

Original Article

PNIE 2023;4(2):72-78 https://doi.org/10.22920/PNIE.2023.4.2.72 plSSN 2765-2203, elSSN 2765-2211



Estimating Population Density of Leopards in Semi-Arid habitat, Western India

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ABSTRACT

The leopard (*Panthera pardus*) is one of the most widespread felids worldwide. Despite their wide distribution, reliable data on leopard population densities are still inadequate for conservation and management strategies in different landscapes. In the present study, we estimated leopard density using camera traps in the Ranthambhore Tiger Reserve (RTR), Rajasthan, India, between December 2010 and February 2011, where leopards coexist alongside a high density of tigers (*Panthera tigris*), a larger predator (RTR). A sampling effort of 4,450 trap days was made from 178 camera trapping stations over 75 days, resulting in 46 suitable photo captures (25 right flanks and 21 left flanks). In total, 18 individuals (7 males, 8 females, and 3 unknown sexes) were identified using the right flanks, and the estimated leopard density was 8.8 (standard error=2.8) individuals/100 km². Leopard density appeared to respond to small prey (<50 kg weight) richness. As this is the first systematic study to provide baseline information on leopard density in RTR, it could form a baseline for comparison in future investigations.

Keywords: Camera trap, Panthera, Photo-capture, Rajasthan, Ranthambhore, Spatial explicit capture-recapture

Introduction

The leopard (*Panthera pardus*) is the most widespread large cat in the world (Nowell & Jackson, 1996), and occupies a wide range of habitats, including rainforests and desert mountains in temperate regions and the fringes of urban areas (Kitchener, 1991). Despite having the widest distribution, leopards are often assumed to be of low conservation priority among large felids because of the limited information available across their range, except for African studies (Balme *et al.*, 2012). Habitat loss, prey depletion, retaliatory killing, and poaching for trade have

Received November 25, 2022; Revised February 28, 2023; Accepted March 7, 2023

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caused a decline in leopard populations (Nowak, 1999; WPSI, 2006), which are currently categorized as near-threatened by the International Union for Conservation of Nature (Henschel *et al.*, 2008).

Leopards show plasticity in their behavior as conditions change and are adaptive to dwell near human habitations (Seidensticker, 1990) which often results in direct conflict with people mainly in the form of over-livestock predation (Athreya, 2006). Hence, leopards are prone to retaliatory killing or poaching. Thus, reliable data on the population densities of leopards are needed to develop sound conservation and management strategies (Thapa et al., 2014) and to identify priorities in the allocation of limited resources (Karanth, 2003). Leopards are difficult to monitor because of their nocturnal, cryptic, and elusive behavior; wide home ranges; and low population densities (Cederlund et al., 1998). Traditionally, pugmarks have been used to estimate the abundance of large carnivores (Panwar, 1979), but these techniques have been criticized and found to be less reliable (Karanth et al., 2003). With the development of automatically triggered camera traps, they have been widely used to estimate the abundance of species through individual identification based on their unique coat pattern (i.e., tiger (Panthera tigris), Karanth, 1995; leopard (P.P) (Gray & Prum, 2012)).

In India, leopards are listed in Schedule I of the Indian Wildlife (Protection) Act, 1972, and are under the highest level of protection, but reliable information on the abundance of leopards is still scarce compared to other sympatric carnivores, such as tigers (Jhala *et al.*, 2011; Panda *et al.*, 2022a). The present study was part of a long-term study conducted in the Ranthambhore Tiger Reserve (RTR), India (Singh *et al.*, 2022). We estimated the population density of leopards in a semi-arid habitat of the RTR in western India, which is known to have a relatively high tiger density (Karanth *et al.*, 2004), and provided baseline data for the conservation of this elusive species.

Materials and Methods

Study area

The RTR (25° 54' 26° 12' N, 76° 22' 76° 39' E), situated in the semi-arid region of Rajasthan (Fig. 1), western India, is a transition zone between desert and peninsular India (Rodgers & Panwar, 1988) and is dominated by Northern tropical, dry, deciduous, and thorny forests (Champion & Seth, 1968). The TR is surrounded by 332 villages within 5 km of the reserve boundary, with more than 150,000 people and livestock (Bagchi et al., 2003). People in the region around the reserve chop grass and trees, in addition to grazing livestock. This region receives 800 mm of precipitation each year with temperatures ranging from 2°C in January to 47°C in May (Singh et al., 2013). The RTR has a subtropical dry climate with four distinct seasons: summer (March to June), monsoon (July to August), post-monsoon (September to October), and winter (November to February). The terrain, with 76% of the area categorized as highly undulating, has an eleva-



Fig. 1. Locations of camera traps used in Ranthambhore Tiger Reserve, western India, December 2010 to February 2011.

tion gradient ranging from 200 to 500 m (Singh *et al.*, 2021). Besides the leopard (*Panthera pardus*), other large predators in the RTR include the tiger (*Panthera tigris*) and striped hyena (*Hyaena hyaena*) (Singh *et al.*, 2020). The study area also supports five species of wild ungulates: chital (*Axis axis*), sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelus*), chinkara (*Gazella gazelle*), wild pig (*Sus scrofa*), sloth bears (*Melursus ursinus*), common langur (*Semnopithecus entellus*), and peafowl (*Pavo cristatus*) (Panda *et al.*, 2022b).

Sampling design

For camera trapping, we created a grid system based on distribution maps generated by indirect sign surveys (i.e., tracks and scat). Cameras were built and placed near the most frequently used carnivorous pathways to ensure that every individual in the research area could be identified (Wilson & Delahay, 2001). The sampling region was divided into 1x1 km grids, and the cameras were positioned sequentially across the grid. At any given time, we used 60 remotely triggered cameras: 13 active infrared systems (TrailMaster TM1550; Goodson and Associates, Inc., USA) and 47 digital passive infrared systems. The passive infrared systems comprised 13 Wildview systems (Wildview, USA), 9 Stealth Cam units (Stealth Cam, USA), and 25 Moultrie systems (Moultrie Game Feeders, USA). Each Trail Master unit was connected to a fully automatic 35 mm camera (Canon A1 Mini DX; Canon USA, Inc., USA) with automatic flashes. Considering that different cameras have varying detection zones, we set the cameras in a way ensuring there is enough time to identify an animal and take full-frame photographs of the subject, including three shots constantly taken at short intervals. White flashes could be seen up to 30-35 m away from both the active and passive cameras.

Each sampling grid was composed of a single camera placed 6-7 m away from the road to capture each flank of a passing leopard (Karanth & Nichols, 1998). In "survey design 4", the research area was divided into 3 consecutive spatially separated blocks and systematically sampled in a phased manner (Karanth & Nichols, 2002; Fig. 1). Two camera units were used in the third block during the sampling period; thus, we had 58 sampling stations in that block. Sampling took place between the 5th of December 2010 and the 20th of February 2011, with a 25-day sampling interval in each block. We took 2-3-day breaks after each trapping session (25 days) to download the images from the digital cameras and change the cameras in the following block. The camera traps were operated 24 hours a day, 7 days a week. Because of the good road network, all trapping stations were monitored on alternate days throughout the sampling period. All the covered camera-trapping sites had a minimum convex polygon (Fig. 1) of 233 km².

Leopard density

Individual leopards were identified from photographs obtained using camera traps by visually examining the markings on the pelages of hind limbs, forelimbs, and forequarters (Kalle *et al.*, 2011). Individually identifiable leopards in the photographs were allocated unique identification numbers and the trap site, sample period, date, and time of capture were documented. We created a striped leopard capture history in spatial explicit capturerecapture (SECR) data format for analysis, taking into account a continuous 75-day sampling occasion (1-to-25day sessions in block A, 26-to-50-day sessions in block B, and 51-to-75-day sessions in block C) (Singh *et al.*, 2014).

We followed the SECR approach to obtain maximum likelihood density estimates for leopards using camera trapping data (Efford, 2011).

The likelihood SECR models were subjected to the R packages SECR and DENSITY 5.0 (Efford 2010; Efford *et al.*, 2009; www.otago.ac.nz/density). The detection probability of each individual was modeled using the spatial detection function (Efford, 2004) and was explained by 2 parameters (one-night detection probability at the center of an individual's home range, $[g_o]$, and a function of the scale of animal movements, $[\sigma]$; Efford, 2004). We chose a half-normal detection algorithm because it appears to be acceptable for mark-recapture data from large carnivores and is the most commonly used. By integrating the Poisson distribution of the home range centers and adding a buffer of 10,000 m around the trapping grids, we evaluated the log-likelihood function (Zimmermann *et al.*, 2013).

Results

Based on the total sampling effort of 4,450 active trap days (2 camera traps were stolen) from 178 active trapping stations between December 2010 and February 2011, we obtained 53 photographs of leopards, of which 46 were suitable for individual identification (25 right flanks and 21 left flanks). The right flank photo capture was taken for further analysis, as it involved a larger number of individuals and captures. In total, 18 individual leopards (7 males, 8 females, and 3 unknown sexes) were identified based on the right flank. The statistical test for population closure in the CAPTURE program (Otis *et al.*, 1978; Rexstad & Burnham, 1991) supported the assumption that the sampled population was closed during the sampling period (z=-0.403, P=0.340). Additionally, leopard density was 8.8 (standard error=2.8) individuals/100 km².

Discussion

The leopard density was estimated to be 8.8 per 100 km² in our study area which was similar to that of the Sariska Tiger Reserve (STR) (8.0 per 100 km²; Mondal et al., 2012a), which has a similar habitat and is adjacent to our study region. Both study areas are situated in the semi-arid region of Western India, and the vegetation is composed of tropical open thorny forests with highly undulating topography and high human influence. As. The RTR maintains a high prey density of medium-to-largesized wild prey species (96.5 per km²; Bagchi et al., 2003) which supports the high density of carnivores, as it is believed that carnivore density is positively correlated with prey biomass (Carbone & Gittleman, 2002; Karanth et al., 2004). Leopards in India prefer small-to-medium-sized prey (chitals, wild pigs, and langur), generally weighing less than 50 kg (Harihar et al., 2011; Johnsingh, 1992; Karanth & Sunguist, 1995; Sehgal et al., 2022). Among the prev species, chitals were the most frequently consumed prey item by leopards in the Indian subcontinent (Andheria et al., 2007; Ramesh et al., 2009) and leopard density was positively correlated (R²=0.6) with chital density (Fig. 2). According to Bagchi et al. (2003), chital (31 animal/km²) was the most abundant wild prey in the RTR, followed by common langur (21.75 animal/km²), sambar (17.15 animal/km²), and wild pig (9.77 animal/km²). Furthermore, the leopard density derived from camera traps in the present study was close to the estimates obtained from the prey biomass-carnivore relationship (Carbone & Gittleman, 2002). Similarly, relatively higher leopard density has also been reported in other protected areas (PA) of tropical dry deciduous forests, that is, the Pench Tiger Reserve (9/100 km², Majumdar, 2011); and Mudumalai Tiger Reserve (13.7/100 km²; Kalle et al., 2011). Both PAs had higher prey densities (Majumdar et al., 2012). Howev-



er, the population density estimates of leopards in the PAs of moist deciduous forests of Rajaji National Park were estimated to be 2.07 to 9.72 leopards/km² (Harihar et al., 2011) (Table 1). However, it has been speculated that the fluctuation in the density of leopard populations in the area may be a function of poaching (Johnsingh & Negi, 2003) or a response to the recovery of the tiger population (Harihar et al., 2011). The estimated leopard density in the lowland forest of Manas National Park (MNP) in the Eastern Himalayan Mountains is 3.4 /100 km² (Borah et al., 2014). The MNP, which receives high rainfall (>2,800 mm) and has a closed canopy forest, has high primary productivity in the canopy relative to the ground; hence, a low density of prey and predators may be expected (Datta et al., 2008; Glanz, 1982). Variations in carnivore density between different ecoregions may be a function of vegetation type, prey availability, topography, rainfall patterns, large predator abundance, and hunting pressure (Chapron et al., 2008).



Fig. 2. Leopard density with relation to chital density in Indian-subcontinent (source data: leopard density (RCNP-Thapa, 2011; STR- Modal *et al.*, 2012; RNP- Harihar *et al.*, 2011; MTR- Kalle *et al.*, 2011; PTR- Majumder *et al.*, 2012), chital density (RCNP- Seidensticker, 1976; STR- Avinandan *et al.*, 2008, RNP- Harihar *et al.*, 2011; MTR and PTR- Majumder *et al.*, 2012).

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Study area	Habitat type	Leopard density	Tiger density	Reference ^a
Chilla National Park (2006)	Tropical moist deciduous	9.72	3.31	Harihar <i>et al.,</i> 2011
Chilla National Park (2010)	Tropical moist deciduous	5.81	2.07	Harihar <i>et al.,</i> 2011
Chitwan National Park	Tropical moist deciduous	4.34	2.7°	Thapa, 2011
Mudumalai Tiger Reserve	Tropical dry deciduous	13.7	8.31	Kalle <i>et al.,</i> 2011
Manas National Park	Tropical rain forest	3.4	0.8^{b}	Borah <i>et al.,</i> 2013
Pench Tiger Reserve	Tropical dry deciduous	9	2.5^{b}	Majumdar, 2011
Ranthambhore Tiger Reserve	Tropical thorn forest	8.8	4.72	Present study
Sariska Tiger Reserve	Tropical thorn forest	8.0		Mondal <i>et al.,</i> 2012
Sariska Tiger Reserve	Tropical thorn forest	3.3		Mondal <i>et al.,</i> 2012
Satpura Tiger Reserve	Tropical dry deciduous	5.9	1.57^{b}	Edgaonkar <i>et al.,</i> 2007

Table 1. Leopard and tiger density in Indian subcontinent with respect to habitat

^bJhala *et al.,* 2011; ^cKaree *et al.,* 2012.

Other than prey density, additional factors, such as disease and interspecific competition, also contribute to variations in carnivore densities (Chauvenet *et al.*, 2011; Harihar *et al.*, 2011; Singh *et al.*, 2015). With a simultaneous recovery of tiger populations, the density of leopards decreased from 9.76/100 km² to 2.07/100 km² in Rajaji National Park (Harihar *et al.*, 2011) and 8.0/100 km² to 3.3/100 km² in STR (Mondal *et al.*, 2012b). Our results showed that RTR had a lower tiger density (4.80 individuals/100 km²) than leopards, and a comparison of leopard density with tiger density across different regions suggested that leopard densities appear to be the response of tiger densities.

However, the tropical dry thorns and deciduous forests of India, including the RTR, have potential productive grassland habitats that are enriched with prey (Karanth *et al.*, 2004a). Therefore, a higher leopard population density is expected in tropical dry-forested habitats. Chundawat *et al.* (1999) suggested that there are potential tropical dry forested habitats available in India, which extend to approximately 150,000 km², and if such habitats can be protected, they can support a substantial number of large cats, such as tigers and leopards (Karanth *et al.*, 2004b).

The results of this study provide baseline information on the leopard population in the RTR, and it is assumed that tropical dry forests provide suitable habitats for leopards and can support adequate leopard populations. Thus, it may be suggested that dry regions are potential areas of conservation importance for the maintenance of metapopulations. Thus, wildlife authorities must consider or include leopard populations when formulating conservation and management strategies.

Conflict of Interest

The authors declare that they have no competing interests.

Acknowledgments

We are grateful to the Director and Dean of the Wildlife Institute of India for their help. We are grateful to the Rajasthan Forest Department, as well as the reserve officials and field employees at the RTR for granting permission and allowing our work, as well as for their assistance. Special thanks go to the RTR's nature guides and field helpers, M. S. Gurjar and S. Sharma, for their assistance. The Ministry of Environment and Forests, Government of India provided financial support through the Training Research and Academic Council.

References

Andersen, R., Duncan, P., and Linnell, J.D.C. (1998). *The European Roe Deer: The Biology of Success*. Scandinavian Univer-

sity Press.

- Andheria, A.P., Karanth, K.U., and Kumar, N.S. (2007). Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *Journal of Zoology*, 273, 169-175. https://doi.org/10.1111/j.1469-7998.2007.00310.x
- Athreya, V. (2006). Is relocation a viable management option for unwanted animals? - The case of the leopard in India. *Conservation and Society*, 4, 419-423.
- Avinandan, D., Sankar, K., and Qureshi, Q. (2008). Prey selection by tigers (Panthera tigris *tigris*) in Sariska Tiger Reserve, Rajasthan, India. *Journal of the Bombay Natural History Society*, 105, 247-254.
- Bagchi, S., Goyal, S.P., and Sankar, K. (2003). Prey abundance and prey selection by tigers (*Panthera tigris*) in a semi-arid, dry deciduous forest in western India. *Journal of Zoology*, 260, 285-290. https://doi.org/10.1017/S0952836903003765
- Balme, G.A., Hunter, L., and Braczkowski, A.R. (2012). Applicability of age-based hunting regulations for African leopards. *PloS One*, 7, e35209. https://doi.org/10.1371/journal. pone.0035209
- Borah, J., Sharma, T., Das, D., Rabha, N., Kakati, N., Basumatary, A., et al. (2014). Abundance and density estimates for common leopard Panthera pardus and clouded leopard Neofelis nebulosa in Manas National Park, Assam, India. Oryx, 48, 149-155. https://doi.org/10.1017/S0030605312000373
- Carbone, C., and Gittleman, J.L. (2002). A common rule for the scaling of carnivore density. *Science*, 295, 2273-2276. https://doi.org/10.1126/science.1067994
- Champion, F.W. (1928). *With a Camera in Tiger-land*. Doubleday, Doran & Company.
- Champion, H.G., and Seth, S.K. (1968). A Revised Survey of the Forest Types of India. Manager of Publications.
- Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S., and Clobert, J. (2008). The impact on tigers of poaching versus prey depletion. *Journal of Applied Ecology*, 45, 1667-1674. https://doi.org/10.1111/j.1365-2664.2008.01538.x
- Chauvenet, A.L., Durant, S.M., Hilborn, R., and Pettorelli, N. (2011). Unintended consequences of conservation actions: managing disease in complex ecosystems. *PloS One*, 6, e28671. https://doi.org/10.1371/journal.pone.0028671
- Chundawat, R.S., Gogate, N., and Johnsingh, A.J.T. (1999). Tigers in Panna: preliminary results from an Indian tropical dry forest. In J. Seidensticker, S. Christie, and P. Jackson (Eds.), *Riding the Tiger: Tiger Conservation in Human-dominated Landscapes* (pp. 123-129). Cambridge University Press.
- Datta, A., Anand, M.O., and Naniwadekar, R. (2008). Empty forests: large carnivore and prey abundance in Namdapha National Park, north-east India. *Biological Conservation*, 141, 1429-1435. https://doi.org/10.1016/j.biocon.2008.02.022
- Edgaonkar, A., Chellam, R., and Qureshi, Q. (2007). *Ecology of the Leopard (Panthera pardus fusca) in Satpura National Park and Bori Wildlife Sanctuary*. Wildlife Institute of India.
- Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, 106, 598-610. https://doi.org/10.1111/j.0030-1299.2004.13043.x
- Efford, M.G. (2010). *Secr: spatially explicit capture recapture in R*. Department of Zoology, University of Otago.
- Efford, M.G. (2011). Estimation of population density by spatially explicit capture-recapture analysis of data from area searches.

Ecology, 92, 2202-2207. https://doi.org/10.1890/11-0332.1

- Efford, M.G., Borchers, D.L., and Byrom, A.E. (2009). Density estimation by spatially explicit capture-recapture: likelihoodbased methods. In D.L. Thomson, E.G., Cooch and M.J., Conroy (Eds.), *Modeling Demographic Processes In Marked Populations* (pp. 255-269). Springer.
- Glanz, W.E. (1982). The terrestrial mammal fauna of Barro Colorado Island: censures and long-term changes. In E.G. Jr Leigh, A.S. Rand, and D.M. Windson (Eds.), *The ecology of a tropical forest: seasonal rhythms and long-term changes*. (pp. 455–468). Smithsonian Institution Press.
- Gray, T.N.E., and Prum, S. (2012). Leopard density in postconflict landscape, Cambodia: evidence from spatially explicit capture-recapture. *The Journal of Wildlife Management*, 76, 163-169. https://doi.org/10.1002/jwmg.230
- Harihar, A., Pandav, B., and Goyal, S.P. (2011). Responses of leopard Panthera pardus to the recovery of a tiger Panthera tigris population. *Journal of Applied Ecology*, 48, 806-814. https://doi.org/10.1111/j.1365-2664.2011.01981.x
- Henschel, P., Hunter, L., Breitenmoser, U., Purchase, N., Packer, C., Khorozyan, I., et al. (2008). Panthera pardus. In The IUCN Red List of Threatened Species v. 2015.2. Retrieved Apr 13, 2023 from https://www.iucnredlist.org.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965-1978. https://doi.org/10.1002/joc.1276
- Jhala, Y.V., Gopal, R., and Qureshi, Q. (2008). *Status of the Tigers, Co-predators, and Prey in India*. National Tiger Conservation Authority, Govt. of India.
- Johnsingh, A.J.T. (1992). Prey selection in three large sympatric carnivores in Bandipur. *Mammalia*, 56, 517-526. https://doi. org/10.1515/mamm.1992.56.4.517
- Johnsingh, A.J.T., and Negi, A.S. (2003). Status of tiger and leopard in Rajaji-Corbett Conservation Unit, northern India. *Biological Conservation*, 111, 385-393. https://doi. org/10.1016/S0006-3207(02)00307-5
- Kalle, R., Ramesh, T., Qureshi, Q., and Sankar, K. (2011). Density of tiger and leopard in a tropical deciduous forest of Mudumalai Tiger Reserve, southern India, as estimated using photographic capture-recapture sampling. *Acta Theriologica*, 56, 335-342. https://doi.org/10.1007/s13364-011-0038-9
- Karanth, K. (2003). Tiger ecology and conservation in the Indian subcontinent. *Journal of the Bombay Natural History Society*, 100, 169-189.
- Karanth, K., Nichols, J., Seidenstricker, J., Dinerstein, E., Smith, J., McDougal, C., et al. (2003). Science deficiency in conservation practice: the monitoring of tiger populations in India. *Animal Conservation Forum*, 6, 141-146.
- Karanth, K.U. (1995). Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. *Biological Conservation*, 71, 333-338. https://doi. org/10.1016/0006-3207(94)00057-W
- Karanth, K.U., and Nichols, J.D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79, 2852-2862. https://doi.org/10.1890/0012-9658(1998)079%5b2852:EOTDII%5d2.0.CO;2
- Karanth, K.U., and Nichols, J.D. (2002). Monitoring Tigers and Their Prey: A Manual for Wildlife Researchers, Managers and

Conservationists in Tropical Asia. Centre for Wildlife Studies.

- Karanth, K.U., and Sunquist, M.E. (1995). Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecol*ogy, 64, 439-450. https://doi.org/10.2307/5647
- Karanth, K.U., Chundawat, R.S., Nichols, J.D., and Kumar, N.S. (2004a). Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture-recapture sampling. *Animal Conservation*, 7, 285-290. https:// doi.org/10.1017/S1367943004001477
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., and Hines, J.E. (2004b). Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 4854-4858. https://doi.org/10.1073/pnas.0306210101
- Kitchener, A. (1991). The Natural History of the Wild Cats. Comstock Pub.
- Majumder, A. (2011). Prey selection, food habits and population structure of sympatric carnivores: Tiger panthera tigris tigris (L.), Leopard Panthera pardus (L.) and Dhole Cuon alpinus (Pallas) in Pench Tiger Reserve, Madhya Pradesh (India). (doctoral dissertation). Saurastra University, Rajkot.
- Majumder, A., Basu, S., Sankar, K., Qureshi, Q., Jhala, Y.V., Nigam, P., *et al.* (2012). Home ranges of the radio-collared Bengal tigers (Panthera tigris tigris L.) in Pench Tiger Reserve, Madhya Pradesh, Central India. *Wildlife Biology in Practice*, 8, 36-49.
- Mondal, K., Gupta, S., Bhattacharjee, S., Qureshi, Q., and Sankar, K. (2012). Response of leopards to re-introduced tigers in Sariska Tiger Reserve, Western India. *International Journal of Biodiversity and Conservation*, 4, 228-236.
- Nowak, R.M. (1999). *Walker's Mammals of the World*, 6th ed. Johns Hopkins University Press.
- Nowell, K., and Jackson, P. (1996). Wild Cats: Status Survey and Conservation Action Plan. IUCN.
- Otis, D.L., Burnham, K.P., White, G.C., and Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, 62, 3-135.
- Panda, D., Mohanty, S., Allen, M.L., Dheer, A., Sharma, A., Pandey, P., et al. (2023).Competitive interactions with dominant carnivores affect carrion acquisition of striped hyena in a semi-arid landscape of Rajasthan, India. Mammal Research, 68, 129-141. https://doi.org/10.1007/s13364-022-00663-1
- Panda, D., Mohanty, S., Suryan, T., Pandey, P., Lee, H., and Singh, R. (2022). High striped hyena density suggests coexistence with humans in an agricultural landscape, Rajasthan. *PloS One*, 17, e0266832. https://doi.org/10.1371/journal. pone.0266832
- Panwar, H.S. (1979). A note on tiger census technique based on pugmark tracings. *Tigerpaper*, 6, 16-18.
- Ramesh, T., Snehalatha, V., Sankar, K., and Qureshi, Q. (2009). Food habits and prey selection of tiger and leopard in Mudumalai Tiger Reserve, Tamil Nadu, India. *Journal of Scientific Transactions in Environment and Technovation*, 2, 170-181.
- Rexstad, E., and Burnham, K.P. (1991). User's Guide for Interactive Program CAPTURE. Cooperative Fish and Wildlife Research Unit.
- Rodgers, W.A., and Panwar, S.H. (1988). *Biogeographical Classification of India*. New Forest.



- Sehgal, J.J., Kumar, D., Kalsi, R.S., Allen, M.L., and Singh, R. (2022). Spatio-temporal overlap of leopard and prey species in the foothills of Shiwalik, Himalaya. *European Journal of Wildlife Research*, 68, 18. https://doi.org/10.1007/s10344-022-01568-9
- Seidensticker, J. (1976). On the ecological separation between tigers and leopards. *Biotropica*, 8, 225-234. https://doi. org/10.2307/2989714
- Seidensticker, J., and Sunquist, M.E. (1990). Leopards living at the edge of the Royal Chitwan National Park, Nepal. In J.C. Daniel, and J.S., Serrao (Eds.), *Conservation in Developing Countries: Problems and Prospects* (pp. 415-423). Oxford University Press.
- Singh, R., Krausman, P.R., Goyal, S.P., and Chauhan, N.S. (2015). Factors contributing to tiger losses in Ranthambhore Tiger Reserve, India. *Wildlife Society Bulletin*, 39, 670-673. https:// doi.org/10.1002/wsb.561
- Singh, R., Pandey, P., Qureshi, Q., Sankar, K., Krausman, P.R., and Goyal, S.P. (2020). Acquisition of vacated home ranges by tigers. *Current Science*, 119, 1549–1554.
- Singh, R., Pandey, P., Qureshi, Q., Sankar, K., Krausman, P.R., and Goyal, S.P. (2021). Philopatric and natal dispersal of tigers in a semi-arid habitat, western India. *Journal of Arid Environments*, 184, 104320. https://doi.org/10.1016/ j.jaridenv.2020.104320
- Singh, R., Pandey, P., Qureshi, Q., Sankar, K., Krausman, P.R., and Goyal, S.P. (2022). Temporal variation in tiger population in a semi-arid habitat in India. *Proceedings of the National Institute of Ecology of the Republic of Korea*, 3, 154-164. https://doi.org/10.22920/PNIE.2022.3.3.154
- Singh, R., Qureshi, Q., Sankar, K., Krausman, P.R., and Goyal, S.P. (2013). Use of camera traps to determine dispersal of

tigers in semi-arid landscape, western India. *Journal of Arid Environments*, 98, 105-108. https://doi.org/10.1016/j.jaridenv.2013.08.005

- Singh, R., Qureshi, Q., Sankar, K., Krausman, P.R., and Goyal, S.P. (2014). Evaluating heterogeneity of sex-specific capture probability and precision in camera-trap population estimates of tigers. *Wildlife Society Bulletin*, 38; 791-796. https://doi. org/10.1002/wsb.471
- Thapa, K., Shrestha, R., Karki, J., Thapa, G.J., Subedi, N., Pradhan, N.M.B., *et al.* (2014). Leopard Panthera pardus fusca density in the seasonally dry, subtropical forest in the Bhabhar of Terai Arc, Nepal. *Advances in Ecology*, 2014, 286949. https://doi.org/10.1155/2014/286949
- Thapa, T.B. (2011). Habitat suitability evaluation for leopard (Panthera pardus) using remote sensing and GIS in and around Chitwan National Park, Nepal. (Unpublished doctoral dissertation or master's thesis). Saurashtra University, Rajkot.
- Wilson, G.J., and Delahay, R.J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research*, 28, 151-164. https://doi.org/10.1071/WR00033
- WPS1. (2006). *Skinning the cat: crime and politics of the big cat skin trade*. Retrieved February 21, 2021 from http://www.indiaenvironmentportal.org.in/files/Skinning%20the%20Cat. pdf.
- Zimmermann, F., Breitenmoser-Würsten, C., Molinari-Jobin, A., and Breitenmoser, U. (2013). Optimizing the size of the area surveyed for monitoring a Eurasian lynx (Lynx lynx) population in the Swiss Alps by means of photographic capturerecapture. *Integrative Zoology*, 8, 232-243. https://doi. org/10.1111/1749-4877.12017