

Acquisition of vacated home ranges by tigers

Randeep Singh^{1,2,*}, Puneet Pandey^{1,2}, Qamar Qureshi¹,
Kalyanasundaram Sankar^{1,3}, Paul R. Krausman⁴ and Surendra Prakash Goyal¹

¹Wildlife Institute of India, Post Box # 18, Dehradun 248 001, India

²Amity Institute of Forestry and Wildlife, Amity University, Sector-125, Noida 201 303, India

³Salim Ali Centre for Ornithology and Natural History, Coimbatore 641 108, India

⁴School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona 85721, USA

Understanding the social organization and acquisition of potential home ranges in solitary polygamous mammals is important for their management and conservation. However, such information requires a continuous long-term study. Therefore, limited information is available for mammals from South Asia. We studied the western most distributed Bengal tiger (*Panthera tigris*) population of Ranthambhore Tiger Reserve (RTR), Rajasthan, India, intensively during 2005–2011 using direct observation and intensive camera trapping-based methods. We examined how the home ranges of deceased tigers would be filled. Nine home ranges of tigers were vacated (two males and seven females) because of death, translocation, emigration and dispersal. Vacated female home ranges were filled by neighbouring tigers; 57% of neighbouring females were related to each other and after females vacated their ranges, their daughters acquired these home ranges. Mother tigers shared their home ranges with their daughters to increase the reproductive success of the latter. The home range of adult male tiger (TM-02) was estimated to be 73 sq. km using camera traps. Vacated male home ranges were filled by four transient individuals that were not related to each other. These data help understand the social organization and land tenure system of tigers in semi-arid habitats of India.

Keywords: Camera trap, home range acquisition, land tenure system, *Panthera tigris*, social organization.

In polygamous mammals, territorial behaviour influences social organization, distribution, population structure and dynamics^{1,2}. Social organization, however, facilitates the species to exploit resources, in territory acquisition and to increase their reproductive opportunities³. Tigers (*Panthera tigris*) are solitary carnivores with a polygamous mating system⁴ and are listed as an endangered species by the International Union for Conservation of Nature (IUCN)^{5,6}. Adult male tigers usually have a body weight >200 kg and large territories (>100 sq. km), while female tigers have an average body weight of <150 kg and smaller ranges (10–30 sq. km)⁷ than males. Sub-adult

male tigers generally start dispersing between 19 and 28 months, to longer distances from their natal areas^{8,9}. Females establish territories near their mothers' home ranges; dispersal of female tigers is rarely documented, and is considered to be rare⁸. In the land tenure system, resident animals are confronted directly and indirectly by other conspecifics through territoriality and temporal avoidance through chemical clues that regulate their density^{10,11}. Resident male tigers have intra-sexual territories (male–male competition) and defend their territories assertively influenced by resource competition; but they allow multiple females to use their home ranges^{5,12}. Sub-adults have been killed by adult animals because of territorial disputes in tiger¹³, lion (*Panthera leo*)¹⁴, brown bear (*Ursus arctos*)¹⁵ and jaguar (*Panthera onca*)¹⁶ populations. Thus territory acquisition is important, especially for sub-adult or transient tigers in core habitats where competition is high. Natural or anthropogenic death of resident individuals during dispersal may create vacant home ranges, which can be filled by transient individuals or neighbouring residents^{4,17,18}. Therefore it is important to understand the social organization and acquisition of vacant home ranges in animal ecology, and landscape level conservation and management^{19–21}. We studied the western-most distributed, small and isolated population of tigers in the dry, tropical habitat of Ranthambhore Tiger Reserve (RTR), Sawai Madhopur district, Rajasthan India. The tiger population in the landscape is composed of <50 individuals²². However there is 344 sq. km of potential habitat for tigers in RTR²², which could support additional tigers. In the present study, we examined how the home ranges of deceased male and female tigers would be filled by transient or neighbouring resident tigers. These data help understand the social organization and land tenure system of tigers in semi-arid habitats of India.

Study area

The study was conducted in a semi-arid landscape in RTR, which is situated at the junction of the Aravalli and Vindhya hill ranges. The total area of RTR is 1394 sq. km and it consists of two management units: a

*For correspondence. (e-mail: randeep04@rediffmail.com)

core area which includes the Ranthambhore National Park (RNP; 392 sq. km) and a buffer area, including the Sawai Mann Singh (SMS) wildlife sanctuary (WLS) (330 sq. km) and Kailadevi (KD) WLS (672 sq. km; Figure 1). In RTR, 36 tigers were reported during 2010 (ref. 23), among which 27 were reported from RNP²⁴. The vegetation of RTR corresponds to that of northern tropical dry deciduous forests and northern tropical thorn forest²⁵. The region receives an average annual rainfall of 800 mm, and temperatures can be low as 2°C in January and as high as 47°C in May. The vegetation of RTR is representative of a typical, dry, deciduous dhok (*Anogeisus pendula*) forest. Apart from dhok, the other species commonly found are kadaya (*Sterculia urens*), salai (*Boswellia serrata*), raunj (*Acacia leucophloea*), amaltas (*Cassia fistula*), palash (*Butea monosperma*), tendu (*Diospyros melanoxylon*), gurjan (*Lannea coromandelica*) and jamun (*Syzygium cumini*). Ranthambhore is characterized by a subtropical dry climate with four distinct seasons: winter (December–February), summer (March–June), monsoon (July–September) and post-monsoon (October–November). Large predators include tiger, leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*) and striped hyaena (*Hyaena hyaena*). The RTR supports five species of wild ungulates, including the chital (*Axis axis*), sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelus*), chinkara (*Gazella gazelle*) and wild boar (*Sus scrofa*).

Methods

Monitoring tigers

We monitored the tiger population in RTR through camera traps (1 camera trap/sq. km) in the core area from April 2005 to June 2011 (Supplementary Figure 1). We

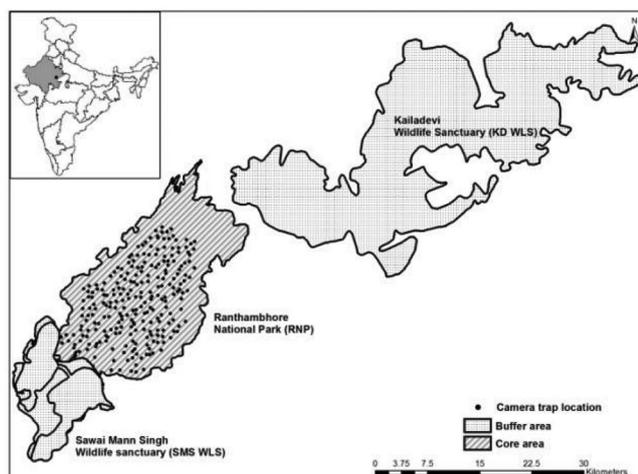


Figure 1. Study area map of Ranthambhore Tiger Reserve along with camera trapping location used for sampling during 2005–11.

established a database of 647 photo-captures of 22 female tigers in RTR from April 2005 to June 2011 (refs 26–28). Tigers were recognized from their stripe patterns on the flanks, limbs and forequarter²⁹, and we identified the sex after carefully observing the secondary sexual traits (i.e. genital portion) in the photo groups. We identified the ranges of individual female tigers from this database, which allowed us to collect information about the reproductive parameters of 15 breeding female tigers (i.e. litter size, inter-birth interval²⁷; and minimum distribution (viz. home range area) of each female.

We also examined the dataset (i.e. photographs) of individual tigers collected from the authorities and tourist guides who regularly (twice/day) visited the Reserve. The scanty vegetation and road network in RTR provided ideal conditions for tiger sightings. Females are philopatric and likely remain in the same area for their entire life, while males often disperse from their natal ranges⁷. We used this information to reconstruct life histories of individual tigers in RTR. Since these data were gathered from multiple sources, the identity of individual tigers was also confirmed through our photographic dataset of tigers using their unique coat patterns³⁰.

Minimum distribution area and vacant home range analysis

We used intensive camera trapping and direct observation of tigers to obtain a minimum distribution area (MDA) used by each animal. We defined resident tigers that resided in a centralized area for ≥ 8 months, which is the minimum time necessary to estimate home-range size³¹. For residents, we generally estimated MDA prior to death, and for replacements we generally estimated home range area for the first 12 months that we documented the individual using the area. The MDA by each adult tiger was calculated using the 100% minimum convex polygon (MCP) using the software package Home Range Extension in ArcView 3.3 (ref. 32). We used MCP over kernel methods because of small sample size. Also, kernel methods require more even distribution of the locations to maintain accuracy^{33,34}. We knew the age of females monitored during the study period, viz. 2005–11. For more details refer to Singh *et al.*^{28,35}.

Results and discussion

During the study period, nine home ranges were vacated (two males and seven females) due to death, translocation or emigration of tigers¹³. The seven resident adult female tigers vacated their home ranges because of death ($n = 3$), translocation ($n = 2$) and emigration ($n = 2$). We documented mothers and related offspring of each sub-adult female born during the study (Table 1)²⁷. The sub-adult female (TF-41; TF is tiger female) at 28 months acquired

Table 1. Detail of home range vacated and acquired by tigers in Ranthambhore Tiger Reserve, India, April 2005 – June 2011

Resident individual identification number	Date of vacated home range	Photo captures	Replacement individual	Date of first photo-capture in vacant home range	Photo captures after acquisition of home range	Relationship	Cause of vacant home range of resident tiger
Female							
TF-01	July 2008	19	TF-19	November 2008	34	Elder sister (previous litter)	Translocation to STR ²⁸
TF-04	April 2009	51	TF-41	May 2010	21	Daughter	Died defending cubs ³⁶
TF-27	January 2010	25				NA	Old age emigration
TF-14	October 2008	7	TF-13	November 2008	42	Daughter	Died natural
TF-15	September 2008	15	TF-18	October 2008	6	NA	Died diseased ³⁷
TF-13	October 2010	75	TF-39	November 2010	15	Daughter	Emigration to avoid infanticide ³⁶
TF-18	February 2009	6	TF-22	February 2009	46	NA	Translocation to STR ²⁸
Male							
TM-12	July 2010	80	TF-24	December 2010	21	NA	Transient
TM-02	December 2008	61	TM-03	December 2008	90	NA	Transient
			TM-21	February 2008	20	NA	Transient
			TM-28	December 2008	96	NA	Transient
			TN-29	December 2008	66	NA	Transient

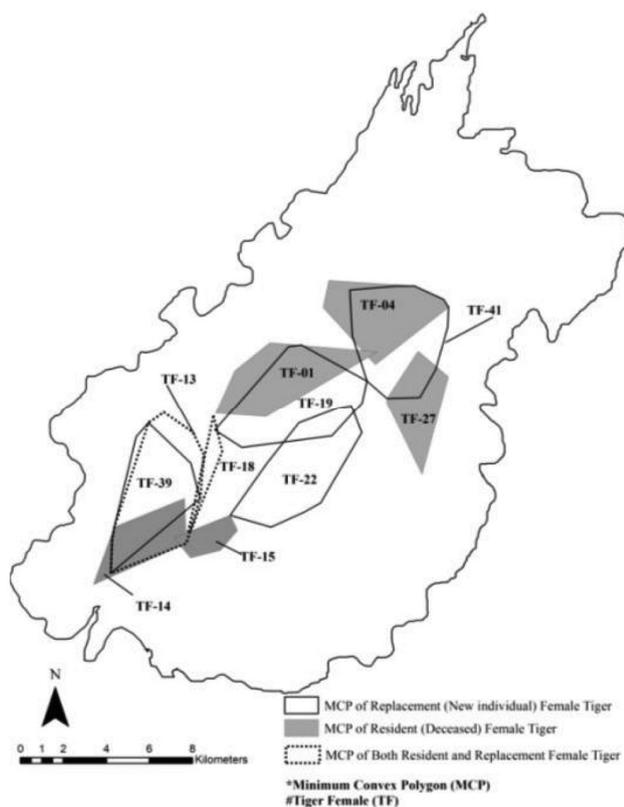


Figure 2. The distribution area of resident (tiger that vacated the home range) and replacement (tiger that replaced the one that vacated) female tigers using 100% minimum convex polygon (MCP), Ranthambhore Tiger Reserve, India, 2005–11.

the entire home range of two adult females (age >72 months) after the death of her mother (TF-04) in April 2009 and a home range vacated by an adult female (TF-27) due to old age emigration (Figure 2). Another

sub-adult female (TF-19; 20 months) acquired the home range of the resident adult female (TF-01); this home range was vacated after her translocation to Sariska Tiger Reserve (STR) in July 2008. Both females were related (sisters). Female TF-13 took over the entire natal home range following the disappearance of her mother TF-14 (Figure 2). The female TF-13 left her natal home range in December 2010 to avoid infanticide³⁶ and the home range was acquired by her daughter (TF-39). Similarly in another case after the death of the resident adult female (TF-15) in September 2008 (ref. 37), the vacated home range was occupied by a neighbouring dispersed sub-adult female (TF-18) and after the translocation of TF-18 in February 2009 to STR. Both females were not related to each other (Figure 2). Most ($n = 4$, 57%) vacated home ranges were filled by neighbouring females. In two other cases, the mothers (TF-9 and TF-16) shifted their home ranges to share with their daughters (TF-11, TF-17 and TF-19; Figure 3). All the daughters gave birth to litters following the division of the maternal home ranges.

Two home ranges were vacated by resident adult male tigers because of death and translocation¹³. The adult male TM-12 (≥ 6 years; TM is tiger male) was translocated to STR and his vacated home range was filled by a neighbouring adult male TM-24 (≥ 4 years) living in the proximate habitat. This male tiger had been previously physically captured approximately 4 km away in a sub-optimal habitat³⁶. The home range area occupied by TM-02 during 2005 to 2010 was approximately 73 sq. km, but after the death of this tiger (≥ 9 years), his vacated home ranges were taken over by four transient males (TM-03, TM-21, TM-28 and TM-29), which dispersed from different areas (Figure 4).

The literature suggests that female carnivores often settle in their natal areas and the mothers assist to increase the reproductive success of their daughters⁸. In this study we observed that the vacant home ranges after the occupants left were filled by neighbouring females for female residents and by transient individuals for male tigers. Similar observations have been documented in tigers by other researchers in India, Nepal and Russian Far East^{31,38,39}. In the degraded habitats carnivore territories remain vacated until habitat conditions not recovered, but with habitat impoverishment the area were gradually occupied by nearby individuals reported in Simlipal Tiger Reserve⁴⁰. Smith *et al.*³⁸ documented the inheritance of maternal home ranges in Chitwan National Park, Nepal, because the mothers shared their home ranges with their daughters, while three other young females acquired similar home ranges after the death of the former residents. Similarly, in Amur tigers in the Russian Far East, two mothers shared their home ranges with their daughters and in two other cases, the females took over the entire natal home range following the disappearance of their mothers³¹. Laing and Lindzey⁴² reported that after the death of the resident mountain lions (*Puma concolor*), the vacant home ranges were occupied by individuals of the same sex. In swift foxes (*Vulpes velox*) after the

disappearance of resident individuals, the vacant areas were re-occupied by new individuals⁴². Sandell⁴³ suggested that in the most solitary carnivores, the spatial organization of females depends on the distribution of resources so that the neighbouring females are aware of the availability of resources in the adjacent home ranges to maximize their foraging and reproductive efficiency.

Researchers of large carnivores suggest that the home-range expansions or shifts to fill vacancies are common^{10,12}. We observed that younger tigers replaced vacancies in home ranges occupied by an old male tiger (TM-02). The age of TM-02 was assessed based on photo-capture records from the Forest Departments. This tiger was first photo-captured using camera traps in 1998 (ref. 30), when he was a sub-adult approximately 2 years old and the approximate age of TM-02 was 12 years in 2008. The large home range of this tiger during 2005 to 2008 is because of the available space for male tigers, as there were only two adult tigers (TM-02 and TM-20) in 2006, which were photo-captured using camera trap, and the tiger habitat (344 sq. km) was occupied by both male tigers. From 2008 onwards when dispersal started, the young transient males compelled the older tiger to restrict its distribution area in the fringes of the park. Hence our data are consistent with other studies.

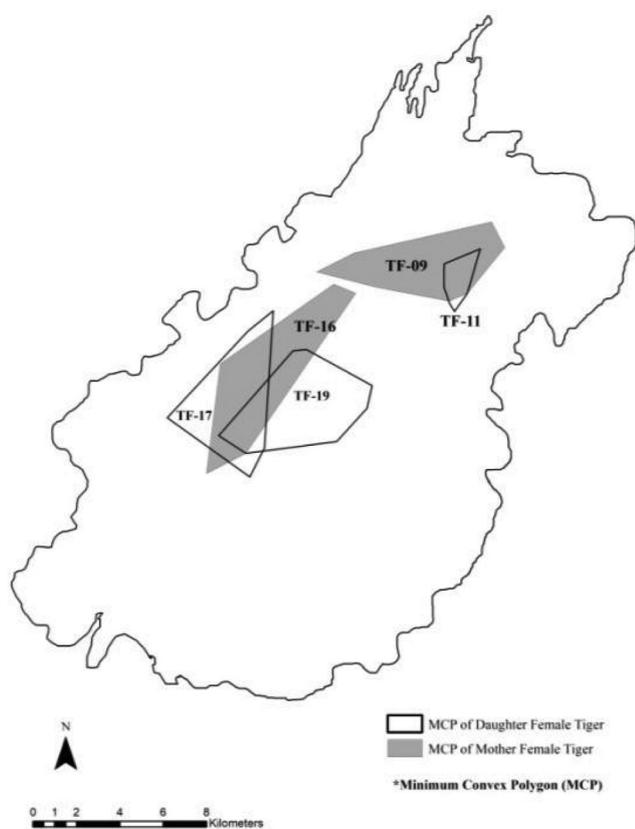


Figure 3. The distribution area of female mothers and with daughters using 100% minimum convex polygon (MCP), Ranthambhore Tiger Reserve, India, 2005–11.

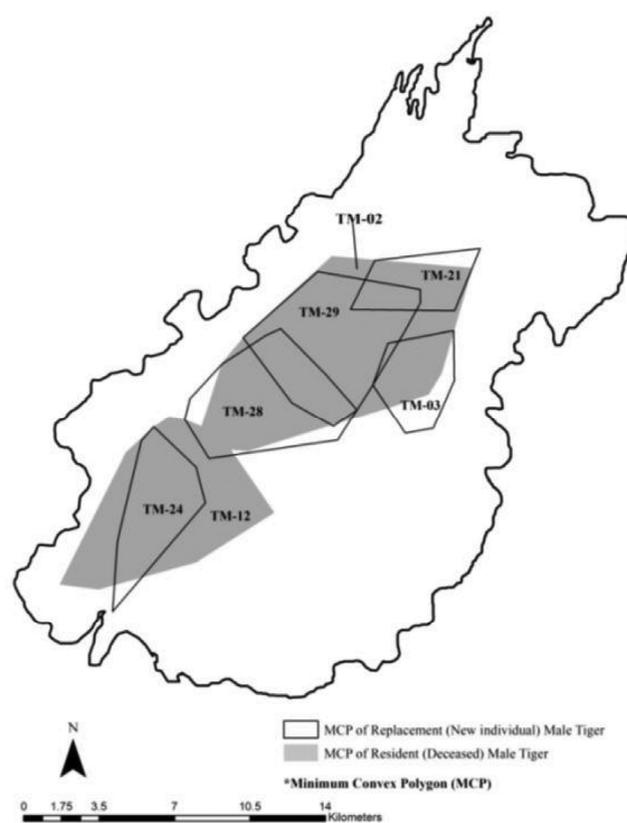


Figure 4. The distribution of resident (tiger that vacated the area) and replaced male tigers using 100% minimum convex polygon (MCP), Ranthambhore Tiger Reserve, India, 2005–11.

The vacant home range of RTR was due to decline of the tiger population in 2005 (ref. 44). Subsequently, after increased protection, the tiger numbers increased from 19 individuals in 2005 (ref. 26), to 36 individuals in 2010 and 45 individuals in 2014 (ref. 45). However the natural and anthropogenic mortality rate of tigers in RTR was 2.4 animals/year (ref. 13). Tigers in RTR have been reported to disperse to nearby areas, including protected areas through 'ridge top' narrow stepping stone connectivity⁹. Reddy *et al.*⁴⁶ reported evidence for movement of tigers to adjoining habitats in Madhya Pradesh across River Chambal. Mallick⁴⁷ reported that during the recovery phase, tigers populations had expanded their distribution ranges in nearby areas, and for the long-term conservation of tigers it is necessary to maintain the forest corridors to ensure the exchange of genes from adjacent areas⁴⁸. Such events may result in vacant home ranges and subsequently these would be filled by the nearby individuals. Thus this study will be useful to enhance our understanding about land tenure social organization and acquisition of vacant home ranges by tigers. It can also be used as baseline information for comparison in the future as part of management and conservation in RTR⁴⁹.

Conflict of interest: The authors declare no conflict of interest.

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ACKNOWLEDGEMENTS. We thank the Director and Dean Wildlife Institute of India (WII), Dehradun for support. We also thank the Rajasthan Forest Department, and park officials and field staff at Ranthambhore Tiger Reserve for the necessary permissions and support; M. Singh and S. Sharma for help during fieldwork, and WII for providing financial support for this study.

Received 23 March 2020; revised accepted 23 August 2020

doi: 10.18520/cs/v119/i9/1549-1554