

Use of bioclimatic region-specific single nucleotide polymorphism reveals cryptic long-distance dispersal of a female tiger from Terai Arc Landscape in northern to western India

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ABSTRACT

Tigers are showing male-biased dispersal and females philopatric. Keoladeo National Park (KNP), India, globally a bird sanctuary, and there has been no history of tiger presence. In 1999, villagers and the forest department sighted a female tiger in the grassland of KNP and was believed that female might have been from nearby tiger populations (c. < 200 km), i.e. Sariska or Ranthambhore in western India. Different approaches such as use of multi locus genotyping and isotope have been used in ancestry determination to either bioclimatic region or population. Because of microevolution, empirical studies have demonstrated presence of fixed SNP in mtDNA gene specific to different bioclimatic regions and has been used to determine ancestry. We compared mtDNA data with existing data on different mtDNA genes for tiger populations across India and revealed the presence of fixed specific SNPs which could distinguish the tigers of India into four broad bioclimatic regions. Therefore, that dispersed tigress had fixed specific SNPs (haplotype) in mtDNA genome which resembles specific to the Terai Arc Landscape (TAL) in the phylogenetic tree. This landscape is about 200 to 350 km from the KNP. Hence, our finding suggests and support occurrence of long-distance dispersal among female tigers.

Keywords: Tigress, dispersal, habitat fragmentation, TAL

INTRODUCTION

Dispersal in carnivores is the movement of individuals from the natal area to establish an independent home range, which helps in the spatial structuring of the population and acts as a population-regulating mechanism (Lidicker, 1975). Additionally, long-distance dispersal is central to ecological processes (Levin et al. 2003; Nathan, 2003), including gene flow (Trakhtenbrot et al. 2005), colonization of new areas, range shift, and helps to maintain functional connectivity between populations (Noss et al. 1996; Weaver et al., 1996; Clobert et al. 2012). Moreover, the long-term population persistence may depend on how successfully individuals traverse through a highly interspersed mosaic of forested areas, agriculture fields, and human settlements to reach another habitat (Watts et al. 2015). Literature with significant conservation and management implications must include information on such long dispersal characteristics.

Among felids, the tiger (*Panthera tigris tigris*), an endangered iconic predator, regulates ecosystem ecological processes (Goodrich et al. 2015). They are habitat specialists but can move longer distances in fractured or fragmented landscapes (Wikramanayake et al. 2010; Sarkar et al. 2016, 2021; Hussain et al. 2022). Hence it is essential to have information about the dispersal pattern and movement path in the landscapes, which helps the conservation and management agencies to act timely to make conservation strategies for the smooth passage of the animals (Wikramanayake et al. 1998). Across the tiger distribution range, the complement methods of non-invasive genetic techniques, radio/GPS telemetry and camera traps have been used to study the dispersal pattern of tigers (Smith 1993, Reddy

et al. 2012, Gour et al. 2013, Singh et al. 2013, Wang et al. 2015, Joshi et al. 2016; Sarkar et al. 2016, 2021; Hussain et al. 2022).

Long-term research work using radiotelemetry in Royal Chitwan National Park, Nepal, documented that dispersal in tigers is male-biased and tigers start dispersing at 19-28 months and disperse over large distances (Smith, 1993). Dispersion among males is generally considered a response to mate competition, resource competition or both (Sunquist 1981; Smith et al. 1987). Records of tiger dispersal events have significantly increased in recent years due to broader monitoring and improved technology. While the sporadic events of long-distance dispersal of tigers have been recorded using camera traps in India (Patil et al. 2011; Singh et al., 2013; Shah et al. 2015; Chatterjee et al. 2017) and Russia (for the Amur tiger, *Panthera tigris altaica*; (Wang et al. 2015). However, with the increase in tiger population over the years (Jhala et al. 2014; Qureshi et al. 2023), incidents of long-distance dispersal movement have been recorded frequently, i.e. (i) tiger dispersed 300 km from Madhya Pradesh and photo-trapped in Gujarat (ii) male tiger was physically captured near Satpura Tiger Reserve, Madhya Pradesh which revealed that the tiger had travelled a distance of 510 km from Chandrapur Super Thermal Power Station, Maharashtra based on comparing tiger stripes database of Wildlife Institute of India (WII) and Maharashtra Forest Department. (Table 1). The recent camera trap-based photo-graphic records and opportunistic sighting evidence suggested that tigers can occasionally move approximately 375 km through human-dominating, fragmented landscapes (Vasudev et al. 2017). Hussain et al. (2022) monitored the dispersal pattern of a sub-adult male tiger using GPS telemetry in

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Central India, and they reported individuals covering a straight-line distance of 315 km over 225 days and a cumulative distance of c. 3000 km. A recent study connected using non-invasive genetics in the central landscape of India has also suggested that male tigers tend to disperse long distances and can disperse as far as 650–700 km (Joshi *et al.* 2016). Because of such long movement and dispersal, tigers have recently been reported in many areas where they were never observed.

Unlike males, female tigers are considered philopatric and establish their territory, usually in the natal area. Familiarity with spatial and temporal variation in resources within the natal area may benefit parental care (Seidensticker *et al.* 1999; Tilson & Nyhus, 2010). Therefore, dispersal among female tigers was thought to be rare and rarely documented (Smith, 1993). Contrary to this belief, Sarakar *et al.* (2021) reported the dispersal of a re-introduced female around 375 km away from its release site in the Central landscape of India.

Considering the empirical studies, understanding the ranging behaviour and dispersal of a species in a metapopulation framework, which occupies different bioclimatic zones, is critical for ensuring long-term conservation goals. However, radio and GPS telemetry have been widely deployed but limited due to the high cost of monitoring many individuals at the landscape level. With the advances in molecular tools, emphasis has been on establishing population/region-specific characteristics using different genetic markers, and significance has been demonstrated to tackle poaching hotspots more effectively and curb illegal wildlife trade at source (Mishra *et al.* 2012; Wasser *et al.* 2015). Considering significance not only for wildlife forensics, but such reference database is also very powerful in understanding cryptic long-ranging behaviour using noninvasively collected samples of elusive species. Kumar *et al.* (2016) could trace the seized elephant tail to its geographic origin using reference DNA sequences. Similarly, Gaubert *et al.* (2016) and Zhang *et al.* (2020) could also match the pangolin scales to phylogeographical

regions of origin. Recently, Zhao *et al.* (2019) elucidated the value of harmonized reference DAN sequences of African elephants in provenance tracing.

Context of the present study:

Keoladeo National Park (KNP), Rajasthan, India, is a globally known bird sanctuary, and there has been no history of tiger presence. In 1999, villagers and the forest department reported a sighting of a female tiger in the grassland of Keoladeo National Park (KNP), Rajasthan, India. It was believed that this female might have been from a nearby tiger population, either from Sariska Tiger Reserve (STR) or Ranthambhore Tiger Reserve (RTR) in the western region of India. Similarly, in August 2010, a male tiger was also reported in KNP. Based on matching stripe patterns to those in the Wildlife Institute of India photo database, it was confirmed that the animal has dispersed from RTR (Singh *et al.* 2013). The aerial distance between KNP in STR and RTR is approximately 95 km and 148 km, respectively. However, the origin of the female tigress seen in KNP in 1999 could not be resolved. Therefore, we used harmonized mtDNA database across the tiger population in India (Sharma *et al.* 2008, 2011; Singh *et al.* 2015; Puneet *et al.* 2018) to document the geographic origin of the female who moved to KNP in 1999.

STUDY AREA

Keoladeo National Park (KNP) is a World Heritage Site situated on the extreme western edge of the Gangetic basin at the confluence point of Gambhir and Banganga rivers in the eastern part of Rajasthan with an extensive natural drainage network (Fig. 1). The total area of the KNP is 29 km². It has a unique mosaic of habitats, including wetlands, woodlands, scrub forests, and grasslands, supporting an incredible diversity of plant and animal species. Forests are dominated mainly by kadam *Mitragyna parvifolia*, jamun *Syzygium cumini* and babul *Acacia nilotica*. KNP has good domestic and wild prey populations.

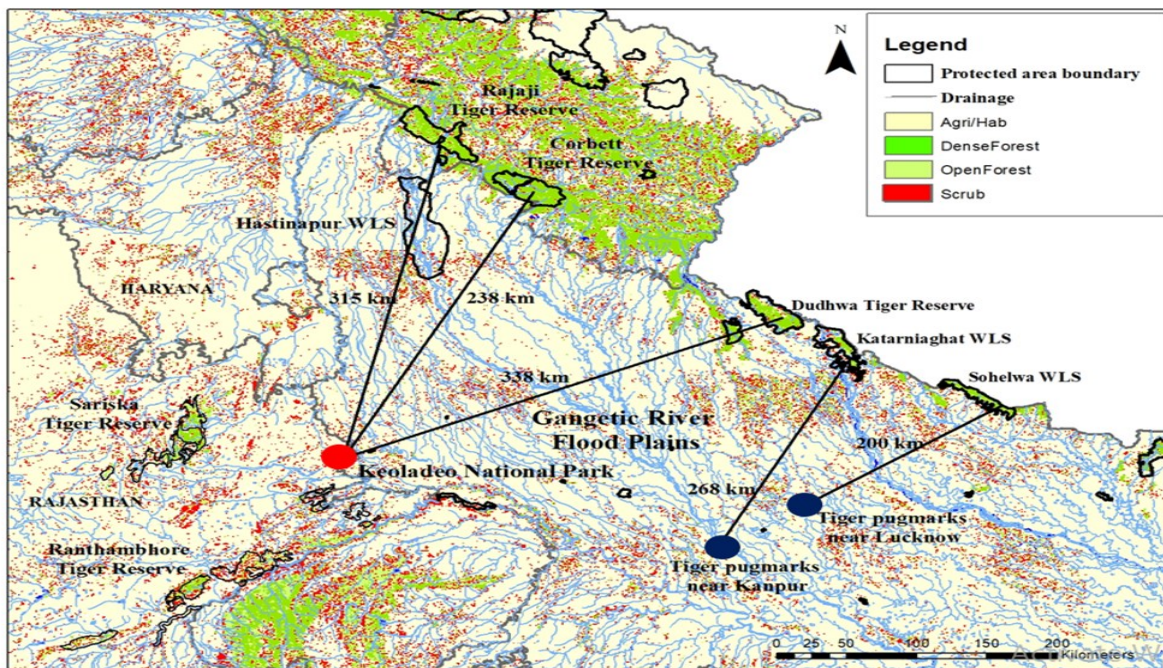


Figure 1. Observed and recorded dispersal of tigers (as per Table 1) from Terai Arc Landscape



(reagents only) were also included during DNA extraction to monitor contamination. To re-confirm the origin (species) of the scat, we targeted the 172 bp region of the mitochondrial Cytb gene and amplified faecal/tissue DNA using felid-specific primers by Sharma et al. (2008). All the amplification reactions were performed on ABI FAST thermocycler (Applied Biosystems) in total volume 10µl, containing 1µl of the DNA extracted from scat sample, 1X of the PCR buffer, 2.5 Mm of the Mgcl₂, 200 µm of each dNTP, 1X of BSA, 0.5U of Taq DAN polymerase (Applied Biosystems) and 0.2 µm of each primer. The thermal profile for the mtDNA amplification was initial denaturation at 94°C for 10 min. Followed by the 40 cycles of denaturation at 94°C for 35s, annealing at 55°C for 45s and extension at 72°C for the 45s, with one cycle of the final extension for 15min at 72°C. The amplified PCR product was subjected to ABI 3130 Genetic Analyzer after Exo-SAP treatment for sequencing. The DNA sequences' quality was determined using Sequence Analysis software (Applied Biosystems) and edited by Sequencher 4.7 (www.genecode.com).

Phylogenetic analysis

We examined the phylogenetic relationship of the dispersed tigress and compared the tigress sequence with all other Cyt b mitochondrial sequences of tigers (Sharma et al., 2008, 2011; Singh et al., 2015; Puneet et al., 2018) and retrieved them from the GenBank.

All the sequences were aligned using CLUSTAL-W implemented in BioEdit (Hall et al. 1999) sequence alignment software. The phylogenetic tree of the Cytb gene was generated based on Neighbor-joining (NJ) methods as implemented in Mega v 5.0. (Tamura et al. 2007).

RESULTS AND DISCUSSION

Empirical studies have indicated that known-origin geographical reference DNA sequences are extremely valuable for provenance tracing (Zhang et al. 2015; Kumar et al. 2016; Gaubert et al. 2016; Zhao et al. 2019). Like these studies, harmonised data on different mtDNA genes indicated the presence of population-specific SNPs, which could distinguish the tiger population of India into four geographic regions viz. Terai Arc Landscape (TAL) in northern India, Ranthambhore-Peninsular, Northeast India and Sundarbans (Fig. 2a) (Sharma et al., 2008, 2011; Singh et al. 2015; Pandey et al. 2018). Multiple sequence alignment method showed that dispersed tigress had mtDNA haplotype specific to the Terai Arc Landscape (TAL) in the phylogenetic tree (Fig. 2b). Therefore, it could be that the female tiger which moved to KNP belonged to the TAL tiger population in Northern India. She could have dispersed from one of TAL's Protected Areas (PAs), i.e., Rajaji Tiger Reserve, Corbett Tiger Reserve, Dudhwa Tiger Reserve. The aerial distance of these PA to KNP is between 238 and 338 km (Fig. 1).

Table 1. Reported tiger dispersal distances.

S.N o.	Species	Sex	Distance, km	Method used	Area	Reference
1	Amur tiger (Panthera tigris altaica)	Male tiger	270	Camera trap	NA	Wang et al. 2015
2	Bengal tiger (Panthera tigris tigris)	Male	280	Camera trap	Bandipur to Shikaripur, India	Patil et al. 2011
3	Bengal tiger (Panthera tigris tigris)	Male	197	Camera trap	Bhadra Tiger Reserve to Dandeli Tiger Reserve, India	Patil et al. 2011
4	Bengal tiger (Panthera tigris tigris)	sub-adult Male	71	Radiotelemetry	Royal Chitwan National Park, Nepal, India	Smith1993
5	Bengal tiger (Panthera tigris tigris)	Male	148	Camera trap	Ranthambhore TR to Kuno Palpur National Park, India	Singh et al. 2013
6	Bengal tiger (Panthera tigris tigris)	Male	220	Camera trap	Ranthambhore TR to Datia MP.	Shah et al. 2015

7	Bengal tiger (<i>Panthera tigris tigris</i>)	Male	510	Physical-ly capture	Chandrapur Super Thermal Power Station, Maharashtra's to Satpura power station, Madhya Pradesh	https://www.timesnownews.com/mirror-now/civic-issues/article/maharashtra-madhya-pradesh-chandrapur-reserve-plant-durgapur-sarni-satpura-reserve-tiger-maneater-maneating/329896
8	Bengal tiger (<i>Panthera tigris tigris</i>)	Male	300	Camera trap	Madhya Pradesh to Gujarat, India	https://timesofindia.indiatimes.com/city/bhopal/tiger-spotted-in-gujarat-walked-all-the-way-from-ratapani-in-mp/articleshow/67985472.cms
9	Bengal tiger (<i>Panthera tigris tigris</i>)	Male	139	Genetics	Ranthambhore TR to Madhav National Park, India	Reddy et al. 2012
10	Bengal tiger (<i>Panthera tigris tigris</i>)	Male	650	Genetics	Kanha TR to Nagarjunasagar TR, India	Joshi et al. 2016
11	Bengal tiger (<i>Panthera tigris tigris</i>)	Male	280	Photograph	Panna TR to Bandhavgarh TR	Murthy (2017)
12	Bengal tiger (<i>Panthera tigris tigris</i>)	Male	250	GPS telemetry	Panna TR	Sarkar et al. (2016)
13	Bengal tiger (<i>Panthera tigris tigris</i>)	Male	340	GPS telemetry	Vidarbha Landscape, Central India	Hussain et al. (2022)
14	Bengal tiger (<i>Panthera tigris tigris</i>)	Female	78	Camera trap	Ranthambhore TR to Chambal WLS, India	Singh et al. 2013
15	Bengal tiger (<i>Panthera tigris tigris</i>)	Female	340	GPS telemetry	Panna TR	Sarkar et al. (2021)
16	Bengal tiger (<i>Panthera tigris tigris</i>)	Female	>238	Genetics	TAL to Keoladeo National Park, Rajasthan	Present study

However, observed such a long-distance (> 200 km) dispersal of female tigers is infrequent and unexpected. The longest dispersal distance so far known is of a sub-adult female of 78 km from Ranthambhore Tiger Reserve to the riverine habitat (Singh et al. 2013) and 340 km from Panna Tiger Reserve (Sarkar et al. 2021). As such, there is no functional connectivity between TAL and western India landscape (Jhala et al. 2008), and most of the areas are Gangetic River flood plains (Fig. 1). This area is the mosaic of extensive drainage spread, scrubland, ravines, scrub area of exotic mesquite, and agricultural fields (Fig. 1). The dispersing tigers might have taken advantage of limited escape cover available in the riverbed and extensive drainage networks (Fig. 1). Such matrices of the landscape have probably provided conducive habitat to the transient animals for long-range movement (Singh et al. 2013, Singh et al. 2017). Besides, the Gangetic floodplain area is highly fertile, and sugarcane (a tall grassland analogue) and rice farming dominate the landscape. Tigers use such habitat for dispersal

and movement (Wickramanayake et al. 2004). For example, it was reported that an adult tigress had taken up residence in a sugarcane field near Pilibhit Tiger Reserve in TAL and raised three cubs (Chanchani et al. 2014). The feral cattle, livestock, small mammals, nilgai and wild boar are the prey available for tigers in such areas. The approximate cattle density in the landscape is ~77.41 cattle/sq. km (Semwal 2005). Shukla (2013) reported that 20% of tigers of TAL stay in sugarcane fields, and their movement increases with stray cattle movement. The sugarcane fields offer a perfect refuge for tigresses for breeding because of the thick cover of tall cane crops, easy food, water and complete protection from other male tigers (Shukla, 2013). The tigers disperse mainly during the monsoon seasons when the livestock are left to graze freely during the peak vegetation growing seasons. Hence, they form easy prey for dispersing tigers (Bargali & Ahmed, 2018). Thus, tall canopy cane fields and feral livestock probably support the tigers to disperse long distances.

Similar to our observations of a female tiger moving through the agricultural landscape, Sarkar *et al.* (2021) reported that female dispersed from Panna Tiger Reserve has also moved using forest patches, water channels, and agricultural fields and avoided human settlements. Hussain *et al.* (2022) reported the use of agriculture landscape matrices by dispersing male tigers in Central India, and the overall movement rate was significantly faster during the night (0.44 km/h) than during the day (0.21 km/h).

However, long-distance dispersal by females is a social state as they can contribute to range expansion, an outbreeding strategy, or counter strategies to avoid infanticide to ensure the survival of their progeny (Singh *et al.* 2014). TAL is a linear habitat of c. 810 km with a width of around 8 to 16 km, and the Corbett Tiger Reserve is a source population in this area with the highest tiger density of 14 individuals/100 km² (Jhala *et al.*, 2020). Recolonization to the adjoining habitats from a source population was also reported when the PAs attained carrying capacity or when anthropogenic disturbances were controlled (Harihar *et al.* 2009). Under such a scenario, individuals of both sexes are known to move in adjoining habitats. In support of this, Bisht *et al.* (2018) monitored the tiger population using a camera trap for six years in Corbett Tiger Reserve, and they reported high reproduction with 54.8 (SE 5.1)% females and high turnover rates (32%–48%) between successive years. Considering population demography and observed ranging behaviour, we presume that one of the females of this landscape might have taken advantage of the intense drainage network for dispersal of the Gangetic plain and finally settled in KNP, which has adequate wild and domestic prey species (Singh *et al.* 2016, 2017). Hence, we suggest (i) the identification of potential dispersal routes for connecting the different landscapes by regular monitoring through presence–absence surveys and the use of a non-invasive genetic sampling approach in more significant landscapes, (ii) understanding human attitudes and perceptions regarding tiger conservation in these potential dispersal routes and (iii) provide adequate protection to dispersal individuals. Such strategies would ensure managing the tiger population in a meta-population framework.

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Declarations:

Ethical statement:

Tiger scat samples were collected noninvasively without animal capture or handling. Therefore, sample collection did not require any handling of the animals. All necessary permissions to collect and store the samples at the national wildlife reference sample repository were obtained from the Ministry of Forest, Environment and Climate Change, Government of India and Forest Department, Uttarakhand (letter No. 1/29/2003-PT).

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