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Cover Image: Red-headed bunting *(Emberiza bruniceps)* and Black-headed bunting *(Emberiza melanocephala)* are long-distance migratory passerines overwintering in India. ©Shantanu Kuveskar.

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Content

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TYPE Commentary

Arrival, rise, fall, and again rise of the Asiatic lion *Panthera leo leo* in India

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Abstract

Many animal populations have shifted their distribution and emigrated to new areas in response to climate change, and lions in India have had a similar story. This commentary examines historical records, environmental barriers, climate change in the region of Indus-Sarasvati rivers that created conditions for lions's entry in India. Recovery of artefacts of several wild animals and near absence of lion in these ancient artworks at any site of the Indus-Sarasvati civilization revealed that lion was absent or rare beyond the east of the Indus River in India before 2000 BCE. Environment progressed from the moist conditions to dry in the Indus-Sarasvati region between 2600 and 1500 BCE, discharge of snow water from the Himalayas declined and many large rivers of Indus-Sarasvati system transformed into seasonal rivers. Also, the dense forests transformed to thorn forests and savannah like vegetation over a period after 2000 BCE. Subsequently, Asiatic lions from the ancient Persian land got suitable environment and opportunity to cross the Indus valley to the east. After a period, lion population flourished reaching its peak in India during Buddha-Mauryan-Gupta period (600 BCE – 500 AD). Hunting records revealed that the distribution and abundance of lions remained at its peak during the Mughal and early British period before end of the Little Ice Age during the mid-19th century. Subsequently, fall of the Asiatic lion was sharp as numbers declined below hundred. After a long critical period of ups and downs, Asiatic lion's number and distribution range is on consistent rise since declaration of Gir Lion Sanctuary Project in the early 1970s. Since then, lion population has increased by five folds (891 individuals in 2025) along with impressive recovery of wild ungulate population, turning management approach into one of the most successful wildlife conservation stories in the world. Considering dispersion trend of the lions and their arrival to Barda forest, an identified alternative site for lion, Gujarat Government has prepared a long term comprehensive project, "The Project Lion @2047-A vision of Amrut Kal" to secure and manage the growing lion population and its potential habitats distributed in entire Saurashtra region.

Keywords: Climate change, Indus valley civilization, lion distribution, lion history, lion population.

Introduction

Before the recent genetic studies on the surviving lion populations from different regions in the world, biologists placed all African lions within a single subspecies, *Panthera leo leo*, and the Asian lions as the second zoo-geographic subspecies, *P. leo persica* (O'Brien *et al.*, 1987; Bauer *et al.*, 2016; Jhala *et al.*, 2019). These two subspecies had possibly diverged around 55,000 to 200,000 years ago (O'Brien *et al.*, 1987). However, recent studies found that the Western and Central African lions are more closely related to the Indian lions in the Gir forests than those found in South and East Africa (Bertola *et al.*, 2022). Their work has improved the subspecies classification, categorizing the surviving lions in two subspecies: *Panthera leo leo*- lions of Central Africa, West Africa, and Asia (India), and *Panthera leo melanochaita*- Southern and Eastern African lions (De Manuel *et al.*, 2020; Bertola *et al.*, 2022). Recent analysis using mt-DNA from the latest and old lion samples shows that the movement of lions from north Africa into Asia started sometime around 21000 years ago and probably continued till the late Holocene, bringing fresh genetic material to the existing Asian lion populations (Barnett *et al.*, 2014). The study found evidence of separate incursions into India from North Africa through Asia Minor. The maternal lineage of the current Asiatic lion population in Gir was found to be a part of the clade of the Northern, Western, and Central African lions (Barnett *et al.*, 2014; Jhala *et al.*, 2019). Research by Bertola *et al.* (2015), who included nuclear as well as mt-DNA markers, found that the Indian lions were a distinct genetic cluster without much admixture from African lions, plausibly evolving separately after migrating to India.

Globally many animal populations have shifted their distribution and emigrated to new areas in response to climate change, including the lions (Barnett *et al.*, 2014). During the period of the Indus Valley civilization, climate-induced vegetation shifts in the forests of the Indus-Sarasvati landscape have been well-documented (Shaffer & Lichtenstein, 1989; Enzel *et al.*, 1999; Staubwasser *et al.*, 2003; Cliff, 2009; Giosan *et al.*, 2012), but there have been no corresponding investigations of wild animal emigration/dispersal. This paper logically clarifies the issue and tries to bring new facts related to the arrival, rise, fall, and again rise of the Asiatic lion in India.

When and how the Asiatic lion crossed the western Himalayan passes and entered the Indian subcontinent has remained a matter of debate due to a lack of extensive and authentic evidence. Fossil records in Sri Lanka (Manamendra-Arachchi *et al.*, 2005) indicate lion's presence as early as the late Quaternary, much before the estimated arrival of both modern lions and tigers into India (Jhala *et al.*, 2019). However, this may not be relevant in the context of the entry of the modern lion into the Indian subcontinent, unless the fossil records of Sri Lanka show links to the current lions in India.

When did the Asiatic lion enter India?

Lions perhaps first entered India from the western Himalayan passes (Singh, 2017a; Rashid & David, 1992). As the lions could not possibly enter mainland India from Asia Minor/Persia without crossing the Indus River and the Indus-Sarasvati landscape. The Indus Valley civilization, also known as the Indus-Sarasvati civilization or Harappan civilization, was a Bronze Age civilization in the north-western regions of the Indian subcontinent, lasting from 3300 BCE to 1500 BCE, with a mature phase from 2600 BCE to 1900 BCE. The seals and artefacts linked to the Indus Valley civilization often depict common animals like tiger, elephant, rhino, bull, antelope, crocodile, etc., but lion is conspicuously absent (Divyabhanusinh, 2008; Dutt *et al.*, 2018). Except at sites of Mehrgarh civilization in the west of the Indus River, lion art was not found on seals, pottery, and terracotta at any of the hundreds of Indus Valley civilization's sites such as Mohenjo-daro, Dholavira, Harappa, Lothal, and Rakhigarhi (Singh, 2017a). A rare figurine of a two-headed lion-like creature was recovered from an Indus Valley site, but it was likely an imported artefact (Divyabhanusinh, 2008; Singh, 2017a).

Surprisingly, lion painting or art on terracotta vessels were recovered at Mehrgarh (Baluchistan) in the west of the river Indus, one of the most important Neolithic (7000 BCE to 1700 BCE) sites in archaeology (Figure 1). The presence of lion in artefacts at the Mehrgarh in the west of the Indus River indicates a close association of the lion with people of western Indus Valley as well as people of the ancient Persian lands. Lions have had a close relationship with humans, as it was reflected in human art and culture wherever both shared the same landscapes. What was the reason for the presence of such artefacts at Mehrgarh and their absence at any other site east of the Indus River? Perhaps, dense moist forest and the mighty Indus River worked as a barrier against the movement of the lions to the east of the Indus River before the progress of aridity in the region. Therefore, the lion was plausibly not present in the east of the Indus River during the mature phase of the Indus Valley civilization.

To understand the period of lions crossing the Indus-Sarasvati region to its east, it is necessary to discuss climate, forests, and conditions of the rivers and environment. The study by Dutt *et al.* (2018) indicates an interval of warm and wet climatic conditions before and during mature phase of the Indus valley

Figure 1. Artefacts depicting a lion-like figure recovered from Mehrgarh, a western Indus Valley civilization site. Source: Singh (2017a) and Google images

civilization with a trend towards deteriorating climate, leading to a protracted period of cold and arid phase from 2350 to 1450 BCE in the Indus-Sarasvati region. During this protracted dry spell, the Indian summer monsoon weakened depleting the water resources in the region that likely had triggered the gradual desertion of the Harappan cities. Study suggests a more than 900 years long event of dry spell in the North-West Himalayas beginning at about 2350 BCE, which decreased the precipitation and snow melting in the Northwest Himalayas and subsequently the discharge in the Indus River system (Dutt *et al.*, 2018). A shift in temperatures and weather patterns over the Indus valley at the beginning of 2500 BCE caused summer monsoon rains to gradually dry up, making agriculture difficult or even impossible close to Harappan cities (Giosan *et al.*, 2012).

Shaffer & Lichtenstein (1989) envisaged a wet climate during early Harappan times, placing the mature phase in an already marked trend of aridity. The planktonic oxygen isotope ratios of the Indus delta were examined by Staubwasser *et al.* (2003). According to their research, the climate changed over the past 6,000 years, with the most notable shift occurring during the last phase of the fully developed Indus Valley civilization with a reduction in water flow in the Indus River. They observed that the 2200 BCE event aligns with the drying rivers and sudden decline of urban Harappan civilization in the Indus Valley (Enzel *et al.*, 1999; Staubwasser *et al.*, 2003; Cliff, 2009). Gupta *et al.* (2006) collected studies on the monsoon and other climate factors from a variety of sources, including their own, and came to the conclusion that the arid phase in the Indian subcontinent started during the mature phase of the Indus Valley civilization, coinciding with a stepwise weakening of the south-west monsoon. The arid phase might have intensified during 2000 – 1500 BCE, as has been in the Himalayas, western peninsula, and north-western India. Danino (2016) also wrote that the early mature Indus Valley civilization was the time when, in the east of the Indus system, the mighty Sarasvati dwindled to a minor seasonal river. Evidence in these scientific publications suggest that the savannah habitats existing today in western India are young.

Based on abovementioned studies, it appears to be well recognized now that climatic and environmental disruptions were a significant factor in the decline of moistness of environment, transformation of many mighty rivers into seasonal rivers, gradual change of high forests into thorn forests and savannah like vegetation, leading to final break-up of the Indus civilization. In other words, early phase or at the beginning of the mature phase of the Indus Valley civilization, the environment of the Indus-Sarasvati region was wet with dense, moist to semi-moist tropical forest, and large rivers acting as a barrier against the movement of the lion to the east of the Indus River. When many rivers of the Indus-Sarasvati system changed seasonal, discharge of snow water from the Himalayas declined in the rivers and dense forests transformed to thorn forests or savannah like vegetation over a period, lions from the Persian region in the west of the Indus River got suitable environment and opportunity at some time, most likely after 2200 BCE, to cross the Indus valley to its eastern lands in India.

There could be two reasons for the presence of lion artifacts at the site of the Mehrgarh. First, it was an extension of the Persian civilization where the lion was the dominant big cat. Second, perhaps lions crossed the Bolan pass (near Quetta) and lived in the region west of the Indus River, indicating continuity of lion distribution from the ancient Persian land to Mehrgarh through the Bolan Pass. However, the dense, moist forest in the lower Indus Valley and a bigger Indus River could have acted as an environmental barrier for the lion.

M. A. Rashid and Reuben David, the two known lion experts from India, wrote that the lion migrated to India through the north-western passes much before 6000 BCE (Rashid & David, 1992), but no authentic evidence was mentioned to substantiate it. The *Rigveda*, one of the oldest texts in the world (approximately 1700–1100 BCE), places great importance on lions, bulls/cows, and horses. The early part of the *Rigveda* does not mention the tiger, but the lion is mentioned, perhaps because the bulk of this text originated either in the north-western Himalayas or northern Persia, which had lions. Subsequently, the lion in culture was carried on by the people in the Rigvedic land to the Indian subcontinent.

A fresh controversy emerged after the publication of a book, "Exotic Aliens: The Lion & the Cheetah in India" (Thapar *et al.*, 2013). The statement in the book about the Asiatic lion being introduced in India by humans was contested by wildlife experts like Divyabhanusinh and Ranjitsinh (Jhala *et al.*, 2019). Such views of anthropogenic introduction of the Asiatic lion, opined by some naturalists and historians, have been negated by genetic studies. O'Brien (2013) wrote that no African genetic lineage was ever discovered among the wild Gir lions sampled. A comprehensive analysis of molecular phylogeny indicated a clear genetic distance between the present Gir and African lion populations, indicating separate populations for a long period and no evidence of gene flow between African and Asiatic lions after the Holocene (Barnett *et al.*, 2014; De Manuel *et al.*, 2020). This curtails the scope for continuing discussion on the points raised by Thapar *et al.* (2013).

Rise of lions – Abundance and historical range in India

The lion came to India at a time when tigers and leopards had already settled in the subcontinent (Rashid & David, 1992; Bernett *et al.*, 2014). Perhaps the lion was present in the areas inhabited by the new human migrants (*Aryans*) and on the route through which they migrated to India. The close proximity of lion may explain its prominence in their art and literature and the absence of tiger. It is also likely that the lions followed their prey, the livestock, and fresh genetic pool of lions entered in mainland India following human migrants and their cattle and thus began to colonize the northern and western parts of the country. Within a millennium, they expanded their habitat up to the rivers Narmada and Ganga. It may be inferred that the lion's history in the Indian subcontinent may not be more than 4,000 years old. Kailash Sankhala, in his book "Tiger! The Story of the Indian Tiger", says that the tiger seems to have lost its supremacy in India for some time after about 1500 BCE (Sankhala, 1978). The lion was frequently mentioned in religious and cultural works, including the *Rigveda*, Buddhist *Jatakas* stories, *Panchatantra*, and Sanskrit literature in general. Lions guarded the gates of the majority of temples of the ancient and early medieval periods. In the late medieval period, the lion dominated human culture in north-west India. Following Independence, the lion capital of the Ashoka pillar (300 BCE) was chosen as India's emblem and, subsequently, its national animal. The lion, which had dominated India for over 3,000 years, was replaced by the tiger as the country's national animal only in 1972–1973.

The *Rigveda* has more than fifteen references to the lion (*Simha*). Aryan *devatas*- *Rudra* and *Agni*- are compared to a lion in the *Vedas*. In *Dev-Asur yug*, Narsimha, a Lord Vishnu incarnation or avatar who is half man and half lion and killed Hiranyakasyipu, a great Asur king, thereby restoring *Dharma*. In the early *Rigvedic* period, before the epic age (earlier than 600 BCE), Bharat, son of the great king Dushyant and Shakuntala, played fearlessly with lion cubs in a sage's *ashram*, a testament to his bravery. In the war of the ten kings, Indra, king of the *Devas*, provided aid to *Rigvedic* king Sudas of the Bharat clan against the vast host of enemies. In this war, the defeat of ten kings is compared to the defeat of a lioness by a ram. There is an interesting story in both the *Ramayana* and *Raghuvamsa* of a lion attempting to kill the cow, *Nandini*, who was saved by king Dilip, an ancestor of Lord Rama. These mythological stories indicate the presence of lions in the lands of their kingdoms.

It is likely that the period from the entry of the lion in India to 600 BCE saw an increase in the lion's distribution range in the north-western and north-eastern India up to Bihar - Bengal and up to the Narmada River in the south. The Harappan civilization used the bull, the elephant, the rhino, and the tiger as cultural symbols. In Asia Minor, Europe, and Egypt, every god, goddess, and king was 'lionized'. But in India, before Mahavir (540 BCE to 468 BCE), none of the twenty-three *Tirthankars* of Jainism had the lion as their symbol. Every one of them selected plants and animals, including snakes, as their symbol. King of *Ikshwaku Vansh* of Simhpur (now Sarnath, near Varanasi) was the father of the 11th Tirthankar, Lord Shreyansnath. The name of the kingdom, Simhpur, suggests that the lion perhaps existed when Lord Shreyansnath was born in the city (Singh, 2017a).

Queen Trishala, mother of Vardhman, who was later named as Lord Mahavir, dreamt fourteen beautiful and auspicious events after conception, including a magnificent lion, at midnight. The dream was interpreted that her son would be as powerful as a lion. He would be fearless, mighty, and capable of ruling the entire world. The lion became a symbol of Tirthankar Mahavir, but this royal animal could not become a symbol of other *Tirthankars* before him.

Siddhartha, who was later called Gautam Buddha after achieving enlightenment around 524 BCE, was born around 560 BCE to Sakya chieftain. He was also known as *Sakyasimha*, the lion of the *Sakya* tribe. His first sermon at Sarnath is known as *Simhanad*, the roar of a lion, since his voice was as loud and effective as the roar of a lion. While other gods and kings in ancient India were symbolized with animals like elephant and bull, the lion was chosen as a symbol for Gautam Buddha, Mahavir Jain, and the *Mauryans*. The domination of the lion in culture during the time of the Mahavir Jain, Buddha, and the *Mauryas* around the sixth century BCE indicates that the distribution and population of the lion reached a peak during those periods. By the time Jainism and Buddhism grew in significance, lions had a well-established distribution range in India.

During the time of Buddha, the Asiatic lion roamed from Sindh in the west to Bengal in the east. The Himalayan foot-hills and the Ganga plains formed their northern and eastern limit, while the Narmada seemed to be its southern boundary, although unconfirmed report of the lion south of Narmada River have also emerged (Rashid & David, 1992; Singh, 2017a). A question might be raised as why the lions did not reach the eastern plains of the Ganga River. There could be two reasons: first, the lions could not get enough time to cross the mighty Ganga in the plains, and the second reason could be that the dense, moist forests and Ganga river acted as an environmental barrier. Lions were abundant in the Gupta period (300 AD to 600 AD), as kings of the period – Chandragupta II and Kumargupta hunted lions and minted lion coins. There are plenty of records of lion hunts during the Mughal period and early British period (mid-15th century to 19th century AD). Thus, the Asiatic lion flourished from the first millennium BCE to the mid-19th century AD in the north-west of India.

Fall after the Little Ice Age – A critical period a hundred years ago

The Asiatic lions are now restricted to a single population in and around the Gir forests in Gujarat State of India. Due to un-restricted hunting and habitat loss, lions were extirpated from Asia Minor and a major part of the habitats in India by the end of the 19th century (Figure 2; Singh, 2017a).

Except for lion hunting records of the Mughal and British period, the history of lions in India before the 19th century, especially beyond the Gir forest, is poorly documented. Kazmi (2021) has described chronological records of lion hunts in Hurrianah (now Haryana) and the region around Delhi. His research established the existence of a good number of lions, and their large-scale hunting, which involved wiping out entire prides, including the killing or capturing of lion cubs in Haryana, leading to their extinction in a short period. He listed 26 references dealing with lions in the Haryana landscape between the years 1809 to 1823. The records also provide very interesting information on the ecology of lions in Haryana. These references mention sightings of a total of 129 to 141 lions, out of which at least 109 were conclusively killed by the hunters. Of them, as many as 80 lions were killed in a mere five-year period (1810–1815). The British record of June 18, 1811, mentioned that the lions were very plentiful in the area around Hansi, Haryana, where tigers and leopards also occurred. Kazmi (2021) also mentioned the travel diaries of Maria Nugent, the wife of Sir George Nugent, the Commander-in-Chief of India (1811–1813), who kept record of lion hunts. William Fraser, who was part of Lady Nugent's camp, hunted plenty of lions in Haryana, mostly on foot or on horseback. Divyabhanusinh (2008) also mentions that the

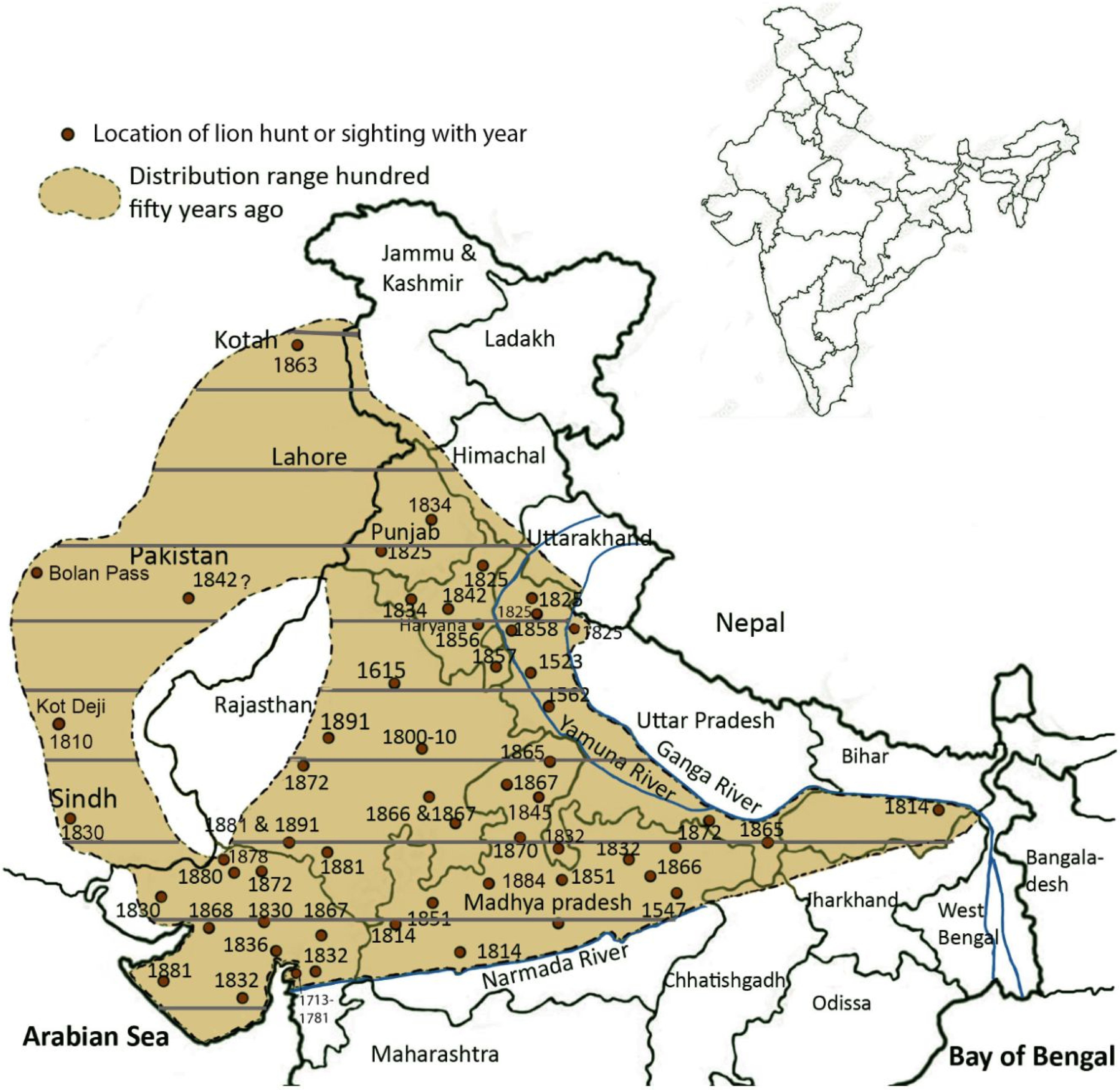

Figure 2. Lion distribution in India and hunting records by the mid-19th century. Sources: Joslin (1973), Rashid & David (1992), Divyabhanusinh (2008)

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British encountered plenty of lions in the region around Delhi. Naturalists Richard Lydekker and J. G. Dollman claimed that Colonel George Acland Smith hunted 300 Indian lions during his stay in India (out of which about 50 lions were killed in the Delhi district) in the years leading up to and just after 1857, although this statement was contested by some naturalists (Thapar *et al.*, 2013; Kazmi, 2021) . Available records indicate that population and distribution range declined drastically after the First War of Independence (1857) in India, which was also the ending phase of the Little Ice Age (1300 AD to 1850 AD).

During the Little Ice Age, from the early 14th century through the mid-19th century, when mountain glaciers expanded, the climate was cooler than the present days. Subsequently, habitat loss and rampant hunting, combined with the impact of a hot environment, perhaps caused a drastic decline in the distribution range and population of lions.

Available records suggest that lions occurred in almost all parts of Saurashtra during the Mughal period, and lion hunts were recorded in all districts of the region (Gee, 1964; Rashid & David, 1992; Singh, 2017a). By the 1880s, lions were restricted in and around the Barda and Alech hills, Mitiyala, Girnar, and Gir forests in the Saurashtra peninsula of Gujarat (Jhala *et al.*, 2019). Subsequently, lions were extirpated from Barda and Alech hills and were restricted to Gir forest and adjoining areas. Since 1880, there has been an increased concern about the falling numbers of the Asiatic lion in the Gir forest. The last three decades of the 19th century and the first two decades of the 20th century were the worst for the Indian lion as its population was estimated below a hundred individuals, with few naturalists mentioning a population below 50 individuals (Gee 1964; Rashid & David, 1992). Although most of these estimates were opinions rather than a result of systematic surveys. At the beginning of the 20th century, Lord Curzon declined a lion hunt in the Gir forests in Junagadh because the Asiatic lion was on the verge of extinction and instead asked the Nawab of Junagadh to protect the animal. According to Fenton (1909), a British field officer, five or six lions were shot annually within Gir and about eight in the outlying areas, despite protection. The Chief Forest Officer of Junagadh mentions in 1913 that a good number of lions were hunted annually in Mitiyala, a block of forest governed by the princely Estate of Bhavnagar (Anon., 1975; Singh, 2017b).

The Statistical Account of Nawab (ex-ruler) of Junagadh in 1884, through a statement of a Britisher, Col. J. W. Watson, mentioned that the Gir lion population was about a dozen (Divyabhanusinh, 2008; Singh, 2017a). After a tour of the Gir forest in 1913, Wallinger, the Chief Forest Officer, raised alarm about a low number of lions and reported that there were no more than 20 lions in the Gir forest of Junagadh State (Anon., 1975; Singh, 2017a). However, during the same period, Major H. G. Carnagie, in 1905, mentioned about 80 surviving lions (at least 70 lions), and J. R. Ratanagar and Sir P. R. Gadell stated about 50-100 free-ranging lions in the Gir forests in 1920 (Anon., 1975). The scientific discourses later picked the lower number (a dozen to 20 individuals) as a reference of lion population at the beginning of the 20th century for unknown reasons, ignoring observations of other naturalists. At that time, lions occurred in Rajkot and Bhavnagar states beyond the boundaries of the Gir forests governed by the Nawab of Junagadh. During the first census of the Asiatic lion in 1936 in and around the Gir forests, 287 individual lions were counted (Anon., 1975; Singh, 2017b). If the lion number was below two dozens in 1913, how could it reach 287 individuals at the time of the first lion census in 1936? It is evident that the free-ranging lion population most probably never dropped below fifty during the entire history of the Indian lion. Ignoring several reports and logical findings, and sticking to two individual statements, numerous scientific papers and books have been published discussing and ascertaining an unrealistic population rebound. These scientific publications have created an improbable narrative that the present population of the Gir lion is built up from a dozen lions that survived in the Gir forests. These narratives need recalibration to correct the distorted recent history, and future discourses must be more careful.

Accurate information about the distribution range and abundance of lions in India before the first lion census in 1936 in the Gir forest is not well understood. However, it is evident that the distribution range and population of lions reached their lowest level at the end of the 19th century and the beginning of the 20th century. At present, the Gir forest is synonymous with the Asiatic lion.

Rising again - Recovery from the verge of extinction

Along with Asiatic lions, other carnivores such as the Indian leopard (*Panthera pardus fusca*), striped hyena (*Hyaena hyaena*), Indian golden jackal (*Canis aureus*), jungle cat (*Felis chaus*), Indian fox (*Vulpes benghalensis*), honey badger (*Mellivora capensis*), and rusty-spotted cat (*Prionailurus rubiginosus*) occur in the Gir landscape. Nine wild prey species, consisting of seven wild ungulates (spotted deer *Axis axis*, sambar *Rusa unicolor*, blue bull *Boselaphus tragocamelus*, four-horned antelope *Tetracerus quardricornis*, blackbuck *Antelope cervicapra*, Indian gazelle *Gazella benneti*, and wild pig *Sus scrofa*), one primate (hanuman langur *Semnopithecus entellus*), and one large bird (Indian peafowl *Pavo cristatus*) are the main wild food for major carnivores in the Gir forest (Joslin, 1973; Anon., 1975). Lions are primarily dependent on wild ungulates like spotted deer, blue bull, sambhar and wild pigs, and domestic animals like cattle, buffalo, whereas leopard's dependency is high on spotted deer, sambar, wild boar, Hanuman langur, peacock, Indian hare and medium to small domestic animals (Anon., 1975; Singh, 2017b). Beyond Gir boundaries, lions' dependency for food is high on cattle, buffalo, blue bull, wild pig, and carcasses of domestic animals (Jhala *et al.*, 2019).

The Gir Lion Sanctuary was created in 1965, and the Gir Lion Sanctuary Project was launched in 1972. Before the implementation of the Gir Lion Sanctuary Project, the prey population was very low, and lions' dependency was mainly on domestic livestock-cattle and buffalo (Joslin, 1973; Anon., 1975). Implementation of the project was one of the most successful conservation stories, as the lion population consistently increased by five folds (Figure 3) and seven species of wild ungulates also increased by many folds (5,600 in 1973 to 91,300 in 2019) during the last five decades (Joslin, 1973; Anon., 1975; Singh, 2017b; Jhala *et al.*, 2019; Ram *et al.*, 2023a).

At present, lion is found in seven districts– major parts of Junagadh, Gir-Somanath, Amreli, and Bhavnagar, some parts of Rajkot, Porbandar, Devbhumi, Dwarka, and occasional visits in Surendranagar district. In the winter of 2023, one lion and two lionesses arrived in the Porbandar district and settled in the Barda forest, a site identified in the 1979 as an alternative habitat for lions. Subsequently, they were joined by three more lionesses. Breeding of these lions was documented during the last two and a half years. At present, there are 17 individual free-ranging lions (one male lion, 5 lionesses, 2 sub-adults over one year, and 9 cubs) in the Barda forest. Thus, the restoration and development of an alternate lion population away from the Gir landscape is currently in progress at Barda forest.

In 2015, lion counting was done in about 22,000 km^2, which was further increased to about 30,000 sq. km in 2020, and 35,000 km^2 in 2025 due to continued dispersion of the lion (Gujarat

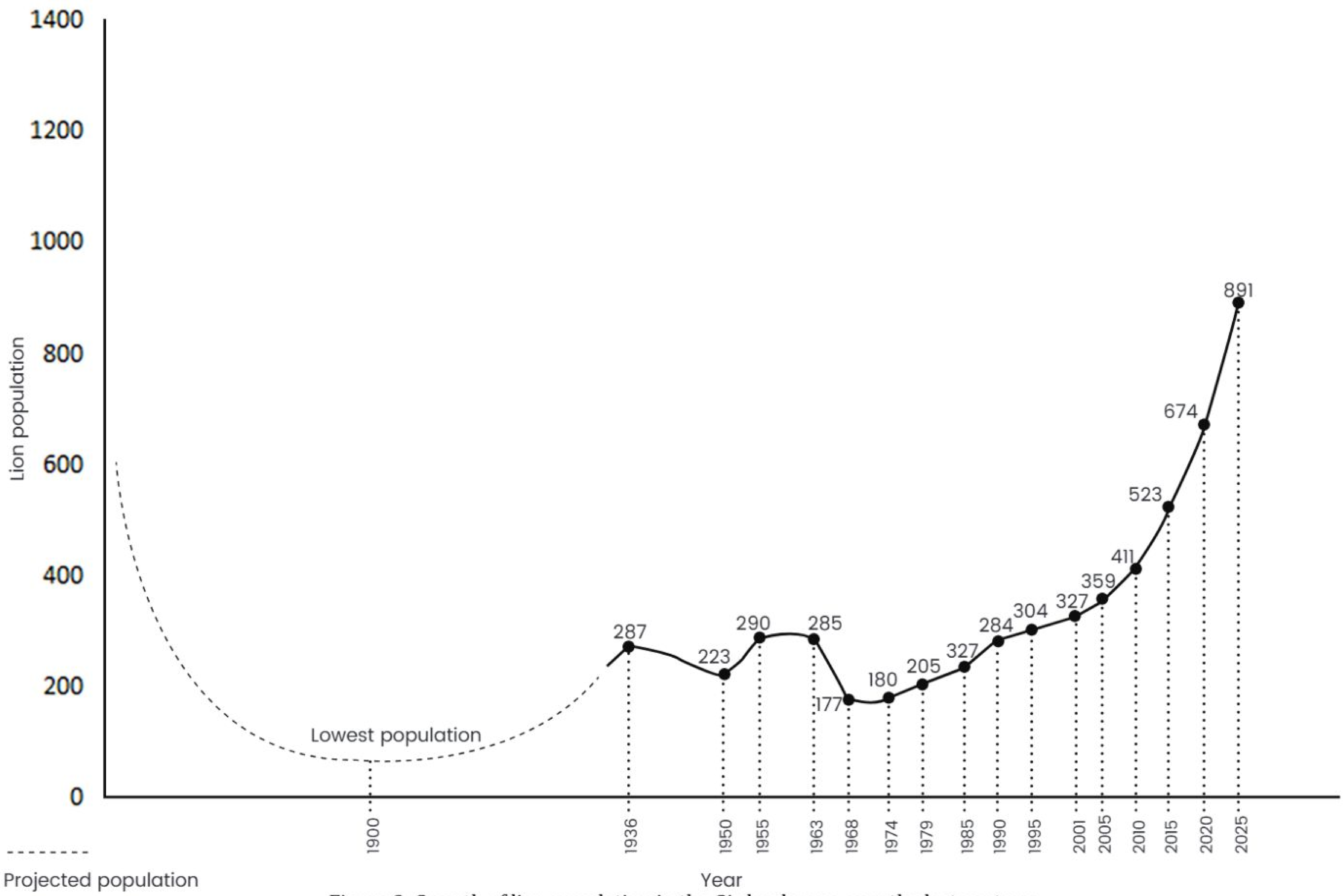

Figure 3. Growth of lion population in the Gir landscape over the last century.

Forest Department, 2025). The population of a minimum of 891 lions at 358 locations in 2025 was female-biased (330 females, 196 males, 140 sub-adults, and 225 cubs). The network of Gir Protected Areas (Gir National Park, Gir Wildlife Sanctuary and Paniya Wildlife Sanctuary), held the largest number of lions (n= 394) as source/core population, followed by seven satellite populations and one alternate population: (i) Savarkundla-Liliya and adjoining areas (n= 125), (ii) the south-eastern coast in Amreli district (n= 94), (iii) Bhavnagar mainland - Hippavadli Zone (n= 103), (iv) Girnar Wildlife Sanctuary and adjoining area (n= 54), (v) the south-western coast in Gir–Somnath district (n= 25), (vi) the coast of Bhavnagar district (n= 15), (vii) Mitiyala Wildlife Sanctuary and adjoining area (n= 32), (viii) Barda Wildlife Sanctuary - an alternative site (n= 17), and corridors and other areas (n= 32) (Figure 4; Gujarat Forest Department, 2025). As per the lion census in May 2025, more lions are outside the Gir forest boundaries (55.8%) than the lions within it (44.2%; Gujarat Forest Department, 2025). Naturalists working in and around the Gir forests have a strong opinion that the lion population is growing consistently at the same or a higher rate. If the compounding annual growth (5.74 %) of the last five years persists in the lion conservation landscape, the population may continue to disperse in the entire Saurashtra region covering 11 districts. Increasing population and detection of death cases during the last ten years also reveal a high population of lions (Ram *et al.*, 2023b). The Forest Department reported in the Gujarat Legislative Assembly that 313 lions died in two years – 2019 and 2020 (154 deaths took place in 2019 and 159 in 2020, comprising 90 lionesses, 71 male lions and 152 cubs) and average annual deaths of lions during the last ten years, from 2015 to 2024, was 122 individuals (pers. comm. Gujarat Forest Department).

The lion count revealed that the lion number within the Gir Protected Area has marginally increased, but the rate of increase was consistently high beyond the boundaries of the Gir forests in the satellite areas. The lion distribution range has expanded from about 10,000 sq. km. in 1995 to about 35,000 sq. km. in 2025 (Singh, 2017b; Ram *et al.*, 2023b; Gujarat Forest Department, 2025). Also, lion densities in Girnar, Savarkundla-Liliya, and the coastal zone of Amreli are higher than the densities in the best lion habitat within the Gir Protected Area. The recovery of the big cat in the lion conservation landscape in the Saurashtra region is a success story, accrediting the efforts of the local community and the Gujarat Government. This story of lions and the people living in proximity in the Saurashtra region of Gujarat provides the world with a plausible model of carnivore co-existence (Singh, 2017b; Jhala *et al.*, 2019).

Emerging future scenario

Establishing a second population of free-ranging lions without dependency on the Gir forest has been the most important conservation priority. Kuno National Park in Madhya Pradesh was identified and developed as an alternative site for the Asiatic lion, but lions could not be translocated till date due to socio-political reasons, despite the direction of the Supreme Court of India. Barda forest in Porbandar and Jamnagar districts was also identified as an alternative habitat within Gujarat by the State Government in 1979, but the lion populations could not be restored there as well. Migration of a lion and five lionesses in the Barda forests (quite distant from the source population in the Gir forest) and the successful birth of litters of all five lionesses in recent years has moved the progress in the right direction. The State Forest Department has initiated several activities to restock Barda and the surrounding area with lions and wild ungulates. Recent development indicates that, in a few years, Barda forest is expected to be fully rehabilitated by the lions, building an alternative site.

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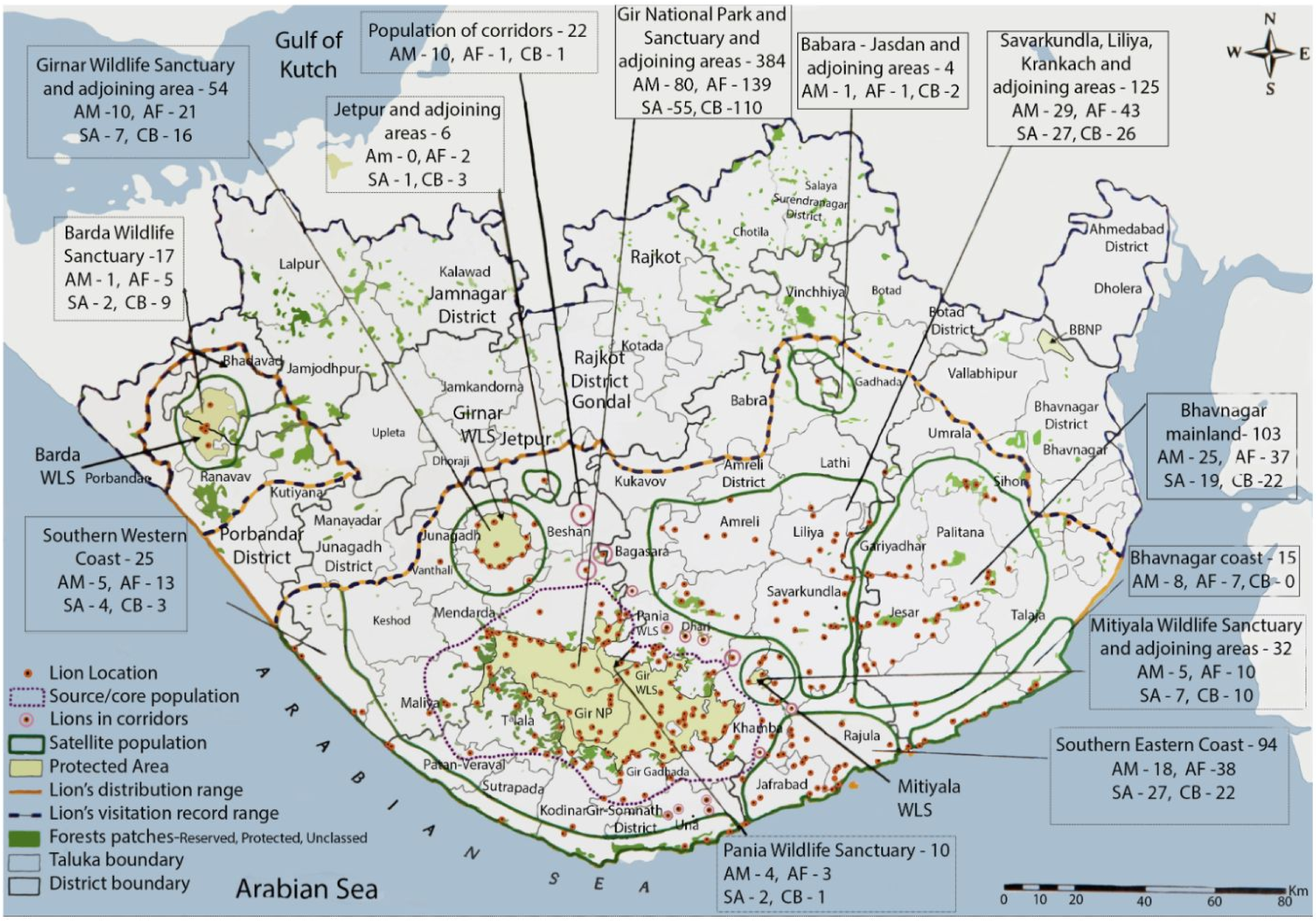

Figure 4. During the latest Asiatic lion census on 12-13 May 2025, a total of 891 lions were recorded at 358 locations across Gujarat, India. Source: Gujarat Forest Department (2025)

When the population reached a saturation level in and around the Gir forests in the 1990s, the lions gradually dispersed to new areas where they had occurred a century ago. The distribution range of the Asiatic lion was doubled in the four districts (Jhala *et al.*, 2019) in three decades, which further expanded to seven districts in 2025 (Gujarat Forest Department, 2025). Conservation measures beyond Protected Areas were extended to the entire lion distribution range. The Gujarat Forest Department reports that the free-ranging population of Asiatic lions is widespread in the multi-use landscape of the Saurashtra region. In several villages, forest patches, wastelands, and community lands are available for resting and sheltering, although not all of them may be suitable sites for lion breeding. Considering the dispersion trend of the lions, the Gujarat Forest Department has prepared a long -term comprehensive project, "The Project Lion @2047- A vision of Amrut Kal", to secure and manage the growing lion population and its habitats (Gujarat Forest Department, 2023a). This project, covering Wildlife Sanctuaries and National Parks, Reserved Forests, Protected forests, Un-classified forests, Reserve *Vidis* (Reserved Grasslands), and Non-Reserve *Vidis* in 11 districts of Saurashtra in Gujarat State, has been approved by the National Board for Wild Life in its 7th meeting at Gir-Sasan held on 3rd March 2025.

With the increasing lion population, the likelihood of negative human-lion interaction is also increasing. However, a high density of the Indian leopard in the lion distribution range is also a big cause of man-wildlife conflict (Vasavada *et al.*, 2020). In 2023, a total of 995 leopards were counted in the lion conservation landscape in the four districts, *viz.*, Junagadh, Amreli, Gir Sasan-Somnath, and Bhavnagar districts (Gujarat Forest Department, 2023b). Thus, over 1,880 big cats with high density occur in the Lion Conservation Landscape. Wild prey biomass within the Gir forests is reasonably high. Due to a high concentration of big cats, human-big cat conflicts are bound to occur. As per the data provided by the Gujarat Forest Department, average annual human deaths due to lion attacks during the last ten years (2015-24) were 3.5 per year, with average annual attacks of 18.9 per year. In comparison, average human deaths due to leopard attacks were 10.5 per year, with average annual attacks of 62 per year during the same period. During the last five years (2020-24), compensation was paid for 28,798 livestock kills (average annual kills- 5760 livestock per year) by lions and leopards, and over 80 % of those were by the lions. There were rare intentional attacks by lions on human beings, as most of the attacks were due to human errors or mischiefs. Payment of adequate compensation plays a crucial role in mitigating conflicts, but leopard attack on human beings are a major cause of human-wildlife conflicts. As lions kill blule bulls and wild boars and protect crops from their raids, people honor this majestic cat and accept its presence in the villages.

Beyond Gir Protected Areas, the population of blue bull and wild pig is good, but the other five ungulates are also present with low density. As per wildlife counting in 2023 by the Gujarat Forest Department, there were 155,360 wild ungulates outside the Gir Protected Area in 11 districts of Saurashtra, but the population of unguarded stray/feral cattle was much more than the wild ungulates. The dependency of the lions for food beyond the Gir forest boundaries is mostly on blue bull, wild boar, stray and domestic cattle, buffalo, and carcasses of the domestic animals (Jhala *et al.*, 2019; Vasavada *et al.*, 2020). The prevailing situation in this human-dominated multi-use landscape beyond the boundaries of Gir Protected Area indicates the scope of successful lion dispersion in other districts of the Saurashtra region in the future.

Conclusion

Recovery of artefacts of several wild animals and absence of any such craft of lion at sites of the Indus-Sarasvati civilization revealed that the lion was absent or rare in India beyond the east of the Indus River during the mature age of the civilization. Subsequently, when many rivers of Indus-Sarasvati system turned seasonal, discharge of snow water from the Himalayas declined and dense forests transformed to thorn forests or savannah like vegetation over a period, lions from the ancient Persian lands in the west of the Indus River got suitable environment and opportunity at some times after 2200 BCE to cross the Indus valley to its eastern lands and entered the Indian subcontinent, bringing major influx of lion population in India. After entering the Indian subcontinent from the Persian region, the lions population reached its peak during the Buddha period (6th century BCE). Lion distribution and abundance remained at the peak during the Mauryan and Gupta period (320 BCE to 550 AD). Hunting records reveal that the lion's distribution range was in the entire North-West India, south of the Ganga River and North of the Narmada River. The records also reveal that, during the first half of the 19th century AD, lions were abundant in Haryana, the region around Delhi, Rajasthan, and a part of Central India and Gujarat.

The period of the Little-Ice Age was over by 1850. Climate change, loss of habitats, and rampant hunting decimated lions from their entire distribution range. By 1880, lions were confined to the Gir-Girnar-Mitiyala landscape with a low number. As per the observation of naturalists and hunting records, the Asiatic lion population was at its lowest range during the period from 1880 to 1920, but several other observations and records, including the Lion census in 1936 (287 individual lions), indicate that the population of lions never dropped below 50 individuals. Subsequent scientific publications have followed a misleading notion that the present population of the Gir lion was built up from a dozen lions that survived in the Gir forests. Prevailing dispersion trend and future vision and plan of the Gujarat State in India for lion conservation may lead to consistent recovery of lion population and expansion of distribution range in the entire Saurashtra region beyond the present Gir Lion Conservation Landscape.

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CONFLICT OF INTEREST

The author declares no conflict of interest.

DATA AVAILABILITY

No additional data was used in this research.

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Annual migration: Strategy for twice-a-year long-distance travel in obligate latitudinal nocturnal avian migrants

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Abstract

Latitudinal avian migrants show comprehensive changes at multiple levels in response to the prevailing environmental conditions, for example, photoperiod, temperature and food availability. These changes aid in decisions when birds begin their migratory flights. Twice-a-year, changes in identifiable, distinct behavioral and physiological phenotypes favor the generation and overall flux of energy required for the nocturnal migratory flight. For example, the accumulated fat stores *via* free fatty acids oxidation in the liver and protein-mediated transport supply energy required by the 'working' (flight) muscles while birds are in migration flight. However, it is still poorly understood how latitudinal migratory species prepare differentially for two similar seasonal travels; southwards in autumn to escape from the harsh winter condition at breeding grounds, and northwards in spring to reproduce. In this brief article, we aim to provide insights into seasonal plasticities that allow an obligate latitudinal migrant to accomplish annual journeys between nearly fixed destinations, based mainly on research in our laboratories on Palaearctic-Indian migratory buntings over the last four decades.

Keywords: Bunting, *Emberiza bruniceps*, *Emberiza melanocephala*, Migrant behaviour, Migrant physiology, Photoperiod response

Introduction

The annual itinerary of a typical avian migrant includes mainly six seasonal life history states (LHSs), namely reproduction, post-breeding moult, autumn migration, wintering, pre-breeding moult (may be sparse or absent in some species), and spring (vernal) migration. Thus, with the migration taking place before and after reproduction, millions of songbirds follow more rigid annual schedules. All seasonal LHSs are identifiable by drastic changes in behavior and physiology as required to begin and end a successful journey of several hundred kilometers. Most important changes are linked with the timely departure of birds to allow them to explore, in particular, feeding resources at the wintering ground, and nesting resources at the breeding grounds in order to enhance the reproductive success (Ramenofsky & Wingfield, 2007; Kumar *et al.*, 2022, 2025; Helm & Liedvogel, 2024).

Regular variations in environmental agents synchronize, if not drive, changes in behavior and physiology to occur at the most profitable time of the year. For example, when the breeding season ends, migrants prepare for their southward travel to the wintering area in response to the post-equinox decreasing autumn (≤12 h) photoperiods, which can still be close to the threshold for photoperiodic induction in spring. Conversely, the overwintering migrants begin to prepare for their northward travel in response to post-equinox increasing spring (≥12 h) photoperiods. The ambient temperature also seems to play a crucial role in the developing the migration phenologies (Singh *et al.*, 2012; Sur *et al.*, 2020). Therefore, the migratory departure decision is the outcome of integrating changes in photoperiod and temperature, along with food availability, that regulates behavioral and physiological phenotypes associated with migration (Kumar *et al.*, 2025).

In this article, we aim to highlight adaptive strategies that migrants employ between non-migratory and migratory, as well as between spring and autumn migratory LHSs. The discussion is based on experimental evidence, mainly from laboratory research carried out in our laboratories over more than four decades using two migratory species, the black-headed bunting (*Emberiza melanocephala*) and red-headed bunting (*Emberiza bruniceps*). These species measure about 16-18 cm in length, although black-headed bunting is relatively larger. The two buntings are sister species and partially overlap their breeding and wintering areas. Both are obligate latitudinal migrants, and follow a predictable annual to-and-fro migration between breeding sites (~40° N in west Asia and southeast Europe, including Indo-European flyway) and wintering sites spread mainly over a large part of central and north India, 20-27°N (Ali & Ripley 1999; Ćiković *et al.* 2021). Further, they represent the Palearctic-Indian migration system, which is the least studied of the major migratory systems of the world (Galbraith *et al.*, 2014). In late September/ October, both bunting species arrive in India. After an overwintering period for about six months, they begin to return very late in March or early April when the natural light period (sunrise to sunset) is ~ 12.5 h and the average ambient daytime temperature nears ~35°C (Ali & Ripley 1999). In the remaining period, buntings seem to spend ~3 months each at breeding grounds and in to-and-fro migratory travels, totalling a distance of about 6000-7000 km (Ali & Ripley 1999; Ćiković *et al.* 2021).

Migratory phenotype

Each sub-annual LHS leading to the beginning and end of the migratory journey is exhibited in a distinct phenotype at multiple levels, including behavioral, physiological, neural and molecular. For example, the birds maintaining normal food intake and body mass during much of the year, begin showing an increased feeding (hyperphagia), accumulation of fat in the adipose and liver tissues to fuel the intense flight activity, and muscular hypertrophy to enhance flight endurance with transition from non-migratory to the migratory LHS. Along with, in most birds that undertake the migratory travel at night, the most distinct change in behavior is the development of nocturnality in the otherwise day-active species with transition from non-migratory to the migratory LHS. This requires a profound shift in behavior with the onset of the migration period (Berthold 1996; Bartell & Gwinner 2005; Rani *et al.*, 2006). In a caged situation, this is reflected by "wing whirring", and called the migratory restlessness or *Zugunruhe* (Wagner 1930). *Zugunruhe* reflects the intensity as well as temporal pattern of actual migration (Czeschlik 1977; Berthold & Querner 1988).

Our research has shown that black-headed and red-headed buntings held captive under the natural daylength and temperature at their wintering latitudes in India (27° or 29°N) show migrant phenotype, identified most visually in the body fattening (accumulation of subcutaneous fat stores), body mass gain, and *Zugunruhe* akin to spring and autumn time nocturnal migratory flight (Gupta & Kumar 2013; Sharma *et al.*, 2022). Jain & Kumar (1995) monitored the black-headed buntings held captives in semi-natural variations of daylength and temperature in Meerut, India (29°N) for food consumption and body mass, and measured the size of gonads and plasma levels of luteinizing hormone, thyroxin and testosterone over a period for ~10 months beginning in January (thus study period covered both spring and autumn migration periods). There were seasonal cycles in all parameters that were examined, with a gain-loss cycle in body mass almost parallel with the testicular growth-regression cycle; however, the seasonal cycle in food consumption peaked much before the peak gain in body mass (Jain & Kumar 1995).

At the physiological level, the development of migratory phenotype is accompanied by significantly higher blood triglyceride levels, but not glucose levels, and growth and involution of specific internal tissues (Trivedi *et al.*, 2014). In black-headed buntings exhibiting the migratory phenotype, for example, the heart is significantly enlarged and weighs heavier while the intestine is significantly lighter in weight (Trivedi *et al.*, 2014). Concurrent hormonal changes include daily levels and rhythm in plasma insulin and corticosterone secretions (Mishra *et al.*, 2017). There is also a significant lipid accumulation in the liver in red-headed buntings exhibiting the migratory phenotype (Sur *et al.*, 2019).

Migration timing

Role of the prevailing environment

Among multiple environmental factors that restrict sub-annual LHSs to the best suited time of the year as well as shape diurnal changes in the behavior and physiology as per non-migrant and migrant periods, the most influential ones include variations in the daily light period (= photoperiod), ambient temperature and food availability (Kumar *et al.*, 2022). These three environmental cues may act in synchrony, and seasonal migration is possibly the net result of their mutually inclusive effects at multiple levels. Changes in the photoperiod and temperature concurrently affect the internal timing system, circadian and circannual clocks, and synchronize many biological processes to maximize reproductive success and eventually the species survival (Kumar *et al.*, 2010). Temperature influences the food availability more directly by its effects on humidity levels; thus, in turn, it affects the photoperiodic induction of seasonal LHSs (Kumar *et al.*, 2001; Visser *et al.*, 2009).

Photoperiod: Migrants are exposed to two types of photoperiod variations: daily changes in the time of sunrise and sunset at their inhabiting latitude, and latitude-dependent amplitude in variations because of wide differences in inhabiting latitudes across seasons. They stay for about one-third of the year at breeding grounds, *i.e.*, higher (temperate) latitudes, and overwinter for about half of the year at lower (subtropics/ tropics) latitudes; the remaining period in the year is spent in to-and-fro annual travels through consistently varying latitudes. In synchrony with prevailing photoperiod variations, the passerine migrants undergo sequential transitions from non-migratory to migratory to the non-migratory LHS, with intervening breeding and moult LHSs.

All migration-related phenologies are faithfully reproduced in captive buntings by manipulating the photoperiod length (Kumar *et al.*, 2022; Sharma *et al.*, 2022; Tripathi *et al.*, 2025). For instance, buntings held captives at the wintering grounds under a non-stimulatory short photoperiod which maintains the physiological state akin to that in late wintering period in the wild when exposed to a stimulatory long photoperiod (mimics increasing spring photoperiods; *e.g.* 10 h ⇢ 13 h light per day), exhibit the spring migration phenotype. Similarly, buntings maintained under a stimulatory long photoperiod in the physiological state akin to that in post breeding period in the wild, when exposed to a decreasing photoperiod (mimics autumn photoperiods; *e.g.*, 14 h ⇢ to11 h light per day) exhibit the autumn migratory phenotype (Trivedi *et al.*, 2014; Sharma *et al.*, 2018). The response to a stimulatory photoperiod can be very rapid; the transcription pathways involved in key biological processes underlying the hyperphagia, body mass gain, metabolism, cellular defence, which are identifiable features of the migration phenotype, are activated on the very first day of long photoperiod exposure in migratory buntings (Sharma *et al.*, 2021).

Ambient temperature: Variation in ambient temperature is concomitant with the photoperiod change; for example, nights are cooler than the day, and autumn/ winter gets progressively cooler than spring/ summer. Increasing evidence suggests the role of temperature in the development of migration phenologies in latitudinal passerine migrants, albeit with species and sex differences (Helm *et al.*, 2017; Sur *et al.*, 2019;

Trivedi *et al.*, 2019). For example, under a stimulatory 13-h photoperiod, black-headed buntings enhance muscle growth and advance the *Zugunruhe* appearance at 35°C, compared to 22°C temperature (Sur *et al.*, 2020). Along with, transcriptional responses suggest temperature effects on the multiple molecular drivers in both regulatory (hypothalamus) and effector (skin, liver, muscle) tissues, culminating in the migratory phenotype. Perhaps, the hypothalamus senses and integrates the ambient temperature information received/perceived by the peripheral (*e.g.*, skin tissues) temperature receptors (Sur *et al.*, 2020).

Food availability: In anticipation of the migratory departure, migrants undergo a period of hyperphagia in order to get an adequate fat fuel load for the upcoming migration flights (Odum, 1960; Blem, 1980, 1990; Newton, 2007; Trivedi *et al.*, 2014). This is species specific, and can account for as much as 100 % of lean body mass in small passerine migrants, for example, a much larger fat store is accumulated accounting for a much higher weight gain in the black-headed bunting than it is in the red-headed bunting even under identical photoperiodic manipulations (cf. Misra *et al.*, 2004; Rani *et al.*, 2005). In a more direct study examining functional linkage between food availability and migratory behavior, black-headed buntings were subjected to food availability such that they did not have food for 2h at the beginning and end of the light period, or had access to food during the entire light or dark period. When the timings of light exposure and food availability overlapped, the light masked the food effect, but food at night alone reduced both duration and amount of *Zugunruhe* (Singh *et al.*, 2012).

Role of internal clocks

The migratory departure at appropriate time (seasons) of the year is achieved by a close integration of internally recurring mutually coupled circadian (circa = about; dies = day) and circannual (circa = about; annum = year) rhythms with prevailing external (environmental) cues, *e.g.*, photoperiod (Kumar *et al.*, 2010; Stevenson & Kumar 2017). Circannual rhythms govern the timing of migration phenologies in interaction with the prevailing photoperiod (Gwinner 1986; Kumar *et al.*, 2010; Kumar & Mishra 2018). It appears that (i) the mechanisms underlying circannual rhythm generation and evolution of photoperiodism (*i.e.*, photoperiodic regulation of a biological event) are mutually inclusive, and (ii) the circannual migration program accommodates consistent variations in the photoperiod across season as well as along the migratory route (Misra *et al.*, 2004; Stevenson & Kumar 2017).

At the same time, circadian rhythm seems to be involved in daily changes in behavior and physiology as required during the migration. This is most obvious in a nocturnal migrant, which otherwise is a diurnal species. Underlying circadian rhythms regulating diurnal patterns in behavior and physiology seems to redefine itself with the onset of the migratory season (Bartell & Gwinner 2005; Rani *et al.*, 2006). This allows a diurnal species to fly at night, when it is cooler and the sky is relatively predator free. This suggests inherent flexibility in the internal clock system, which is evidenced by alterations in the waveform of circadian oscillations of *period 2, cryptochrome 1, brain muscle arnt like 1 (BMAL1), and circadian locomotor output cycles kaput (CLOCK)* genes that comprise the core of the molecular clockwork (Singh *et al.*, 2015). Indeed, 24-h clock gene oscillations show alterations in the acrophase and amplitude in both regulatory hypothalamus and effector liver tissues between photoperiod-induced non-migratory and migratory LHSs in migratory buntings (Singh *et al.*, 2015; Mishra *et al.*, 2017).

Energy management

Storage of fat fuel

An exceptionally high demand for energy during migration is met by the accumulation of fat fuel stores prior to migratory departure, albeit with species and population differences (Blem 1990). Some species fatten to the extent of gaining weight up to 100 % of the lean body mass, but others put on only a small weight with a little amount of fat. A varying degree of fat fuel storage appears linked to the foraging strategy, essentially differing between species those can replenish and those cannot replenish depleting energy stores (Biebach 1990; Bairlein & Simons 1995). A species with very low fuel stores will need feeding at stopovers every day en route to the migratory destination. Importantly, these fat stores get fully depleted, and birds return to their normal (lean) body mass once the migration is over. Interestingly, the lipid accumulation varies between spring and autumn; autumn migrants carrying a smaller fat fuel load. Spring migrants have a larger store of fat fuel, which they need to travel at a higher speed, with longer night-flight and shorter stopover durations (Bairlein & Schaub 2009; Newton 2007; Nilsson *et al.*, 2013; Yavuz *et al.*, 2015).

The fat fuel storage is mainly in the adipose and flight muscle tissues (Battley & Piersma 1997). There is a copious amount of fat deposits visibly seen lying subcutaneously. The pectoralis major and minor flight muscles also show increased lipid storage, and as a result, they are hypertrophied. There is also a change in the structure of muscle fibers at both the anatomical and molecular levels (Sharma & Kumar 2019; Sur *et al.*, 2019). More specifically, significant changes in the expression of myogenic differentiation 1 protein responsible for muscle differentiation (Legerlotz & Smith 2008; Zanou & Gailly 2013) and parvalbumin protein that quickens the relaxation-contraction ability of muscle fibres (Celio & Heizmann 1982) have been reported in migratory buntings (Sharma & Kumar 2019; Sur *et al.*, 2019).

Energy supply and efficiency

When in migration flight, migrants adapt to voluntary anorexia; conversely, they feed vigorously during the stopover period en route to their migratory destination. Per unit of time, avian migrants are in low-income and high energy expenditure state, as compared to when they are in the non-migratory and stopover period of high-income and relatively low energy expenditure state. Thus, a high metabolic turnover is needed to support the migration flight, which requires a strategy for overall energy homeostasis. This is exemplified by reduced energy expenditure by the onset of hypothermia and minimized activity prior to migration. Consistent with this, the energy supply sources, for example, carbohydrates and lipids, undergo significant seasonal fluctuations.

The major energy source is lipids, which when metabolized yield energy required for the migration flight. Indeed, circulating triglyceride levels show LHS-linked differences in migratory sandpipers (*Calidris mauri*: Guglielmo *et al.*, 2002) and black-headed buntings (Trivedi *et al.*, 2014). Increasing serum triglyceride levels correlate with pre-migratory body fattening in migratory songbirds (Guglielmo *et al.*, 2002; Jenni-Eiermann & Jenni, 1994; Williams *et al.*, 1999). However much less dependence is on carbohydrates as the energy source for migration. There is almost no change in blood glucose levels and expression of genes associated with carbohydrate metabolism between non-migrant and migrant periods in several migratory songbirds (godwits, *Limosa l. taymyrensis*: Landys *et al.*, 2005; Canada geese, *Branta canadensis interior*: Mori & George, 1978; sandpiper, *Calidris mauri*: Guglielmo *et al.*, 2002; blackcap, *Sylvia* *atricapilla*: Jenni-Eiermann & Jenni, 1996; robin, *Erithacus rubecula*: Jenni-Eiermann & Jenni 1996; red knot, *Calidrus canutus islandica*: Jenni-Eiermann *et al.*, 2002; black-headed bunting: Trivedi *et al.*, 2014).

The fuel supply for migration flight is from fat stores *via* free fatty acid (Ramenofsky 1990; Sharma & Kumar 2019). Sharma & Kumar (2019) found significantly higher blood levels of free fatty acids in migratory LHS in buntings. There is an exceptionally high rate of fatty acids oxidation in the liver and protein-mediated transport to 'working' muscles in order to generate and maintain the overall flux of energy as required consistently during the migration flight. This involves multiple regulatory steps, several transporter proteins (*e.g.*, fatty acid binding protein and fatty acid transporter/ cluster of differentiation 36) and enzymes, namely carnitine palmitoyl transferase, enzymes of the tricarboxylic acid cycle: malate dehydrogenase, α-ketoglutarate dehydrogenase (Guglielmo 2010). Trivedi *et al.*, (2015) found concomitantly increased citrate and malate dehydrogenase enzyme levels, suggesting an increased cellular metabolism, possibly by the oxidative phosphorylation, during migratory LHS in buntings. Importantly, corresponding to the seasonal LHS, the required metabolic alternations are regulated at the transcriptional level (Trivedi *et al.*, 2015). Thus, the transcription levels of genes coding lipid metabolism-associated proteins and enzymes in both liver and flight muscles can be contingent upon the metabolic requirements of the seasonal LHS. Indeed, the expression pattern of metabolism-associated genes shows significant differences between non-migratory and migratory as well as between spring and autumn migratory LHSs (Sharma & Kumar 2019).

Behavioral adaptation

Activity behavior

Change in daily activity-rest pattern is the most conspicuous alteration in behavior of migrants. There is a profound shift from diurnal to nocturnal activity pattern in many passerine migrants which are otherwise diurnal (active during the day and inactive at night). These birds travel several thousands of kilometers at night albeit with species-specific daytime stopovers in order to forage intermittently and replenish the depleted energy reserve (Berthold 1996). A GPS-based field study on long-distance avian migrants (rough legged buzzard *Buteo lagopus*, white stork *Ciconia Ciconia*, greater white fronted goose *Anser albifrons*, Himalayan vulture *Gyps himalayensis*) found that the activity period was strongly dependent on daylight exposure duration, irrespective whether they were ground foragers (storks and geese) or flying foragers (buzzards and vultures), or whether they reproduced in temperate (storks and vultures) or the arctic (buzzards and geese) zone (Pokrovsky *et al.*, 2021). The ground foragers showed an almost consistent activity throughout the daytime, while flying foragers changed uniformly their season-specific daytime activity with sun (Pokrovsky *et al.*, 2021). Notably, the drastic change in temporal activity pattern without necessarily a change in the overall daily activity seems a part of overall adaptive mechanism in a species for its nocturnal migration. Sharma *et al.*, (2018) found significant differences in both intensity and duration of *Zugunruhe* between photo-periodically induced spring and autumn migration phenotypes in captive buntings.

Food choice and feeding behavior

In preparation for the forthcoming migration, migrants eat more than what is required for keeping the body mass stable, switch to a more beneficial diet, and increase the assimilation efficiency (a more efficient assimilation of ingested food with reduced loss in excreta and feces). Many migrant birds show seasonal shifts in their food choice (Bairlein & Gwinner 1994; Bairlein & Simons 1995; Bairlein 2002). For example, a species feeding extensively on plants appears to rely more on lipids and less on proteins compared to those feeding extensively on arthropods. Likewise, several passerine migrants switch from fruits, the major or exclusive diet, in the pre-migratory period to an insect diet during the spring migration period (Izhaki & Safriel 1985; Bairlein & Simons 1995). There seem to be changes in both quantitative and qualitative availability of required food resources at stopover sites so that migrating individuals can replenish their depleted energy reserves, as required (Bairlein & Simons 1995). Interestingly, Mediterranean autumn migratory passerines show a shift from insect to fruit diet, but they completely rely on an insect diet during the spring migration period when fruits are almost entirely unavailable in the region (Bairlein & Simons 1995).

Conclusion and perspective

Twice-a-year, long-distance migratory travels of avian migrants represent a remarkable evolutionary adaptation strategy involving a careful coordination of the timing of migration, environmental responsiveness of physiological systems, and energy management. As a consequence, with the transition from non-migratory to migratory LHS, the obligate latitudinal migrants exhibit significant differences in behavior and physiology along with concurrent adjustments in the olfaction, visual and hypothalamic neural circuits. To support migratory flights, migrants utilize fat as a major flight fuel supplied by the adipose tissues *via* free fatty acids. The mechanisms underlying the generation and overall flux of energy involve the oxidation of fatty acids in the liver and concurrent protein-mediated transport to the 'working' muscles. Thus, there are neural and metabolic plasticities to respond to the prevailing environment, leading to seasonal homeostasis at both regulatory and effector system levels. Interestingly, there are differences between the two annual migrations, which differ in the timing, context, and prevailing environment. For example, spring migration requires a faster pace with fewer stopovers for timely arrival to be able to reproduce and raise offspring within a relatively narrow temporal window of favorable season. This translates into long nocturnal flights, and with relatively less time to re-fuel, spring migrants need to acquire a copious amount of fat stores before the migration flight. More so, males need to arrive earlier at the breeding grounds, in order to define their territories and build nests, which serve as key determinants of a successful reproduction. There can thus also be a sex-dependent strategy, at least for the spring migration. Next, migrants are in a different state of physiological responsiveness in relation to the prevailing environment. For example, in relation to the stimulatory effects of photoperiods, birds are in sensitive and refractory states at the beginning of spring and autumn migrant periods, respectively. Furthermore, migrating birds face differences in the direction of photoperiod (and perhaps temperature) change between two seasonal migrations–they experience consistently decreasing and increasing photoperiods during autumn and spring journeys, respectively.

This brings us to a few important questions at present. First, how the habitat loss affects the avian migration? Undeniably, along the migratory route, there is continued destruction of habitat, such as forest, wetland and coastal areas, along with the climate change. Alterations in temperature, weather conditions and food availability can significantly influence avian migratory patterns by shifting the timing and routes of migration. In addition, increasing urbanization, leading to a large part of the world experiencing brighter nights due to artificial lighting at night (lighted nights), is altering the temporal separation of day-night, which has been a key selection pressure in defining the biological processes. This can affect nocturnal migrants in multiple ways, including disorientation, migratory pattern disruption, and increased mortality rates during stopovers in urbanized environments. Therefore, it is important to assess whether and if so, how much these emerging environmental issues have begun posing threats to avian migrants. This, in turn, enables us to learn and make efforts systematically towards the conservation of habitats and the necessary conditions for birds to continue their successful annual migrations.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY

No additional data was used in this research.

AUTHORS' CONTRIBUTION

VK and VT conceived the idea and wrote the initial draft; VT and SK reviewed the draft. VK produced the final version. All authors approved the final version.

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Living on the Edge: Assessing spatio-temporal dynamics of Human-Elephant Interactions in Udalguri, Assam

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Abstract

Landscape transformation due to expanding agriculture and infrastructure in Asia has led to extensive habitat loss and fragmentation for Asian elephants (*Elephas maximus*), intensifying human-elephant conflict (HEC) across their range. India, home to nearly 60% of the global Asian elephant population, faces a rising conservation challenge as elephants increasingly venture into human-dominated landscapes, resulting in frequent crop raiding, property damage, and casualties on both sides. This study investigates the spatiotemporal dynamics of HEC in Udalguri district, Assam, a critical elephant landscape bordering Bhutan. Using 13 years (2011–2024) of data obtained from forest departments and validated through ground truthing and community interaction. We quantified seasonal trends in human casualties, property damage, crop raiding, and elephant mortality to identify conflict hotspots. A total of 221 human casualties (144 deaths, 77 injuries) and 96 elephant deaths (14.5% due to electrocution) were recorded, with monsoon and post-monsoon showing the highest conflict intensity. Males were disproportionately affected in human casualties and elephant mortality. Crop raiding was most frequent in the post-monsoon, with paddy being the primary target. Generalized Linear Mixed Model (GLMM) analyses revealed significant effects of season, crop type, and sex on HEC patterns. Conflict hotspots were concentrated near Bornadi Wildlife Sanctuary (BWS) and Khalingduar Reserved Forest (KRF), highlighting the role of forest edges, paddy fields, and tea estates as high-risk zones. Our findings emphasize the need for adaptive, seasonally informed management strategies that integrate habitat restoration, corridor protection, cross-border coordination, and community-based interventions. Reducing anthropogenic threats, improving compensation schemes, and enhancing early warning systems are critical for fostering coexistence. The study offers a robust empirical foundation for designing region-specific mitigation strategies and reinforces the urgency of transboundary, multi-stakeholder approaches to secure the future of Asian elephants in Northeast India.

Keywords: Asian elephants, crop-raiding, habitat fragmentation, HEC, seasonal patterns, tea, transboundary

Introduction

Rapid expansion of human settlements and agriculture in Asia and Africa has led to significant loss of elephant habitats, reduced forage availability, and diminished landscape connectivity, resulting in a marked decline in elephant populations (Thouless *et al.*, 2016; Calabrese *et al.*, 2017). As habitats shrink, elephants are forced into closer contact with human-dominated landscapes, leading to frequent and severe negative interactions over space and resources, including crop raiding and fatal encounters (Leimgruber *et al.*, 2003; Newmark, 2008; McDonald *et al.*, 2009; Western *et al.*, 2009; White & Ward, 2010; Liu *et al.*, 2017). HEC poses a significant challenge in regions where the livelihoods of local communities and the conservation of elephants are closely intertwined, as ongoing landscape transformation further increases the risk of lethal interactions (Naha *et al.*, 2020; Cabral de Mel *et al.*, 2022; de la Torre *et al.*, 2021).

Considering these escalating challenges, the status of Asian elephants (*Elephas maximus*) highlights the urgency of comprehensive conservation efforts. According to the International Union for Conservation of Nature (IUCN, 2024), Asian elephants are classified as “Endangered” on the IUCN Red List, and the species is included in Appendix I of the Convention on International Trade in Endangered Species (CITES). Asian elephants are protected under Schedule I of the Wildlife (Protection) Act, 1972. Their populations are estimated to range between 41,410 and 52,345 individuals across 13 Asian countries, now confined to just 5% of their historical range (Sukumar, 2006). Ever-increasing human population and extensive habitat fragmentation have reduced their available habitat, with only 51% of their range consisting of large, contiguous forested landscapes (Leimgruber *et al.*, 2003). Native to India, Sri Lanka, Thailand, and other Southeast Asian nations, these elephants inhabit diverse forest and grassland ecosystems (Sukumar, 2003).

India harbors the world’s largest Asian elephant population, which accounts for nearly 60% of the global total, with estimates of 25,000 to 30,000 individuals spread across approximately 163,000 km^2 of diverse habitats (Pandey *et al.*, 2024b). Asian elephants are long-lived, wide-ranging mega-herbivores whose survival depends on their ability to travel great distances in search of food, water, and social opportunities (Sukumar, 2003). Moreover, a typical family herd, comprising approximately 5 to 20 individuals, occupies a home range spanning 100 to 1,000 km^2 (Fernando & Lande, 2000; Williams *et al.*, 2001; Alfred *et al.*, 2012). Additionally, elephants play a critical ecological role by dispersing seeds and enhancing the survival of large-fruiting trees in protected areas, an engineering effect that underpins the integrity of forest ecosystems (Fritz, 2017; Sekar *et al.*, 2017). Recognizing their ecological and cultural significance, India designated the species as a National Heritage Animal in 2010 (Pandey *et al.*, 2024a).

HEC in India epitomizes the complex interplay between wildlife conservation and development. Fragmentation and disruption of traditional migratory routes for wild Asian elephant populations (Sukumar, 2003; Rangarajan *et al.*, 2010) force elephants out of their natural habitats and into areas dominated by human activity. This trend is especially evident in forested regions such as the Western and Eastern Ghats and in northeastern states like Assam, where intensified human pressure further escalates negative interactions (Choudhury, 2004). Within these human-altered landscapes, elephants frequently forage on crops and encounter roadways, further intensifying negative interactions that threaten their survival and impose considerable socio-economic burdens on local communities. India alone reports approximately 500 human fatalities and 100 elephant deaths annually from such incidents, with an estimated 500,000 families affected by crop damage (Somu & Palanisamy, 2022). In response to these escalating challenges, India has implemented robust measures to safeguard its wild elephant population and mitigate negative interactions. Project Elephant, launched in 1992, protects elephants and their migratory corridors by establishing 33 Elephant Reserves across 14 states, covering approximately 80,777 km^2 (PE-MoEFCC-WII, 2024). These conservation efforts have broadened their focus beyond mitigating habitat degradation and reducing direct mortality to also address issues such as ivory poaching, trafficking, and growing competition for space (Sukumar, 2006). Complementing these initiatives, legal frameworks such as the Wildlife (Protection) Act, 1972 and the Forest (Conservation) Act, 1980 regulate habitat destruction and infrastructure development, fostering integrated strategies that promote coexistence and effective management of negative interactions (Pandey *et al.*, 2024a).

In Northeast India, Asian elephants are found in states including Assam, Arunachal Pradesh, Meghalaya, Nagaland, Manipur, Tripura, Mizoram, and Sikkim (Choudhury, 2004). The region is estimated to support approximately 10,139 wild elephants, with Assam alone hosting 5,719 individuals, making it the state with the highest elephant population (MOEFCC, 2017). In response, the Government of India has declared five Elephant Reserves that collectively cover approximately 10,967 km^2 (MOEFCC, 2017). Moreover, maintaining connectivity in fragmented habitats is critical. So far 30 key elephant corridors have been designated to link habitat patches in Northeast India, with Assam holding 12 of these corridors (MOEFCC, 2017; Pandey *et al.*, 2024b). These protected areas and corridors are at the core of the integrated management strategies designed to mitigate negative interactions and ensure the long-term survival of this keystone species, although continued rapid human development is likely to further exacerbate HEC.

In Udalguri district, Assam, the increase in human activities near forest areas has intensified HEC, posing significant challenges for both conservation efforts and local communities. The district includes parts of the Tiger Reserve, which serves as a corridor for elephants. Between 2010 and 2019, the Dhansiri Forest Division (FD) in Udalguri district reported 62 elephant and 155 human fatalities due to HEC (Banerjee, 2022). In 2024, a synchronized elephant population estimation recorded 97 elephants in the Dhansiri FD (Piraisoodan *et al.*, 2024).

This situation underscores the importance of understanding the spatial and temporal patterns of human-elephant interactions to develop effective mitigation strategies and ensure the long-term survival of elephants. This study aims to (a) quantify and characterize seasonal trends in HEC in Udalguri over 13 years, focusing on human fatalities, elephant deaths (both human-induced and natural), and crop-raiding incidents, and (b) map the spatial distribution of negative interaction, identifying hotspots for human casualties, crop raiding, property damage and elephant deaths. By providing a baseline understanding of these dynamics, this study would help to inform future monitoring efforts and offer valuable insights into the current state of human-elephant interactions in the region.

Study Area

Udalguri district, administered under the Bodoland Territorial Council (BTC), is in northeastern Assam, India (Figure 1). The district spans approximately 1,852.16 km^2 and is situated at about 26° 46′ N latitude and 92°08′ E longitude (Khanikar, 2017). Established in 2004 following the bifurcation of Darrang district, Udalguri is bounded by Bhutan and West Kameng district of Arunachal Pradesh to the north, Sonitpur district to the east, Darrang district to the south, and Baksa district to the west. The name Udalguri denotes a place surrounding the Udal tree (*Sterculia villosa*), also known as the elephant rope tree, with "Udal" meaning tree and "Guri" meaning surrounding area.

The landscape of Udalguri is a diverse mosaic of agricultural fields, tea estates, forest tracts, and riverine zones. According to the Tea Board of India, Assam has 845 registered tea estates, with 25 located in Udalguri (Baro, 2021). According to The Indian Express (2015), tea estates serve as natural corridors for elephants. Moreover, key forest areas include the Dhansiri Forest Division and the Khalingduar Reserve Forest, both of which contribute significantly to the region’s ecological balance. Bornadi Wildlife Sanctuary (BWLS) and Khalingduar Reserve Forest (KRF) are key parts of the Manas Tiger Reserve (MTR), with the BWLS at the core and the KRF acting as the buffer. The Neoli Proposed Reserve Forest, located in the Nunoi range, connects these two areas (BWLS and KRF), enhancing landscape connectivity. In contrast, Bhairabkunda Reserve Forest (BRF), situated near the Indo-Bhutan border, extends the protected

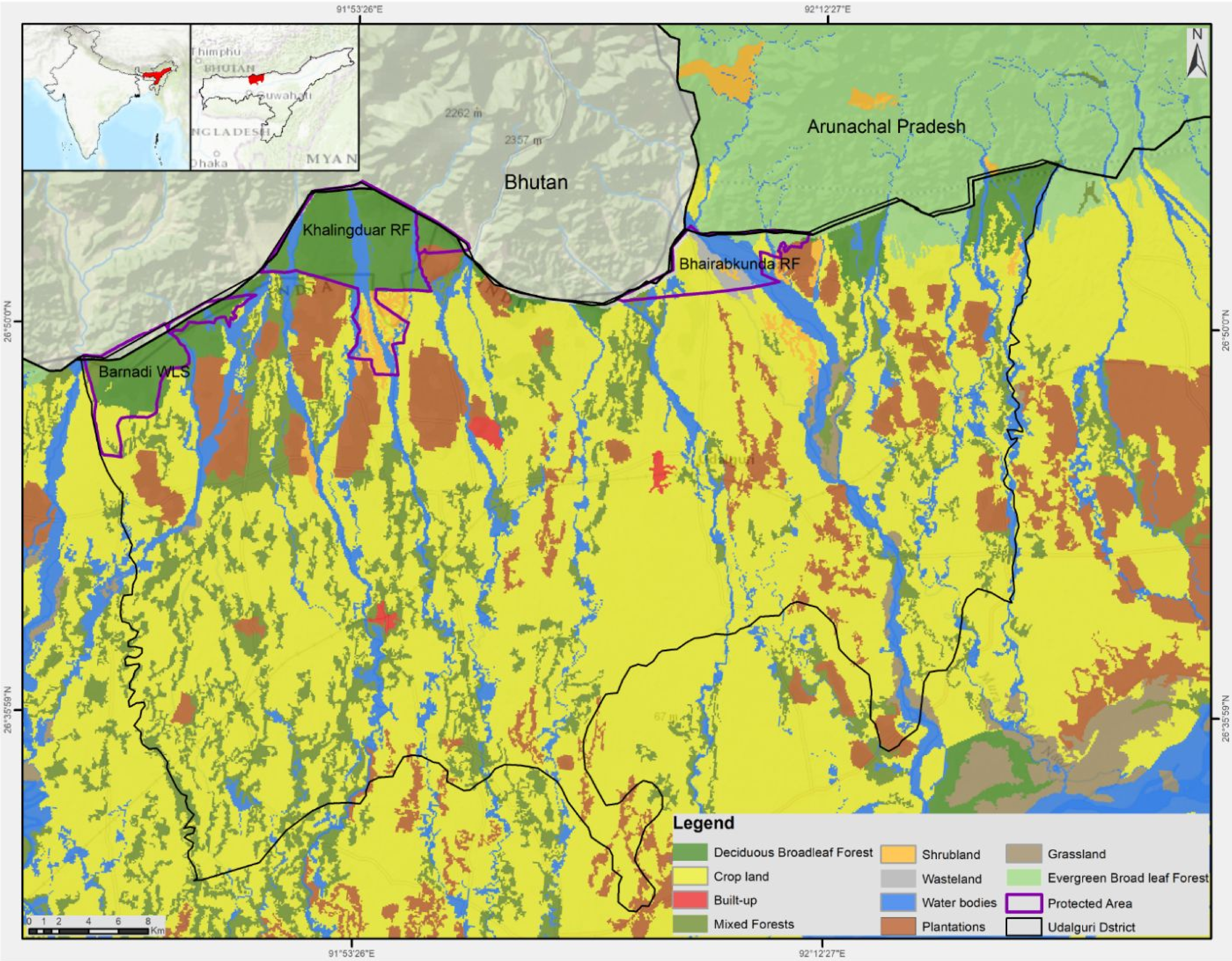

Figure 1. Study area map of Udalguri District, Assam showing the land use, land cover (LULC), and protected area (PA's) boundaries.

landscape beyond the national boundary (Khanikar, 2017; Banerjee & Sharma, 2022). Climatically, the district has a subtropical humid climate characterized by semi-dry, hot summers and cold winters. Agro-climatically, Udalguri falls under the North Bank Plain Zone (Khanikar, 2017). During summer, from May to early September, the region experiences heavy rainfall due to the south-west monsoon, often resulting in flooding. The district receives an average annual rainfall of about 2,000 mm, with temperatures ranging between a maximum of 34.5°C and a minimum of 13.5°C. Relative humidity typically ranges between 82% and 88% (Khanikar, 2017).

According to the 2011 Census, Udalguri district has a population of 831,668, marking an increase of 9.8% since 2001. The district has a literacy rate of 66.6% and a gender ratio of 966 women per 1,000 men, with a population density of 449 inhabitants per square kilometer. Scheduled Castes and Scheduled Tribes account for 4.55% and 32.15% of the population, respectively. The district is multi-ethnic and multi-religious. Bodo constitutes the largest ethnic group, comprising 33.76% of the population. The Adivasi community forms nearly 23.12%, while Bengali Muslims account for about 12%. In urban areas, Assamese and Bengali Hindus are more prevalent, and there is also a scattered presence of the Nepali-speaking Indian Gorkha community, estimated at around 5% of the district's population.

Methodology

HEC data collection

HEC data were collected from the Divisional Forest Office (Dhansiri) and Range Offices (Bornadi, Nunoi, and Mazbat) in Udalguri district, Assam, for a duration between 2011 to 2024. The dataset included incident locations, division names, and dates, along with human casualties (death and injury) by gender, elephant deaths (with date, cause, age class, and gender), and records of crop raiding and property damage with village names and dates. For analysis, the data were categorized seasonally as: Pre-monsoon (March to May), Monsoon (June to August), Post-monsoon (September to November), and Winter (December to February).

Moreover, information obtained from forest department records were cross-verified through ground-truthing at incident locations (for both human and elephant mortality) and discussions with local communities to confirm the accuracy of event details and GPS coordinates.

Data Analysis

Trends of HEC were examined on a yearly and monthly basis for human fatalities, injuries, and crop-forage incidents. Similarly, elephant mortality data were analyzed annually and seasonally, with further breakdowns by age class, gender, and cause of death. Inferential analyses were performed using chi-square tests of independence to evaluate whether the observed differences

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among categorical variables were statistically significant. In instances where expected cell frequencies were below five, Monte Carlo simulations (10,000 replicates) were employed to obtain robust p-values. When an overall chi-square test yielded a significant result, post hoc pairwise comparisons adjusted using the Bonferroni correction were conducted to identify the specific group differences driving the association. The intensity of HEC, including property damage, crop raiding, and human casualties, was mapped using a kernel density estimator in ArcGIS 10.8.

We assessed habitat preferences using the adehabitatHS package in R (version 4.4.0; R Core Team, 2024). Available habitat, based on data from the National Bank for Agriculture and Rural Development (NABARD, 2016), was comprised of paddy fields, home gardens, and tea estates. Habitat use data were collated from the collected HEC records and compared against availability using Manly's selection index (Wi). We used GLMM via the glmmTMB package in R (version 4.4.0; R Core Team, 2024) to analyze two aspects of human-elephant interactions. A Poisson GLMM was applied to assess the effects of season and sex on human casualties, with year included as a random effect. For elephant crop raid incidents, a negative binomial GLMM was used to model the influence of season and crop type, including year as a random effect.

Result

Human Casualties

Between 2011 and 2024, Udalguri reported 221 human casualties from elephant interactions, including 144 deaths and 77 injuries. Men were more affected (198 cases: 129 deaths, 69 injuries) than women (23 cases: 15 deaths, 8 injuries). However, no trend was observed in elephant attacks on humans during the study period (Figure 2). Monsoon and post-monsoon seasons each recorded 73 incidents, followed by pre-monsoon (41) and winter (34). Of 144 human deaths, only 21 occurred within PA (BWLS and KRF), and 123 occurred outside PA. Similarly, 5 of 77 injuries were inside PA (Figure 3). Elephant attacks were significantly lower in winter (β = –0.75, $p < 0.001$) and pre-monsoon (β = –0.43, p = 0.026) compared to the monsoon season. Men-related incidents were substantially higher (β = 1.16, $p < 0.001$) (Supplementary S1). Yearly variation (variance = 0.25±0.5 (SD)) was modest but included in the model (Table 1).

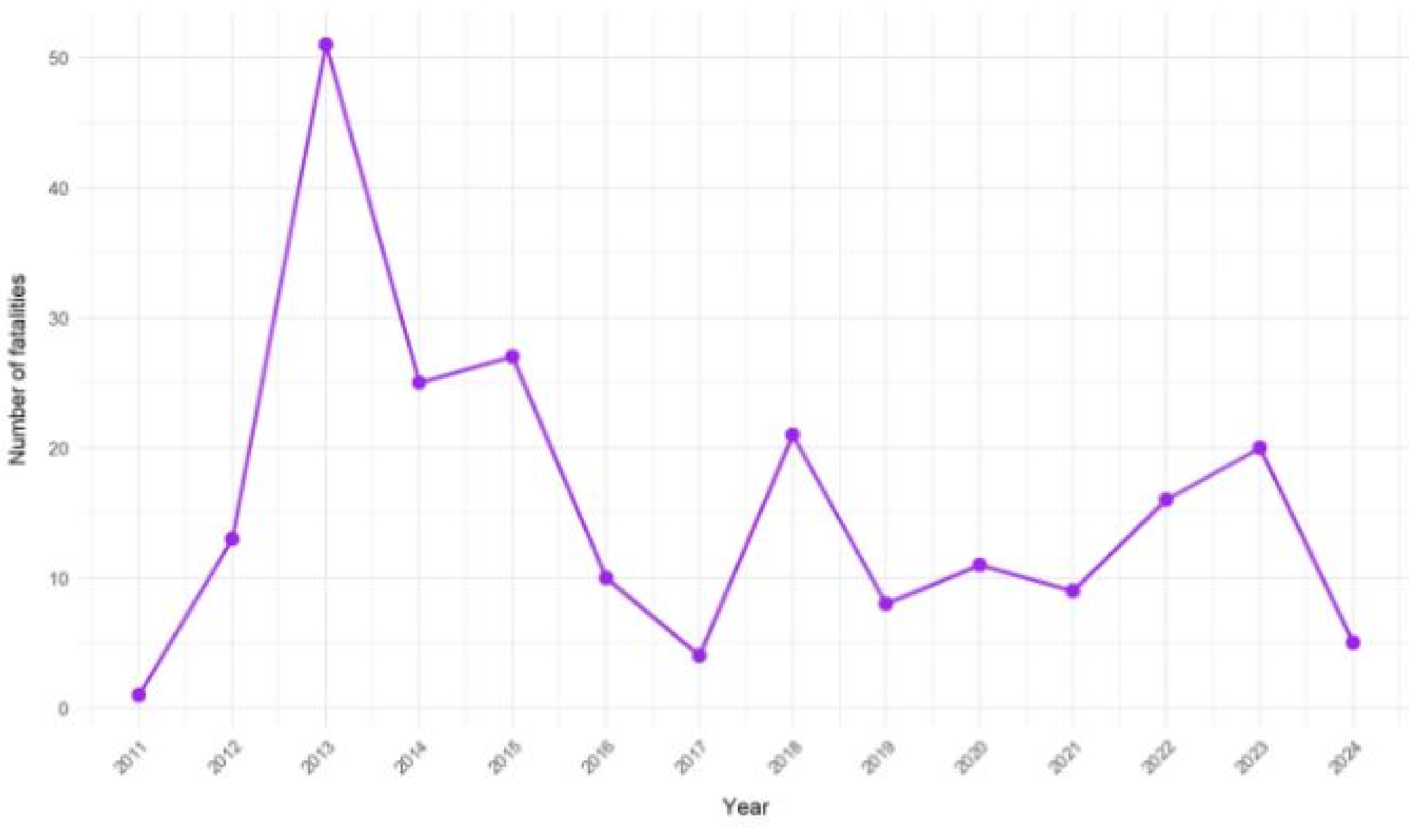

Figure 2: Annual trend of human casualties in Udalguri, Assam (2011–2024).

Table 1. Parameter estimates (β with standard errors, SE) and statistical significance (z-values and p-values) for the effects of season and sex on human casualties due to elephant attacks, with the year as random effect.

Predictor	Estimate (β)	Std. Error	z-value	p-value
(Intercept)	0.54	0.27	2.02	0.043 *
Season: Post-monsoon	-0.22	0.18	-1.18	0.23
Season: Pre-monsoon	-0.43	0.19	-2.22	0.026 *
Season: Winter	-0.74	0.22	-3.43	0.0006 **
Sex: Male	1.16	0.23	4.94	7.6e-07 **
Random effect (Year)	Variance= 0.25±0.5 (SD)			

*Note: * *Statistically significant at <0.05 level,*
*** Statistically significant at < 0.01 level*

Crop Raiding: Seasonal Patterns

A total of 1,171 crop-raiding incidents were reported in Udalguri between 2011 and 2024, with paddy being the primary target, accounting for 90.18% of the incidents. Other affected areas included arecanut plantations (4.24%), tea estates (3.28%), and home gardens (2.30%) (Figure 3). Incidents peaked during the post-monsoon season (592), followed by monsoon (318), winter (146), and pre-monsoon (115), with paddy raids dominating across all seasons. (Figure 4). According to NABARD data (2016), paddy (69.48%) was the predominant crop in the study area, followed by home gardens (23.52%) and tea estates (1.50%) as notable land-use types. Scaled selection ratios (Supplementary S2) indicated a strong elephant preference for tea estates (B_i = 0.59) and paddy (B_i = 0.39), while home gardens (B_i = 0.02) were the least selected. Manly's index confirmed the active selection of tea estates and paddy.

GLMM analysis (with year as a random effect; variance = 2.86±1.69 (SD)) showed that paddy experienced significantly higher raiding incidents (β = 2.63, $p < 0.001$), while home gardens were raided significantly less (β = –1.42, p = 0.045). Crop raiding was significantly lower during winter compared to the monsoon season (β = –1.90, p = 0.013). A significant increase in paddy raiding was observed in the post-monsoon season (β = 2.05, p = 0.011) (Table 2).

Property damage

A total of 2,984 property damage incidents were reported; the properties affected included houses (2,886), grocery shops (44), community structures (35), and storehouses (6). The damage varied significantly across seasons (χ^2 = 30.99, df = 12, $p < 0.05$), with monsoon and post-monsoon linking to the greatest impact (Supplementary S3). Our spatial analysis revealed that most crop raiding and property damage incidents occurred along forest boundaries, particularly near BWLS and KRF (Figure 3). These areas, dominated by paddy and tea estates, create a high-risk interface between human activities and elephant habitats.

Elephant mortality

A total of 96 elephant deaths were reported, with 21 attributed to anthropogenic, 20 to natural, and 55 to unknown causes. However, the anthropogenic cause of elephant mortality showed significant associations with gender (χ^2 = 3.86, p = 0.049), season (χ^2 = 18.00, $p < 0.001$), and age class (χ^2 = 8.86, p = 0.012) (Supplementary S4, S5, and S6). Males and sub-adults were more affected, with most deaths occurring in the post-monsoon season. Mostly the deaths occurred close to the protected areas except one juvenile male that died in the southern part of Udalguri district (Figure 5).

Table 2. Parameter estimates (β with standard errors, SE) and statistical significance (z-values and p-values) for the effects of crop type and season on elephant crop raiding and damage incidents with the year as random effect.

Predictor	Estimate (β)	Std. Error	z value	p-value
(Intercept)	−0.057	0.65	−0.087	0.93
Season: Post-monsoon	−1.264	0.69	−1.830	0.067 .
Season: Pre-monsoon	−1.177	0.662	−1.779	0.075 .
Season: Winter	−1.898	0.764	−2.485	0.013 *
Crop type: Home garden	−1.423	0.711	−2.002	0.045 *
Crop type: Paddy	2.627	0.526	4.993	<0.001 ***
Crop type: Tea plantation	−0.719	0.608	−1.184	0.236
Post-monsoon × Home garden	−0.638	1.42	−0.449	0.653
Pre-monsoon × Home garden	0.001	1.156	0.001	0.999
Winter × Home garden	1.072	1.197	0.896	0.37
Post-monsoon × Paddy	2.053	0.808	2.541	0.011 *
Pre-monsoon × Paddy	−0.413	0.811	−0.509	0.611
Winter × Paddy	1.224	0.891	1.373	0.17
Post-monsoon × Tea plantation	−0.617	1.098	−0.562	0.574
Pre-monsoon × Tea plantation	−0.026	0.972	−0.027	0.979
Winter × Tea plantation	0.252	1.101	0.229	0.819
Random effect (Year)	Variance = 2.86±1.69 (SD)			

*Note: * Statistically significant at <0.05 level,*
**** Statistically significant at <0.001 level*

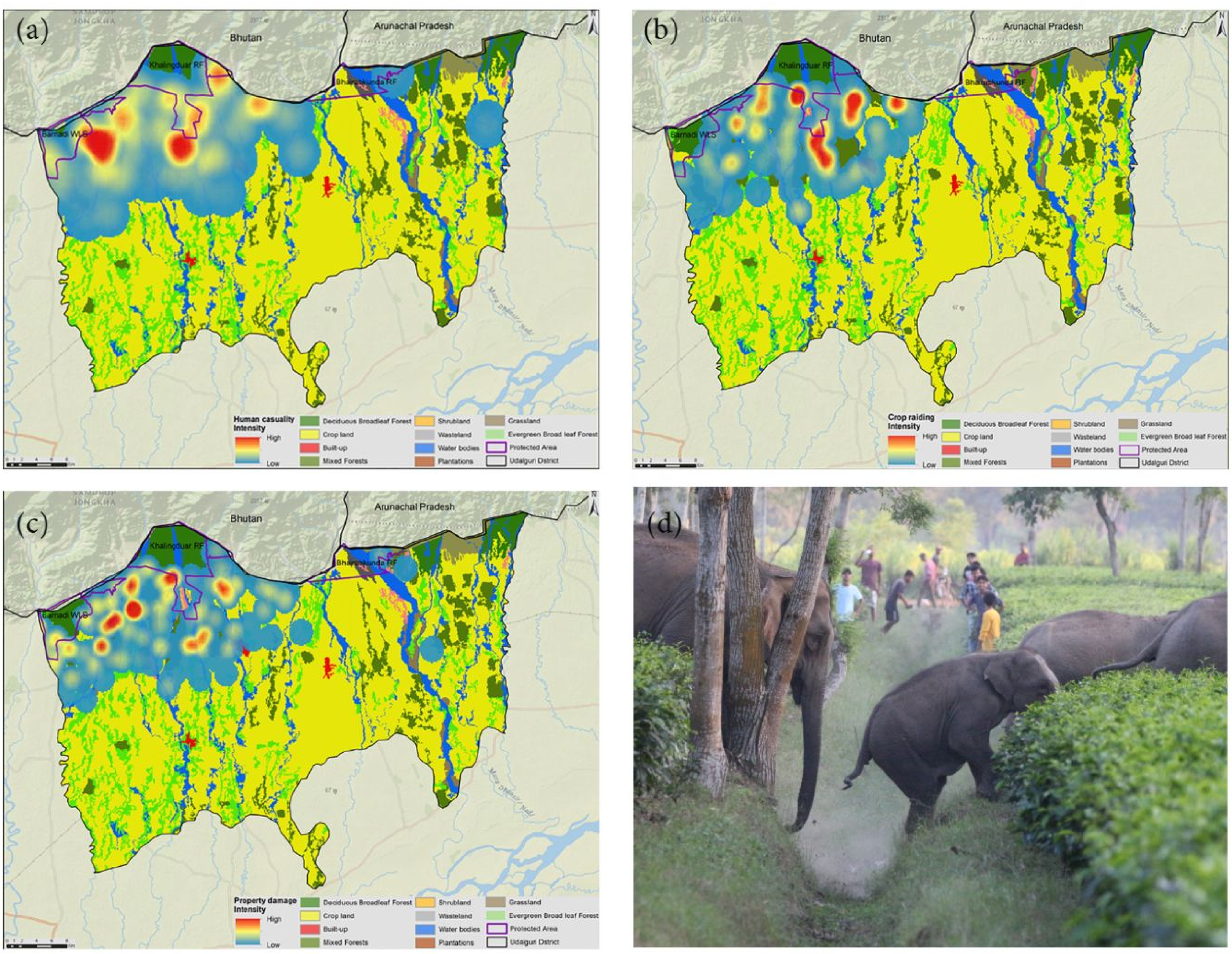

Figure 3: Map showing the hotspot of (a) human casualties, (b) crop raiding, (c) property damage caused by elephants and (d) an incident of human-elephant interaction in Udalguri, Assam (2011-2024).

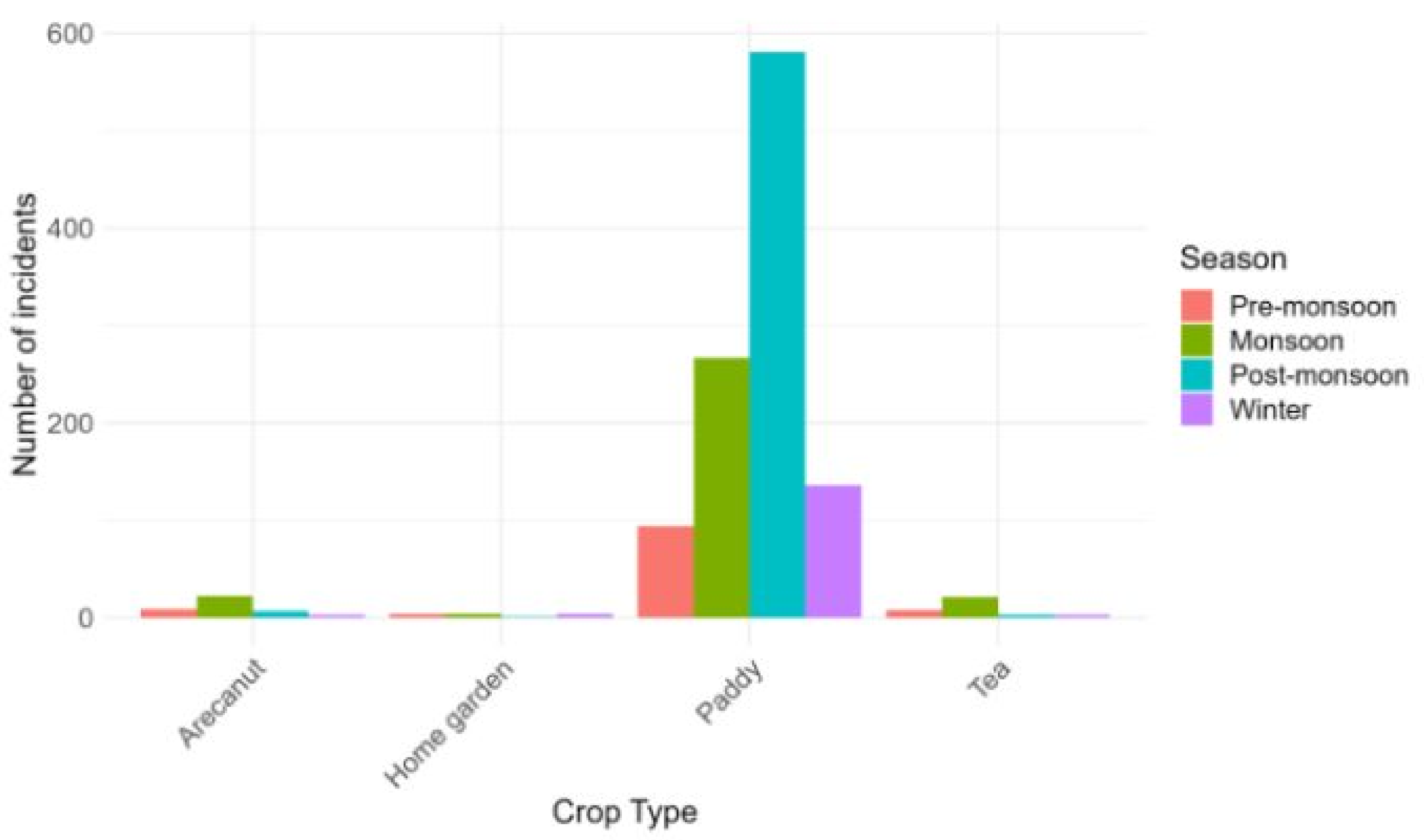

Figure 4: Bar graph depicting the number of elephant crop raiding and damaging incidents by crop type and season.

Discussion

Our study revealed significant annual and seasonal variations in human casualties, pointing to spatiotemporal trends that are crucial for managing HEC. Most incidents occurred outside the forest area, particularly along the boundaries of reserves such as BWLS and KRF, emphasizing the need for mitigation strategies that extend beyond the study area. This pattern aligns with findings from other regions of India, where communities living on the edges of wildlife habitats face heightened conflict (Mohanty & Mishra, 2017; Gubbi, 2012; Nath *et al.*, 2009). In these peripheral zones, including tea estates, often serve as de facto corridors and temporary shelters for elephants that bridge forest patches, croplands, and human settlements (Talukdar *et al.*, 2024; Kashyap, 2015). Although elephants do not forage on tea, their presence in tea estates frequently coincides with crop raiding and village intrusions, intensifying HEC (Vasudev *et al.*, 2020; Wilson *et al.*, 2013; Sukumar, 2003).

Crop raiding and property damage, influenced by seasonal resource availability and elephant movement patterns, are key drivers of HEC. Our findings, consistent with earlier studies, indicate that human casualties peak during the monsoon and post-monsoon, marked by heightened elephant activity and increased crop availability (Dangol *et al.*, 2020; Naha *et al.*, 2020; Rohini *et al.*, 2016; Wilson *et al.*, 2013). In addition to crop raiding, elephants frequently damage properties near forest edges while searching for food (Tripathy *et al.*, 2021 a, b; Gross *et al.*, 2020; Joshi *et al.*, 2020). In Udalguri district, the clustering of human settlements near forests has increased the frequency and severity of such incidents. Men face disproportionately higher casualties due to their involvement in field-based activities near the forest boundary (Sarker *et al.*, 2015). Meanwhile, between 2007 and 2016, elephant activity in Assam led to the destruction of 8,333 houses and damage to 1,400 hectares of cropland (BehanBox, 2023). Notably, in 2015 alone, 108 houses built under the Indira Awaas Yojana were destroyed in villages such as Nonaikhuti,

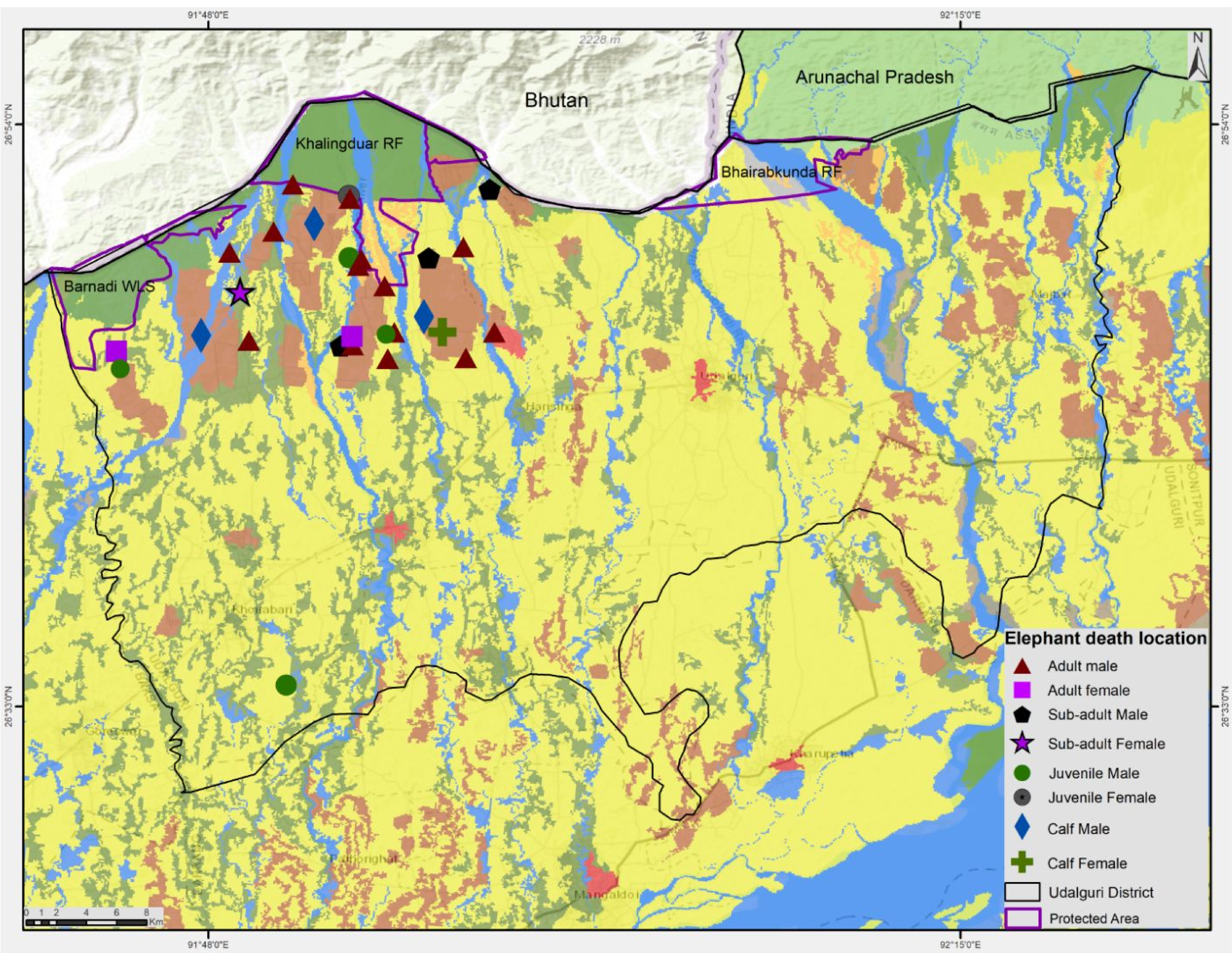

Figure 5: Spatial distribution map of Elephant Mortality in the study site by Age Class and Gender.

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Bamunjuli, and Rajagarh (Earth Journalism Network, 2019), highlighting the vulnerability of state-supported housing located in high-risk zones. These temporal and spatial patterns in elephant- driven damages underscore the urgent need for targeted, seasonally adaptive mitigation strategies with an emphasis on safer land use planning in elephant-prone areas.

Elephant deaths, largely attributed to human-induced causes, can impact overall population dynamics. Notably, many reported cases are labeled as unknown but are likely linked to anthropogenic activities. Males, particularly adults and sub-adults, exhibit higher mortality than females due to their solitary and wide-ranging behavior, increasing their exposure to risks (LaDue *et al.*, 2021; Naha *et al.*, 2020; Srinivasaiah *et al.*, 2019; Palei *et al.*, 2014; Fernando *et al.*, 2009). Mortality peaks during the monsoon and post-monsoon seasons, when increased resource availability draws elephants into human-dominated areas, exposing them to threats such as electrocution from power lines and poorly designed fences (Kalam *et al.*, 2018; Haturusinghe & Weerakoon, 2012).

Conservation Implementation

The spatial analysis showed that areas adjacent to forest areas dominated by paddy fields and tea estates, particularly near BWLS and KRF, are hotspots of HEC. Restoring corridors can help link fragmented habitats, reducing the pressure on elephants to venture into human-dominated landscapes. By creating safe passage routes and managing edge effects, it is possible to minimize encounters between elephants and humans, thereby reducing HEC incidents. As Udalguri borders Bhutan and lies within a transboundary elephant movement zone, cross-border coordination in mitigation, law enforcement, and monitoring is crucial to manage HEC effectively. Seasonal variations in HEC further emphasize the need for adaptive management strategies. The monsoon and post-monsoon periods, when HEC peaks, should be targeted for season specific interventions. Implementing early warning systems, increasing patrols, and local community-based monitoring during these high-risk seasons can help mitigate HEC.

Additionally, raising awareness among local communities about non-lethal deterrence methods and improving compensation mechanisms for crop and property losses are essential to foster a cooperative approach to coexistence. Compensation for crops and property damage is a vital component of successful conservation efforts, serving not only to mitigate the immediate financial losses incurred by local communities but also to foster long-term coexistence between people and elephants.

Reducing human-induced threats to elephants is another key consideration. Our observations indicate that elephant mortality is significantly linked to human activities such as electrocution and poisoning. Addressing these issues through the retrofitting of electrical infrastructure and stricter regulation of toxic substances near elephant habitats can help decrease unintended fatalities. Long-term monitoring, combined with local knowledge, is essential for developing practical, site-specific conservation strategies. Effective management of HEC requires coordinated efforts among forest departments, local communities, and conservation organizations.

A multi-pronged, transboundary approach (Tshering *et al.*, 2024) is vital to address governance challenges and sustain elephant populations:

- Institutional arrangements should be established to support transboundary elephant conservation, including political and legal frameworks, conflict mitigation protocols, and enforcement mechanisms.
- Regional cooperation can be strengthened through soft diplomacy and multi-stakeholder platforms to align efforts across administrative boundaries.
- Community engagement is key through cooperative guarding, solar fencing, and education programs that raise awareness about elephant conservation.
- Initiatives integrating capacity-building and law enforcement can help standardize monitoring, reduce illegal activities, and improve data sharing.
- Innovative land-use planning, such as extending eco-sensitive zones across national borders, is needed to preserve contiguous forest habitats and enable long-term conservation beyond political boundaries.

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CONFLICT OF INTEREST

Bilal Habib & Parag Nigam hold editorial positions at the Journal of Wildlife Science. However, they did not participate in the peer review process of this article except as authors. The authors declare no other conflict of interest.

DATA AVAILABILITY

All data are presented in the paper.

AUTHORS' CONTRIBUTION

AN, BH, PN Conceptualized the study, designed the methodology, and supervised data collection. RS, DB, AN collected data. AA, RS, RB, AN, BH help in analysis, interpreted results. RKP, DM, AMG, PN provided critical insights and assisted in manuscript revision and final approval. All authors have read and approved the final manuscript.

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First photographic evidence of Indo-Pacific Humpback Dolphin (*Sousa chinensis* Osbeck, 1765) from the tidal river Rupnarayan, in Bardhhman district, West Bengal, India

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Sousa chinensis (Osbeck, 1765) of the genus *Sousa* (subfamily Delphininae) also known as the Indo-Pacific Humpback Dolphin (IPHD from hereon), is classified as 'Vulnerable' (VU) according to the IUCN Red List (Jefferson *et al.* 2017). This species is protected under Appendix I of (Conservation of International Trade of Endangered Species of Flora and Fauna (CITES) and is also listed in Appendix II of the Convention on Migratory Species (CMS). Jefferson *et al.* (2014) discovered four species of *Sousa* in their taxonomic analysis of humpback dolphins, with the IPHD being distinct from the other species.

IPHD is found in the coastal waters of the eastern and western Indian Ocean, as well as in the northwestern, southwestern, and western central Pacific oceans (Jefferson *et al*. 2017). These dolphins have been observed throughout the Indian coastline (Blandford 1888–91; Lydekker 1903, 1908; Lal Mohan, 1982, 1983; Pillai & Kasinathan 1988; Parsons 1998; Kumarran 2002; Sutaria & Jefferson 2004; Afzal *et al.* 2008; Muralidharan 2013; Sule *et al.*, 2015; Panicker & Sutaria 2013; Sutaria 2009; Jefferson & Smith, 2016). On the western coast of India, most sightings are concentrated along the Malabar shoreline in Kerala (Pilleri & Gihr 1974; Leatherwood & Reeves 1989; Lal Mohan 1995). Observations and specimens have been documented along the coast of Andhra Pradesh, and Saurashtra and Surat in Gujarat (Owen 1866; Leatherwood & Reeves 1989; Pilleri & Gihr 1972; Sutaria *et al.*, 2015; Kumaran, 2002; Sathasivam, 2000). Pilleri & Gihr (1972, 1974) reported the sightings of humpbacked dolphins further north in Pakistan and the Indus Delta. These dolphins are known to venture several kilometers upstream in rivers, particularly in China, including the Yangtze and Pearl Rivers (Wang & Sun 1982; Parsons *et al.*,1995). However, reports from the midwestern coast of India are comparatively scarce. These dolphins have been reported to occupy a variety of habitats in coastal areas, including estuaries (Parsons, 1998; Muralidharan, 2013; Ross *et al.*,1994), mangrove islands (Cagnazzi *et al.*, 2011; Durham 1994), enclosed bays (Karczmarski *et al.*, 1999; Chen *et al.*, 2009), and shallow rocky reefs (Karczmarski *et al.*, 2000), and often enter rivers (Singh, 2003). *Sousa chinensis* prefers shallow inshore waters ranging from a minimum of ~1 m to a maximum of 21-30 m depth (Ross *et al.*, 1994; Sutaria & Jefferson, 2004).

As part of the rangewide river dolphin estimation project, the Wildlife Institute of India surveyed river dolphins from December 2022 to March 2023 in the tidal river Rupnarayan, a tributary of the Hooghly river in West Bengal. The Rupnarayan river in West Bengal experiences substantial tidal effects over its entire course. During the survey, the team recorded sightings of IPHD with its calf in Panshuili village (22.597348^0 N, 87.851851^0 E), where the Rupnarayan and Mundeswari rivers meet, on March 3, 2024 at approximately 09:50 h IST (Figure 1 & 2). The width, depth, and salinity of the site were determined to be 270 meters, 2.8 meters, and 1 ppt, respectively. The sighting was approximately 130 km from the mouth of the Bay of Bengal and no IPHD has been recorded in a tidal river upstream, at this distance, globally.

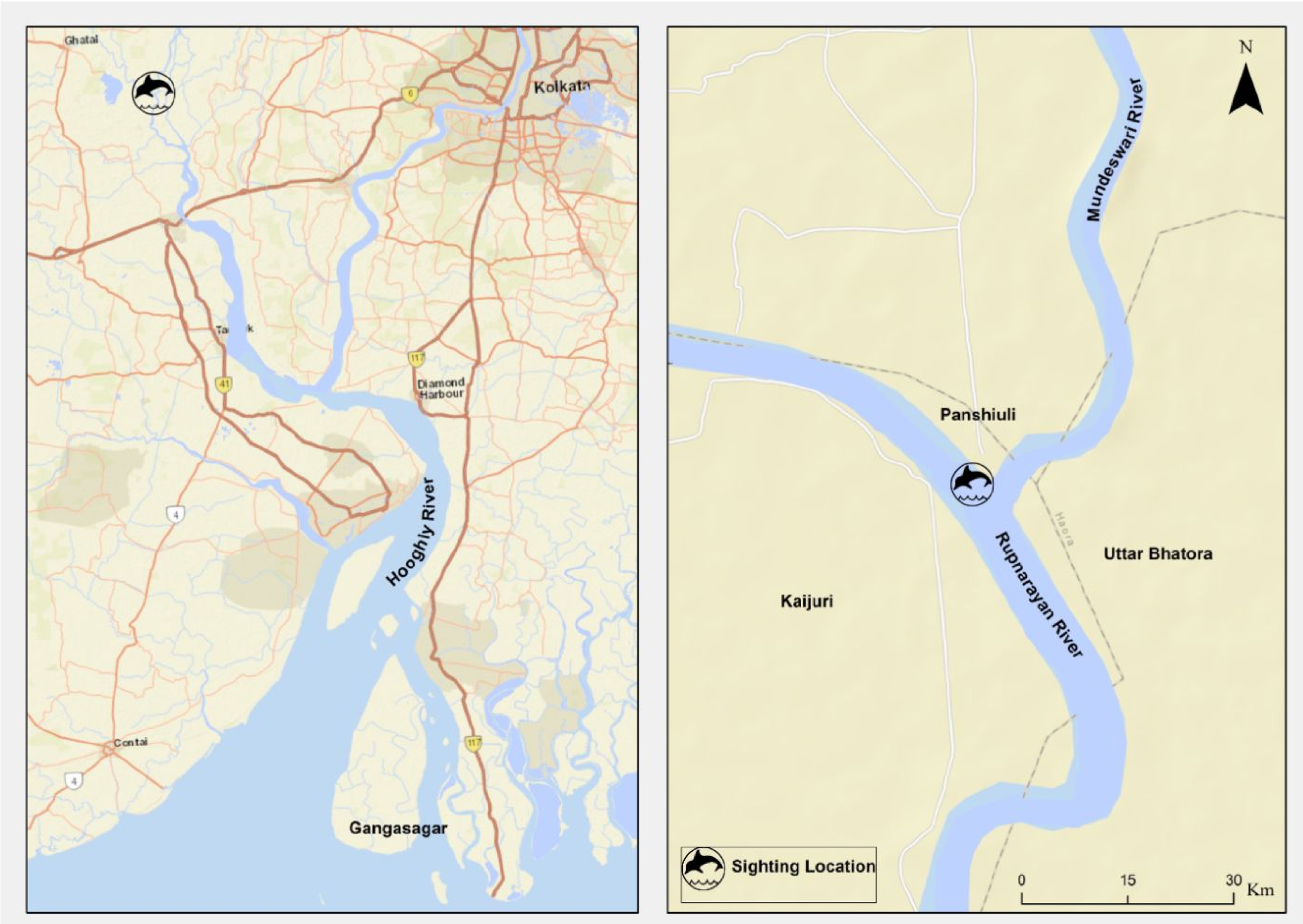

Figure 1: Location of the Indo-Pacific Humpback Dolphin sighting in the Rupnarayan river (March 2024)

Figure 2: Photographs of Indo-Pacific Humpback Dolphin with calf, as recorded in Rupnarayan river (March, 2024)

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Tidal rivers are vulnerable ecosystems that act as transitional zones where freshwater and saltwater converge. Marine mammals may be driven to specific areas to seek out alternative habitats depending on changes in water quality, temperature, or habitat availability. Their presence, behavior, and population dynamics can reflect the overall condition of the ecosystem, including water quality and habitat integrity (Wang *et al.* 2019). Observations of IPHD in this tidal river—more than 100 kilometers from the mouth of the bay—highlight the importance of these intermediate habitats between freshwater and marine environments. This situation prompts us to consider the implications of changing riverine salinity and the persistence of intermediate habitats in light of climate change. A more detailed study is required to understand whether encounters with IPHD are a regular occurrence. There is an immediate need to identify such zones for awareness and capacity building in case of stranding or entanglement. These observations are also crucial for the sustainable management of aquatic ecosystems as a unified entity (both freshwater and marine), serving as a reminder to assess our preparedness for emerging challenges.

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CONFLICT OF INTEREST

Qamar Qureshi & Vishnupriya Kolipakam are both academic editors at the Journal of Wildlife Science. However, they did not participate in the peer review process of this article except as authors. The authors declare no other conflict of interest.

DATA AVAILABILITY

No additional data was used in this research.

AUTHORS' CONTRIBUTION

DG, GRC, KR, PB contributed to fieldwork. DG prepared the first draft.
GRC, VK, QQ, SR provided inputs on the draft.

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First record of a clouded leopard predating on a Bengal slow loris

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Abstract

We present the first photographic record of a mainland clouded leopard *Neofelis nebulosa* predating on a Bengal slow loris *Nycticebus bengalensis* in Dehing Patkai National Park, Assam, India. This finding, made through camera trapping, contributes to our understanding of predatory behavior and diet, highlighting the significance of conservation efforts for both species.

Keywords: Diet, *Neofelis nebulosa*, *Nycticebus bengalensis*, predatory behavior

The mainland clouded leopard, a medium-sized felid in the family Pantherinae, is categorized as 'Vulnerable' by the IUCN and listed under CITES Appendix I, reflecting threats from poaching and illegal trade (Hearn *et al.*, 2013; Gray *et al.*, 2021). Due to their elusive nature, it becomes difficult to ascertain the preferred prey species of clouded leopards (Nowell & Jackson, 1996). During a camera trapping study to assess the population of clouded leopards in its distribution range in India, a clouded leopard was photo captured carrying a Bengal slow loris (*Nycticebus bengalensis*) held by its nape on a broad forest trail (20:58 hrs; December 07, 2024; 164 m asl) (Figure 1). Earlier, its congener, the Greater slow loris (*Nycticebus coucang*), was recorded as a prey species of the clouded leopard by Grassman Jr. *et al.* (2005) based on scat analysis in Thailand, which was erroneously cited by another study (Rasphone *et al.*, 2022) as Bengal slow loris. The habitat comprised a tropical wet evergreen forest characterized by the dominance of tree species including *Dipterocarpus retusus, Mesua ferrea*, and *Dysoxylum gotadhora*, with an approximate canopy cover of 60%. The location is 1.1 km from the nearest tea garden (Tarajan Tea Garden) and 2.5 km from the closest human habitation. In this report, we provide the first photographic evidence of a Bengal slow loris being preyed upon by a mainland clouded leopard, confirming it as a prey species for this felid.

The Bengal slow loris is the only strepsirrhine primate in north-east India and is categorized as 'Endangered' by the IUCN (Nekaris *et al.*, 2020). It exhibits distinct foraging behavior characterized by the repeated use of the same foraging routes and relatively slow locomotion. Among all the species of *Nycticebus*, the Bengal slow loris is the most specialized exudativore, dedicating approximately 86.5% of its total feeding time to consuming plant exudates in arboreal habitats (Swapna *et al.*, 2010). Considering the Bengal slow loris' weight ranges from 850 to 2100 g (Nekaris *et al.*, 2010), and it is arboreal and nocturnal, it is likely that clouded leopards in this area may target this species as relatively easy to hunt prey.

The available literature highlights the diverse range of prey species preferred by clouded leopards, including small and medium sized ungulates, primates, porcupines, pangolins, birds, rodents, and even domestic animals (Davies, 1990; Hazarika, 1996; Nowell & Jackson, 1996; Grassman Jr. *et al.*, 2005; Lam *et al.*, 2014). There is a significant lack of information regarding the preferred prey of the clouded leopard. Therefore, this photographic record fills in the information gap on the prey preference of the clouded leopard in its Indian distribution range.

Figure 1: The clouded leopard predating on a Bengal slow Loris captured on a foresttrail (motorable road) in the Soraipung range of the Dehing Patkai National Park, Assam, India

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CONFLICT OF INTEREST

Dr. Govindhan Veeraswami Gopi is an academic editor, and Dr. Bilal Habib is the managing editor at the Journal of Wildlife Science. However, they did not participate in the peer review process of this article except as authors. The authors declare no other competing interests.

DATA AVAILABILITY

No additional data was used in this research.

AUTHORS' CONTRIBUTION

Rameshwar Ghade: Writing-Original Draft Preparation (lead). Writing-Review & Editing (equal), Field work (equal). Azam Khan: Writing-Original Draft Preparation (supporting), Writing-Review & Editing (equal), Field work (equal). Tribhuwan Singh: Writing-Original Draft Preparation (supporting). Writing-Review & Editing (equal). Daniel Miranda: Writing-Original Draft Preparation (supporting), Writing-Review & Editing (equal). Bilal Habib: Funding Acquisition (lead), Writing-Original Draft Preparation(supporting), Writing-Review & Editing (lead), Gopi G. V.: Writing-Original Draft Preparation(supporting), Writing-Review & Editing (supporting)

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TYPE Natural History Note

First report of albino rhesus macaque *Macaca mulatta* (Zimmerman, 1780) from Barak Valley, Assam

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Keywords: Albinism, India, melanin, pigmentation, South Assam.

On 22nd February 2022 at 10:30 hours, we recorded an albino rhesus macaque infant at Ramkrishna Nagar town (24°50’31.5708″N, 92°23’11.6916″E) in Sribhumi district of Assam (Figure 1). The locals knew the individual by its ethereal appearance and bestowed the name ‘*Pandur*’ (meaning pale, colorless) upon this unique and colorless primate. The monkey was spotted while it was feeding and roaming around the place with the group near the town. The group roamed the suburban town and adjacent areas in the quest for food. The group, consisting of approximately 72 members, including 24 offspring, 29 females, and 19 males, was the only rhesus macaque troop known to inhabit this vast area. Within the troop, the albino baby received constant care and protection from its mother, always staying near her (Figure 2). However, the albino baby faceds some social challenges within the group. Other members of the group exhibited hesitation in interacting and playing with the albino individual, often displaying behaviors of irritation or avoidance. Nevertheless, the albino baby explored its surroundings under the watchful guidance of its mother, vocalizing frequently throughout its daily activities.

Even though the birth of an albino animal is considered a sacred or auspicious event in some cultures, research suggests that some albino animals have reduced fitness in the wild (Uieda, 2000; Hall, 2019). The lack of natural camouflage and increased susceptibility to environmental factors make them more prone to predation (Uieda, 2000). Consequently, the birth of an albino animal raises concerns about the ability of animals or animal groups to thrive and perpetuate their species in their natural habitats. Although rare in nature, albino animals have been spotted in diverse animals (Abreu *et al.*, 2013; Leroux *et al.*, 2022). Among the primate species, it was reported in the toque macaques *Macaca sinica* (Fooden, 1979), bonnet macaques *Macaca radiata* (Mahabal *et al.*, 2012), western lowland gorilla *Gorilla gorilla gorilla* (Prado-Martinez *et al.*, 2013) and black-handed spider monkey *Ateles geoffroyi* (Espinal *et al.*, 2016). With the exception of one or two accounts, the albino individuals were not found to interact with other members within their troops. Leroux *et al.* (2022) observed that the unique morphological features of an infant albino chimpanzee prompted infanticide by other members of the community in Budongo Forest Reserve, Uganda. In contrast, Montilla & Link (2022) found no discrimination in the conspicuous interaction of an albino Caribbean night monkey within the troop.

The expression of albinism in animal populations appears to be closely associated with specific ecological conditions and factors (Bensch *et al.*, 2000). Observations indicate that albinism tends to appear more in areas where animal group densities are relatively low or in decline (Bensch *et al.*, 2000). Furthermore, continuous inbreeding has been identified as a contributing factor to the expression of albinism within populations (Bensch *et al.*, 2000). Albinism serves as an important warning signal, highlighting potential challenges to long-term continuity and genetic health of a species population. Thus, it is needed to monitor the populations regularly for albinism and genetic or morphological anomalies. Such monitoring can help keep an eye on the health of the wild populations. Additionally, creating awareness among local communities about how to coexist harmoniously with non-human primates is of utmost importance.

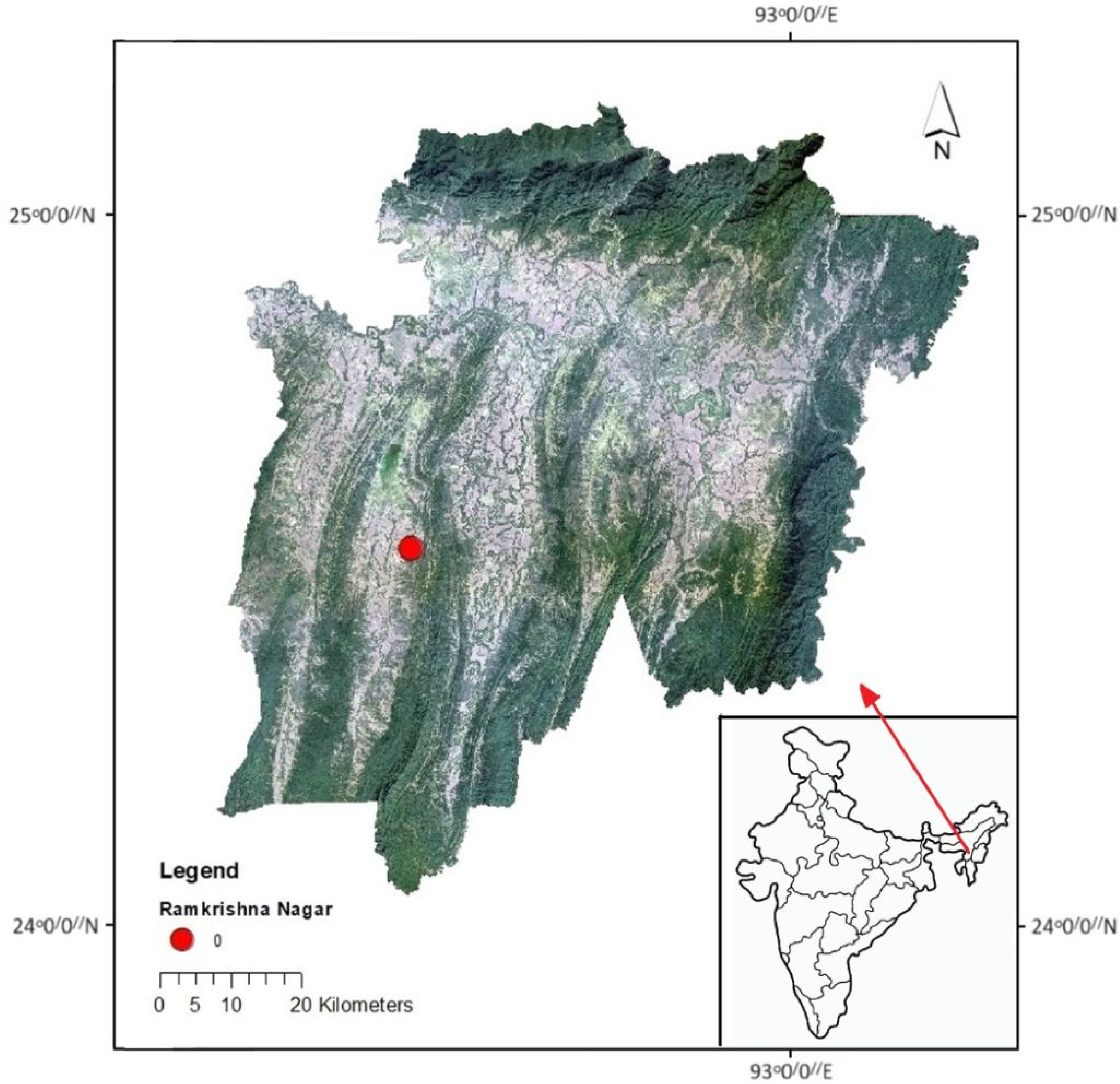

Figure 1. Sighting location of albino rhesus macaque in Ramkrishna Nagar, Sribhumi, Assam, India

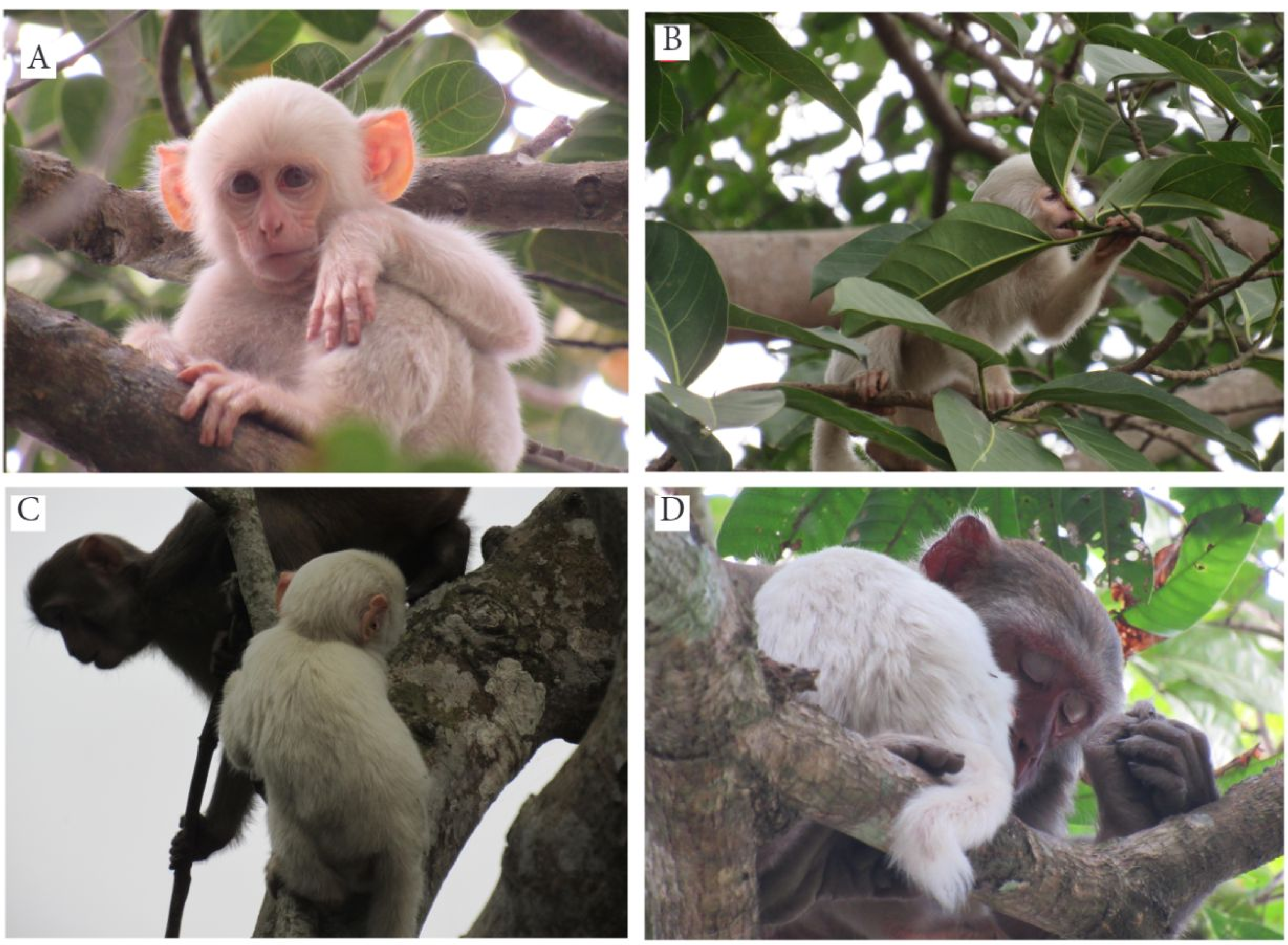

Figure 2. Juvenile albino rhesus macaque individual. A. frontal view, B: feeding on fruits of a banyan tree, C: playing with other members of the troop, D: albino offspring and the mother female sleeping on a branch.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY

Data is available in the manuscript.

AUTHORS' CONTRIBUTION

BS and NRT conceived and designed the study. BS and NRT carried out field study. BS, NRT and BS analysed the data. BS & NRT wrote the first draftof the MS. PC reviewed and edited the final draft.

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