (Fig. 3). The mean sigma was greater for tigers (3.28±0.14 km, Table S2B), followed by hyenas (2.62±0.14 km, Table S10B), and leopards (2.28±0.23 km, Table S4B). Higher σ values were observed in males (tiger: 4.14±0.26 km, Table S7B; leopard: 2.41±0.31 km, Table S9B), compared to females (tiger: 2.63±0.52 km, Table S7C; leopard: 1.88±0.11 km, Table S9C).

The density-based contour plot revealed that leopard density was higher in areas where tiger density was very low (Fig. 4). This inverse relationship was particularly pronounced during the summer season, with leopard density highly concentrated in regions where tiger density was extremely low (Fig. 4b), comparatively to winter (Fig. 4a).

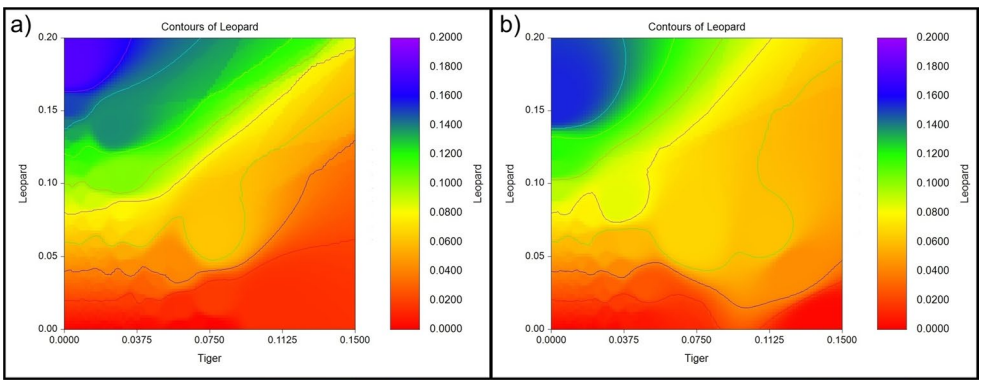

Fig. 4 Contour map showing leopard density against tiger density for both the seasons (**a**) winter and (**b**) summer. Density of tiger and leopard was derived from ML-SECR

We observed a declining trend in sigma (derived from B-SECR) for all carnivores as the density of tigers increased during the study period. The declining sigma was not significant in relation to the density for tigers (♂: −0.00 ± 0.09, $P = 0.95$; ♀: −0.31 ± 0.18, $P = 0.17$) and hyenas (−0.63 ± 0.55, $P = 0.32$). However, for male leopards, there was a significant relationship between σ and density (♂: −1.06 ± 0.35, $P = 0.04$), but not for female leopards (♀: −0.79 ± 0.67, $P = 0.30$, Fig. 5).

Discussion

Large carnivore population dynamics reflect inter and intra specific nature of ecosystem response (Andersen et al. 2004; Bolnick et al. 2011). Studies have shown considerable disparity in tiger density across tiger reserves in India, ranging from as low as 0.27 ± 0.12 (Kalakad Mundanthurai Tiger Reserve) to 14.65 ± 0.92/100 km² (Corbett Tiger Reserve; Qureshi et al. 2023). Following the successful reintroduction of tigers in PTR, tiger population density increased from 2.9 ± 0.9 to 3.18 ± 0.43/100 km² (Ramesh et al. 2013; Qureshi et al. 2023). PTR's tiger population density was similar compared to other tiger reserves in the central Indian landscape (Table 4). This study documented substantial fluctuations in tiger density within the core area of PTR, with a 77% fluctuation over four years, akin to the 62% fluctuation observed over seven years in Huai Kha Khaeng, Thailand (Duangchantrasiri et al. 2016). Furthermore, we observed a slight increase in male and female tiger density over the study period, indicating a relatively stable population within the park. Such fluctuations are common to tiger populations and arise from demographic stochasticity in the number of breeding females, adult or cub survival, and subadult dispersal (Sunquist 1981; Smith 1993; Goodrich et al. 2008). The high survival rate of the reintroduced tiger population

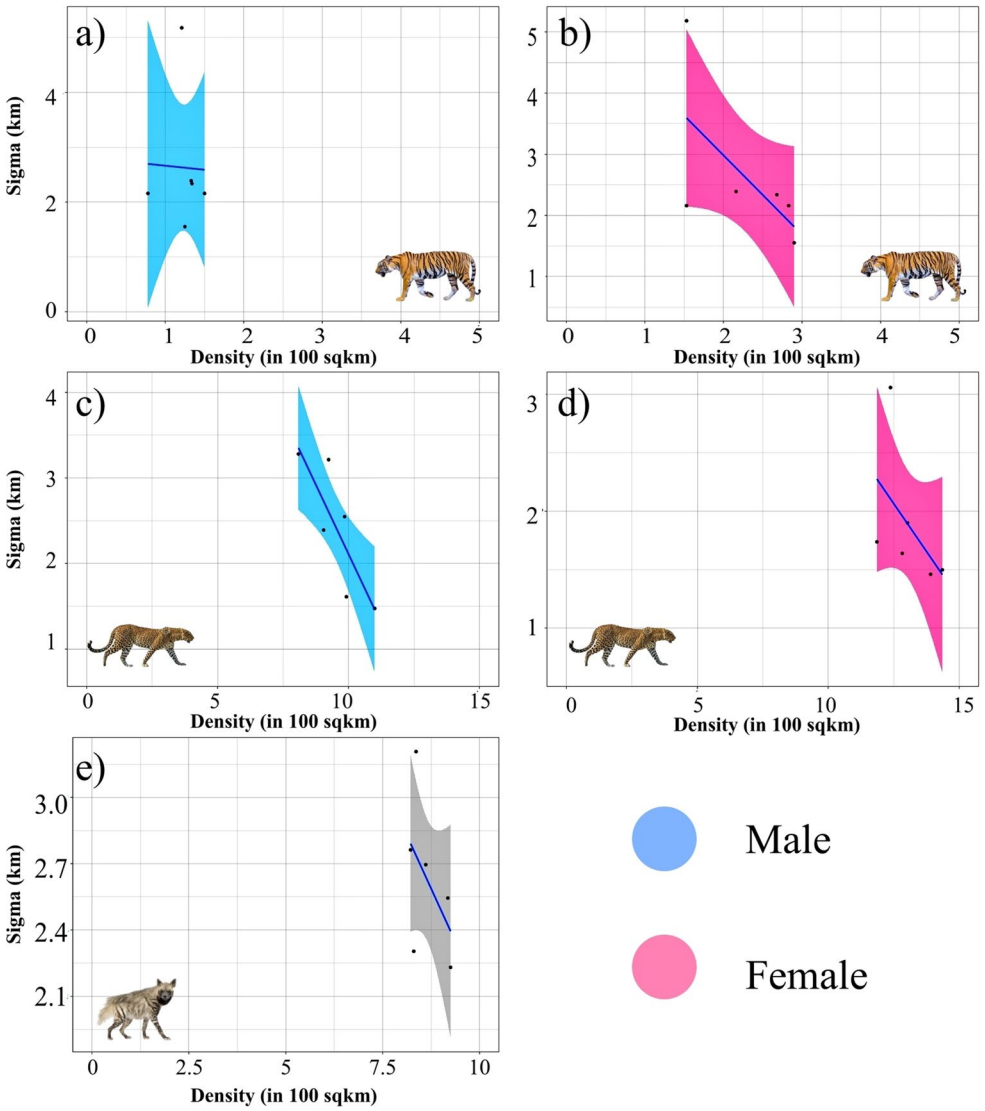

Fig. 5 Plots showing the relationship between sigma, an index of home-range, with density of tigers (*Panthera tigris*) (**a**) male, (**b**) female, leopards (*Panthera pardus*) (**c**) male, (**d**) female and (**e**) hyenas (*Hyaena hyaena*)

Table 4 Comparison of estimated tiger (*Panthera tigris*), leopard (*Panthera pardus*) and hyena (*Hyaena hyaena*) densities in different protected areas of India

Study Site	Density/100 km^2			Reference
	Tiger	Leopard	Hyena	
Mudumalai TR	8.31 ± 2.73	13.17 ± 3.15	-	Kalle et al. 2011
Ranthambhore TR	4.6–7.5	-	5.49 ± 1.27	Sadhu et al. 2017; Singh et al. 2014
Pench TR, MP	5.7 ± 0.87	4.97 ± 0.88	-	Chatterjee et al. 2023
Kanha TR	4.82–5.21	6.63–8.64	-	Kumar et al. 2019
Rajaji TR	3.31–5.81	2.07–9.76	5.67 ± 3.15	Harihar et al. 2011; Harihar et al. 2009
Bandhavgrah TR	4.71 ± 1.20	3.03 ± 0.78	-	Rather et al. 2021
Achanakmar TR	-	12.04 ± 2.98	4.54 ± 1.75	Mandal et al. 2017
Sariska TR	-	7.6 ± 0.6	15.1 ± 6.2	Mondal et al. 2012; Gupta et al. 2009
Sawai Mansingh WLS	-	-	12 ± 0.03	Panda et al. 2022
Panna TR	*3.77–6.69*	*23.87–30.07*	*13.76–16.58*	*Present study*

*all densities were estimated in ML-SECR method

triggered the fast population recovery (82%, Dutta and Krishnamurthy 2024), compared favourably to the other high-density tiger reserves (Table 4).

Analogous to tigers, leopard densities exhibit notable variability across India, both within and outside tiger reserves, with variation from 0.74 ± 0.18/100 km² (Dachigam National Park; Noor et al. 2020) to 28.9 ± 7.2/100 km² in Mudumalai Tiger Reserve (Kalle et al. 2011). Earlier studies in central Indian landscapes have reported comparatively lower leopard densities as compared to our result (Table 4). In this study, we recorded the highest leopard density (30.07 ± 2.31/100 km²) among all tiger reserves in India. Leopard density declined with a little increase in winter 2021, fluctuating by 21%, aligning to previous studies (Jhala et al. 2021; Qureshi et al. 2024). Male leopard densities remained relatively stable, while female densities fluctuated continuously over the study duration.

The reduced home-range size of female leopards (estimated lower sigma) likely reflects their dependence on resource availability, with limited spatial flexibility compared to males (Fattebert et al. 2016). High intra-guild competition may force sub-ordinate predators to be displaced by apex predators (Linnell and Strand 2000). With reference to these patterns, our results suggest that leopard density may be spatially restricted in this landscape, specifically where tiger density is low, with distinct spatial segregation observed during summer. Similar patterns have also been documented by the clumped distribution of major prey species during the summer (Gupta and Krishnamurthy 2023), that could be another reason for the spatially restricted carnivore distribution. A high density of leopards, along with a notable population turnover rate among female individuals (Table S12), suggests intense intrasexual competition. Female leopards, in particular, often experience intensified competition for denning sites and critical resources required for rearing offspring, which directly affects survival and population persistence (Balme et al. 2009; Fattebert et al. 2013). Findings from Rajaji Tiger Reserve indicate a negative correlation between leopard and tiger densities (Harihar et al. 2011). In that area, the densities of tigers and leopards were nearly similar. However, in this study, leopard density was found to be 5–6 times higher than that of tigers. This suggests that population declines of leopards may be due to their intra-specific competition, rather than the influence of tiger density. Similar to Sabi Sand, South Africa, leopard densities remained unaffected by the presence of apex predators such as lions (Balme et al. 2017). However, in PTR, the observed movement of female leopards from the core area towards adjoining buffer regions may indicates potential increase in human-wildlife conflict (Athreya et al. 2011).

Hyena density is highly dependent on resource availability (Singh 2008). Beyond the protected areas in India, hyena densities are significantly lower, ranging from 3.67 to 5.03 individuals/100 km² (Singh et al. 2010; Athreya et al. 2013). The estimated density in our study was found similar to Sariska Tiger Reserve (Gupta et al. 2009), and found high compared to other tiger reserves within the central Indian landscape (Table 4). High predator density provides ample opportunities for mammalian scavengers to acquire food. As hyenas heavily rely on locating carcasses, the site fidelity (den centric; Cooper 1993) movement behaviour of hyenas is one of their limiting factors. Limited availability of the den within the study area may restrict the hyena density (Singh et al. 2010). Therefore, neither we were evident to any significant changes in hyenas' density seasonally nor annually. Additionally, consistent high turnover rate (67.8%, Table S12) in hyena population represents poor land tenure strategy within suitable habitat at PTR. Hyena density appears to be mediated by resource availability, particularly carrion, suggesting that populations respond adaptively to spatial variation in food resources (Singh et al. 2014). Consequently, by restricting their population density, hyenas effectively mitigate the challenges associated with resource competition. This strategic adjustments in their population

density are much required as carcass availability is dynamic and subject to prey-predator density and seasonality.

Home range size depends on a species' body size (Reiss 1988). Smaller carnivores are expected to have smaller ranges compared to larger carnivores, especially when both have similar food habits and foraging strategies (Jetz et al. 2004). Therefore, we expected leopards to have a smaller σ compared to tigers. These results supported our hypothesis, further suggesting that leopards' high adaptability allows them to survive well in areas of high tiger density by restricting their spatial extent. Population density also influences the home range size of many species (Hoset et al. 2008; Trewhella et al. 1988). This scenario suggests that home range size adjusts like an elastic disk to changes in density (Krebs 1971). Once carrying capacity is reached, further decreases in home range size are no longer possible. Results of this study suggested that the σ of both tigers (female) and leopards showed a linear decline with density. This interpretation is further supported by recent findings demonstrating that the top carnivore population in PTR is adequately sustained by the available prey base (Dutta et al. 2026). Similar to our findings, Efford et al. (2016) demonstrated an exponential decline in σ with increasing tiger density at landscape scales. Observed changes in female tiger and leopard densities were associated with a reduction in home-range size, consistent with density-dependent space-use patterns reported in carnivores (Šálek et al. 2015). The home range of the leopard population within the core area was significantly compromised due to the intense intra-sex competition and high turnover rate, this situation is common in other carnivore studies (Chanchani et al. 2018). However, contrary to Kumar et al. (2019), the horizontal slope in case of male tiger density ensured their strong territoriality and lesser space to accommodate more male tigers within the study area, and reduction of home range size is not further possible (Goszczyński 2002). On the other hand, the stable density of hyenas exhibited minimal change in home range size, indicating high stability (reached to the carrying capacity) in their spatial extent and den centric movement (Jänecke et al. 2019; Stewart et al. 2021). This indicates a high level of territoriality (Boydston et al. 2001), which, in turn, facilitates area-specific searching for carcasses.

Conservation implications

Large carnivores require extensive spatial areas to meet their ecological needs. Consequently, the high population densities of large felids within the core region of the PTR demand substantial resource availability. Effective management of mosaic habitats is essential to sustain prey diversity and density, thereby supporting high carnivore density. The high densities of carnivores in the core areas of PTR may potentially lead to higher dispersal rates in the future. An influx of young tigers is anticipated to occupy the buffer zone of the PTR, placing considerable pressure on the existing leopard population to disperse into more degraded forest areas. Although the current leopard population in the core area exhibits a non-sex-biased structure, the high density of tigers, along with resource and spatial constraints, may be driving a gradual displacement of females (leopard) from the core to adjoining areas. If this pattern persists, it could potentially result in a male-biased population structure in the future. Such population fluctuations among carnivores may have serious demographic consequences. Furthermore, enhanced management practices in buffer zone forests, primarily habitat restoration, are expected to accommodate higher densities of both tigers and leopards within these areas. However, that would potentially intensify human-wildlife conflicts through increased livestock depredation incidents.

Conclusions

Across six sampling sessions conducted over four years, the three focal carnivores exhibited contrasting short-term population patterns in PTR. Tiger density increased until summer 2020 before declining during winter 2021, whereas leopard density showed moderate temporal fluctuations and a marginal overall decline. Striped hyena density varied among sessions but showed no significant directional trend. ML-SECR and B-SECR produced different absolute estimates of density and abundance, although both approaches generally identified similar temporal patterns. The spatial scale of detection declined with increasing density for male leopards, whereas corresponding relationships were not statistically supported for female leopards, tigers, or striped hyenas. Thus, the results provide limited evidence for a generalized density-dependent compression of space use and do not demonstrate a causal effect of increasing tiger density on the density of leopards or hyenas. Continued standardized monitoring across the core and buffer zones, together with information on prey availability, demographic turnover, movement, and anthropogenic pressures, will be necessary to determine whether the observed short-term variation represents persistent population change.

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Author contributions S.D. Conceptualization, Methodology, Data collection and processing, Analysis, Visualization, Writing - original draft preparation, Writing - review and editing.G.M. Conceptualization, Methodology, Supervision, Writing – review and editing.R.K. Conceptualization, Methodology, Project administration, Supervision, Funding procurement, Writing – review and editing.

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Data availability The data used in this study will be available upon acceptance of this article.

Declarations

Competing interests The authors declare no competing interests.

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