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**Title** Ecological baselines and emerging threats: Evaluating the status of the Black softshell turtle (*Nilssonia nigricans*) in Assam's protected floodplain habitats

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**Abstract** This study provides a comprehensive assessment of the morphology and current distribution of the critically endangered black softshell turtle (*Nilssonia nigricans*), with insights into its natural history and habitat ecology across four key protected areas in Assam. We used an integrative approach that combined visual encounter surveys with community-based engagement methods such as informal focus groups and semi-structured interviews with local communities and forest personnel. We examined the ecological characteristics and life history traits of *N. nigricans* in the wild, including its seasonal activity patterns, basking and habitat preferences, opportunistic feeding behaviour, and documented the primary anthropogenic threats to the species based on information gathered from interviews and habitat surveys. We provided a refined understanding of the distribution of *N. nigricans* in the Brahmaputra River floodplains by integrating 244 hours of transect survey effort and 73 georeferenced observations compiled from field surveys and secondary sources from 2002–2024. Our systematic review indicates a wide distribution of the species across eight states in northeast India, Nepal, and Bangladesh. Importantly, its presence extends beyond protected areas and temple ponds to encompass the broader floodplain landscape, including community-managed ponds. Additionally, we analysed habitat use patterns and identified critical habitat features such as sandy nesting banks and undisturbed basking sites that are essential for the survival and reproduction of the species. The results underscore the importance of prioritising specific habitats within these national parks for targeted conservation action. The study also highlights the role of community stewardship in supporting in-situ conservation through habitat protection and awareness programs. This research forms a foundation for future ecological research, including GIS-based habitat suitability mapping to identify priority corridors and telemetry-based movement studies, and management strategies aimed at securing the remaining wild populations of *N. nigricans* in Northeast India.

**Keywords** Black softshell turtle, distribution, Brahmaputra floodplains, ecology, research gaps

## Introduction

Turtles are among the most threatened vertebrates globally, with 20% of all species listed as ‘critically endangered’ and approximately 60% of all species classified as ‘at risk of extinction’ (Stanford et al. 2020). Among them, softshell turtles face additional pressures including subsistence hunting, illegal meat trade, accidental drownings, disease risks, and road mortality —underscoring the urgency of regional studies for their conservation (Lovich et al. 2018; Butler 2019). Rapid conversions of floodplain areas that are used as breeding and nesting grounds are further contributing to declining trends indicated for softshell turtles. However, as is common for many freshwater turtle species, reliable population baselines are lacking (Moll and Moll 2004), and therefore declining trends in population numbers cannot be gauged. Assam, a state in northeast India is a part of the World’s Top Priority Freshwater Turtle Conservation area, as the region covers a wide variety of habitats suitable for the occurrence of diverse freshwater turtles and tortoises (Buhlmann et al. 2009). The Brahmaputra River floodplains in Assam itself harbours 19 out the 30 known freshwater turtle and tortoise species in India. The alluvial floodplains are natural habitats, often undisturbed by anthropogenic factors and are an integral mixture of the Eastern Himalayas and Indo-Burma biodiversity hotspots, with one of the richest turtle diversities of the world (Buhlmann et al. 2009). The black softshell turtle (*Nilssonina nigricans*) occurs in sympatry here with two congeners belonging to the Genus *Nilssonina* — the Ganges softshell turtle (*Nilssonina gangetica*) and the Peacock softshell turtle (*Nilssonina hurum*). This sympatric distribution is ecologically and conservation-wise significant, as it raises key questions about how these species coexist, partition resources, and respond to shared environmental pressures in the Brahmaputra basin. *Nilssonina nigricans* is a large turtle with a flattened leathery carapace measuring up to 91 cm, as recorded from captivity, where it can possibly grow even larger. They have proboscis-like snouts, long retractable necks, paddle-like limbs with three claws on each, and undergo ontogenetic morphological variation. Juveniles have distinct ocelli markings on their carapace like their congeners, while the adults develop a distinct dark, blackish grey colouration on their carapace (Das 1995). The species was previously thought to be ‘extinct in the wild’ since its 1875 description from the Bostami shrine in Chittagong, Bangladesh (Anderson 1875). After decades without records, small populations of individuals were identified from temple ponds in Assam, and it was eventually discovered in the wild from the surrounding areas of Nameri National Park in Assam by Praschag and Gemel in 2002, with further evidence across Assam and northeast India reported in the last two decades. The current known distribution of *N. nigricans* includes records from temple ponds and the wild across the Brahmaputra River basin in West Bengal, Assam, Nagaland, Arunachal Pradesh, Tripura, and Mizoram in India, as well as from Nepal and Bangladesh. Most of the life history information on the species is obtained from anecdotal information across temple ponds that they are primarily associated with, with virtually no ecological information available on wild, free-ranging turtles. *Nilssonina nigricans* was downgraded from Extinct in the Wild (EW)

to Critically Endangered (CE) in 2021 by the IUCN Red List (IUCN 2025) and is listed in Schedule I of the Wildlife (Protection) Act, 1972. The black softshell turtle is considered sacred across temple ponds of Northeast India and Nepal, as it is believed to be the holy incarnation or ‘Kurma’ avatar of the Hindu God Vishnu (Chakrabarti and Sen 2016), and it is also believed to be the ‘Mazari’, embodiments of spirits in the Bostami shrine (Das 1995). While the cultural and religious significance of turtles can be leveraged to improve awareness and conservation of the species, it currently results in the occasional transfer of turtles from the wild to temple ponds, further endangering wild populations of this rare species.

The habitat mosaics of protected areas along the Brahmaputra River basin are conducive to supporting a rich diversity of freshwater turtles, yet these vast protected areas have not been surveyed extensively for wild populations of *N. nigricans*. These protected habitats thus serve as ideal study sites to assess the population status of wild living *N. nigricans* to understand their habitat requirements and threats. This ecological information is crucial to ensure their conservation across their distribution range. In this study we (1) identified stable adult populations of the black softshell turtle across four protected areas of Assam along the Brahmaputra floodplain; (2) documented the current distribution of *N. nigricans*, its morphology, and ecological characteristics from dedicated field surveys; (3) assessed the preferences of *N. nigricans* within the floodplain habitats they inhabit; and (4) evaluated key threats to the persistence of *N. nigricans* in the wild and provided recommendations for its conservation and management.

### Study area

We conducted dedicated surveys and interviews from March 2019 to April 2021 (all months except June to September during the flood season) across four National Parks (NPs) in Assam to assess the status of wild *N. nigricans* populations and learn more about their ecology. Kaziranga and Orang NPs are situated along the main stem of the Brahmaputra River, while Nameri and Manas NPs are situated along two major tributaries of the Brahmaputra River, in the floodplain region. These four protected areas thus captured a landscape gradient from main river to tributary systems in the Brahmaputra floodplains. The habitats in the four NPs comprise of large, protected stretches of the main Brahmaputra River, multiple tributaries and channels, marshy grasslands, and moist deciduous and swamp forests. The climate of the floodplain region can be categorized into three distinct seasons by the variation in temperature, rainfall, and humidity — Pre-monsoon (February–May), Monsoon (June–September), and Post-monsoon (October–January). The minimum and maximum temperatures during surveys ranged between 20 and 38 °C. The average relative humidity in the study area ranged between 67–85%. The mean annual rainfall during dry seasons was 390 mm, whereas the monsoon season averaged 1160 mm. Details on the habitat types of each protected area are provided below.

*Kaziranga National Park*

Kaziranga NP lies along the north and south banks of the Brahmaputra River along Biswanath, Nagaon, and Golaghat districts of Assam. The alluvial deposits of the Brahmaputra River and its tributaries replenish the floodplains every year in the monsoon (Gilfellow et al. 2003; Rao et al. 2020), and this forms most of the park area that gets inundated in the annual floods. The river forms and removes alluvial river islands and banks every year. As numerous channels of the Brahmaputra River criss-cross the park area, several deep-water wetlands, also known as 'beels', of various sizes and depths, exist and serve as permanent wetland habitats. There are approximately 58 tributaries and streams, and 191 small and large beels in the park. On the south bank of the park, a major tributary is the Diffluo River that flows east to west through the south bank of the park. Deopani and Mora-Diffluo are two other tributaries that drain through the park in addition to numerous small streams (Ahmad and Das 2010). Several well-populated villages bound most of the boundaries of the park. During this study, surveys were carried out in the Bagori, Kohora, and Agoratoli ranges in the south bank and the Biswanath range on the north bank.

*Orang National Park*

Orang NP is located along the floodplains of the River Brahmaputra to the south of the Darrang and Sonitpur districts of Assam. The park is bounded on either side by the Pachnoi and Dhansiri Rivers, which are tributaries joining the Brahmaputra River. The annual monsoon flood repeatedly inundates a large part of the park. The park comprises a mixture of dry and wet grasslands and dry-deciduous forests. Large areas of the park are covered with wetlands and swamps (Talukdar and Sharma 1995). Human habitation and agriculture surround the park along its boundaries, even on the large sand islands to the south of the park. During this study, the entire park was surveyed, including all beels, stretches of the Pachnoi tributary, and the main stretch of the Brahmaputra River.

*Manas National Park*

Manas NP is located in the Baksa and Chirang districts of the Bodo Territorial Region (BTR) in Assam. The southern boundary has several populated villages. The Manas and Beki Rivers are the two main tributaries that flow from the north to the south of the park, with a few seasonal wetlands and swampy areas across the park. The vegetation of the park consists of evergreen, semi-evergreen, and mixed moist-deciduous forests, as well as grasslands and riparian forests (Champion and Seth 1968). During this study, surveys were carried out only in the Bansbari and Panbari ranges of the park, due to safety concerns and lack of infrastructure in the Bhuyanpara range.

*Nameri National Park*

The Nameri NP is situated in the foothills of the Arunachal Himalayas on the northern part of the Sonitpur district of Assam. The Jia Boreli River flows along the western border of the park, which is a tributary that joins the Brahmaputra River at Tezpur. The river floods frequently during the monsoon season, and several seasonal wetlands within the park support rare and endangered migrant bird species. The vegetation pattern of the park ranges from grasslands and riparian vegetation to mixed evergreen and semi-evergreen forests. During the study, surveys were conducted along the entire stretch of Jia Boreli River adjoining the park, along with six wetlands in the southern borders of the park.

## **Methodology**

We utilized an integrated approach, combining stakeholder interviews, visual encounter surveys, and habitat assessments to document life history, and quantify the distribution, habitat-use patterns, and anthropogenic threat levels to *N. nigricans*, given the paucity of baseline data on the species. Preliminary information on species ecology and location records was noted from informal meetings and focus group meetings with local stakeholders that encounter softshell turtles in the landscape. This was followed by semi-structured questionnaire interviews that were conducted with fisher-people living along the Brahmaputra River and along the buffer areas of the national parks, as well as with selected forest staff of the NPs who routinely patrolled riverine and wetland areas. Following this, focused visual surveys were conducted in shortlisted sites based on interviews and from published literature of previous surveys in these parks to assess species presence and their ecology.

### *Questionnaire surveys*

A semi-structured questionnaire was designed with three sections: (i) socio-demographic information (no identifying personal information was collected); (ii) species identification through photo plates; (iii) open ended questions on past sightings and ecological observations of *N. nigricans*, and their perceived threats. The questionnaires were conducted in Hindi and Assamese with oral informed consent taken from each interviewee. A total of 54 interviews were conducted from 2019–2021. The questionnaire interviews were conducted exclusively with forest staff of the four national parks (n = 28), fisher-people (n = 18), and other community members who reside along the boundaries of the national parks (n = 8). Responses of interviewees on the identification of species were analysed using frequency counts, while open-ended responses were analysed through thematic coding to identify recurring patterns and insights.

### *Visual encounter surveys*

Surveys were conducted in two post-monsoon (October–December 2019, 2020) and two pre-monsoon seasons (January–March 2020, 2021). A total of 70 field sites across four national parks were surveyed for

basking or surfacing turtles during peak sunlight hours from 0800 to 1500hrs. A range of habitats along the main Brahmaputra River channel, its tributaries, and sand islands were surveyed using line transects whose lengths were allocated based on mode of surveys: 2 km transects by boat while surveying sand islands and river banks, and 500 m transects surveyed on foot for river banks, wetlands, grasslands, and forested trails along riverine areas. In addition, potential turtle habitats were opportunistically inspected for 10–15 minutes. All direct and indirect signs including tracks, dead remains, nesting pits, burrows, and eggshell fragments, were recorded systematically. Team members were always accompanied by forest guards of the NP. Data on species, age class, sighting time, location, habitat type, and weather were recorded when turtles were visually observed. Turtles that were rescued or captured by forest staff or locals, or fisher-people, were photographed, identified, measured, and then released in their natural habitat at the place of capture. Dead turtle specimens were also recorded. Morphometric information such as straight carapace length (SCL), straight carapace width (SCW), and plastron length (PL) were measured (cm) using the Vernier Callipers (precision of  $\pm 0.1$  mm). Specimens were weighed (WT, kg) using a digital spring balance. For identification of the species, we followed the taxonomic keys and descriptions available in Das (1995) and Praschag and Gemel (2002). Total field effort amounted to 432 hours across the study period. For Sighting Per Unit Effort (SPUE) calculations, we used 244 hours of standardized transect surveys in the four NPs, that met our criteria for consistent methodology and environmental conditions. Sighting per unit effort (SPUE) was calculated as the number of individuals sighted per hour of survey effort.

#### *Distribution mapping*

Location records of *N. nigricans* were classified as either from temple ponds (captive) or from the wild. Data was compiled from field surveys in Assam, published literature, and from citizen science repositories like India Biodiversity Portal, and iNaturalist. Only records in which species identity was confirmed through uploaded photographs and classified as Research Grade (observations with verifiable photographic evidence that is independently validated by multiple identifiers) were retained for analysis. Spatially clustered records ( $< 1$  km apart) were filtered to avoid pseudo-replication. However, observations from our field surveys that occurred within this distance were retained when photographic evidence indicated that they represented different individuals, based on differences in size and colouration patterns. All records were mapped using QGIS v. 3.36.1.

#### *Habitat surveys and threat assessments*

Seasonal variation was assessed using one-way analysis of variance (ANOVA) with seasonal period (Pre-monsoon, Monsoon, Post-monsoon) as the fixed factor and record presence as the response variable. Habitat sites were categorized into four different categories — River, Tributary, Wetland, and Other (forested trails,

grasslands etc.). The habitat of each site was visually assessed for approximate channel width using a Bushnell Prime 1800 rangefinder (accuracy  $\pm 1$  m), and approximate average water depth using a HawkEye DT1H handheld depth sonar (accuracy  $\pm 0.1$  m), wherever direct measurements were feasible. During boat-based transects, depth measurements were taken every 100 m using the sonar. When direct measurements were not possible, sites were categorised into three width classes: small ( $< 50$  m), medium (50–150 m), and large ( $> 150$  m); and three depth classes: shallow ( $< 1$  m), medium (1–3 m), and deep ( $> 3$  m). Associated microhabitat data such as substrate type (sandy/sand-clay/clay/mud), number of river islands, percentage riparian floating vegetation, and presence and type of basking structures were recorded. Habitat preference was calculated using a variation of Manly's selectivity index, the Habitat Preference Rating Index (HPRI), where  $HPRI = \text{proportion of animals in each habitat type (X)} / \text{proportion of availability of each habitat type (Y)}$  (Beyer et al. 2010; Manly et al. 2002). Sampling effort (transect hours) served as our measure of habitat availability, where, where  $HPRI = \text{proportion of sightings in habitat} / \text{proportion of survey effort in habitat}$ .

In addition to recording baseline habitat variables, we assessed five threat categories relevant to protected-area habitats, identified through semi-structured interviews with local stakeholders. These included nest predation, invasive species, pollution, fishing nets, and riverbed agriculture. Each threat was documented at survey sites using a binary scoring system (presence = 1, absence = 0). For the four habitat types where *N. nigricans* was detected, cumulative threat scores were derived by summing the presence values across the five categories.

## Results

Through dedicated visual surveys, we identified two wild populations of *N. nigricans* within Kaziranga NP and Orang NP. Despite ~34 hours and 28 transects in Nameri and Manas NP, our surveys yielded no detections of *N. nigricans*. An unreported community pond population was also identified in Singri, Assam in September 2019, along with unreported photographic records from the floodplain region of Assam that were collated through a network of stakeholders and collaborators through messaging groups from 2019–2023. Herein, we report a comprehensive distribution map of *N. nigricans* in Assam and its current status across four key protected areas of Assam. We also provide an updated distribution of its current known range across India, Nepal, and Bangladesh, that distinguishes between captive/temple pond and wild populations. This study also expands our understanding of morphological variation across age and sex classes, and provides updated information on its habitat ecology, behaviour, and current threats faced by the species.

*Identification of N. nigricans from interviews with stakeholders*

Based on questionnaire surveys conducted with forest staff from four NPs (n = 28), fisher communities (n = 18), and residents (n = 8), only 33% of respondents were able to accurately identify *N. nigricans*, locally known as ‘Lao mura’, from a set of photographs depicting all softshell turtle species found in Assam (Figure 1). A chi-square test indicated no statistically significant association between the respondent category and the ability to correctly identify *N. nigricans* ( $\chi^2 = 0.517$ ,  $df = 2$ ,  $p\text{-value} > 0.05$ ). Nonetheless, qualitative observations suggested that older and more experienced individuals, those residing or working in proximity to the Brahmaputra River for over two decades, demonstrated a higher accuracy in identifying softshell turtles based on morphological traits.

### *Morphology*

The external morphology of *N. nigricans* shows marked ontogenic variation, with distinct changes from hatchlings to fully mature adults. Juveniles of all *Nilssonina* species, including *N. hurum*, *N. formosa*, and *N. nigricans*, display highly similar carapace and head patterns, rendering them morphologically indistinct during early developmental stages (Praschag et al. 2007). In this study, morphometric data collected from six wild sub adult and adult *N. nigricans* specimens contributed valuable insights into the physical characteristics of this poorly studied and critically endangered species. Of the six individuals documented during surveys in Kaziranga and Orang NPs, four were encountered alive and two were found dead due to natural causes. Of the six, we recorded three subadult females, one adult female, and two subadult males, with detailed measurements presented in Table 1. We restricted morphometric assessment to individuals measuring > 20cm in straight carapace length (SCL), as these size classes exhibit clear diagnostic features on the head and carapace that allow reliable identification of *N. nigricans*. Here, we integrate new field observations, photographic evidence, and available literature (Das 1995; Praschag and Gemel 2002) to characterise the external morphology across four ontogenetic stages of *N. nigricans*.

#### Hatchlings and Early Juveniles (Straight Carapace Length: < 15 cm)

Hatchlings observed at hatchery programs at the Assam State Zoo cum Botanical Garden (n = 13) in May 2019, possessed a nearly circular carapace with a dark olive-brown base coloration, interspersed with numerous lighter flecks. A defining feature of this stage is the presence of four (occasionally five or six) ocelli, each composed of four concentric rings: a central black spot, sharply bordered by an orange ring and subsequent lighter rings (Figure 2a) (Praschag and Gemel 2002). These ocelli are considered diagnostic for juveniles and were also observed in hatchlings emerging from incubated eggs (Ahsan and Saeed 1992). The dorsal carapace is slightly flattened with an ill-defined anterior vertebral groove and a more prominent posterior groove, as noted by Anderson (1875). The cartilaginous margin of the carapace extends prominently at the lateral and caudal edges.

#### Juveniles (Straight Carapace Length: 15–20 cm)

Juveniles observed in the temple pond of Nagshankar, Assam ( $n = 4$ ) exhibit rows of elongated tubercles arranged longitudinally on the bony disc of the carapace, with additional scattered tubercles along the posterior carapace rim. A row of 15–20 prominent tubercles is often present in the nuchal region (Praschag and Gemel 2002). The dorsal surface of the head bears large dirty-yellow flecks that become increasingly greenish, resulting in a reticulated appearance (Figure 2b). The upper lips are yellow posteriorly, and the eyelids display a radiating zebra-striped pattern of black and dirty-yellow hues.

#### Subadults (Straight Carapace Length: 20–45 cm)

Subadult turtles exhibit a more uniform carapace coloration, ranging from grey and olive-green to copper or light brown with occasional marbling (Annandale and Shastri 1914). During this stage, the ocelli begin to fade, with previously present yellow spots becoming indistinct and disappearing. The plastron darkens to grey, and the head becomes more robust and blunt, reflecting increased development of the jaw musculature. The proboscis becomes less prominent, and the posterior region of the upper lip transitions to a pale grey or white coloration. A large, somewhat triangular postorbital fleck of grey to yellowish colour remains evident behind the eye, while the diagonal band at the base of the proboscis fades gradually.

#### Adults (Straight Carapace Length: > 45 cm)

In fully mature specimens, the carapace becomes oval and uniformly coloured, typically dark grey, brown, or olive. The carapace does not have any ocelli or yellow speckling. The head, neck, and limbs are predominantly dark grey to black. The head displays a reticulated pattern formed by large pale flecks, contributing to a net-like appearance. The fleshy upper lip remains white in its posterior two-thirds (Figure 2c). In some individuals, a distinct white fleck may be present in the wrinkled skin between the neck and forelimbs. Sexual dimorphism in *N. nigricans* is evident in both carapace shape and tail morphology. Females exhibit a more rounded carapace compared to the relatively elongated shell observed in males (Ahsan and Saeed 1992; personal observations). In addition, males possess noticeably longer and thicker tails. Adult males also tend to attain larger overall body sizes than females (Praschag and Gemel 2002; personal observations).

#### Cranial Morphology

A diagnostic cranial feature of *N. nigricans*, present in both juvenile and adult specimens, is a pronounced bony crest located within the cavity of the mandibular symphysis. This crest is readily visible when the mouth is open and is also evident in osteological material. The width of the mandibular symphysis approximates the diameter of the eye (Praschag and Gemel 2002), further supporting its utility as a distinguishing feature when photos of an open jaw (Figure 2d), or specimens are accessible.

### *Population density*

A total of 244 hours of transect survey effort was conducted between July 2019 and March 2021 across 72 sites within and around four NPs in Assam to assess the presence of *N. nigricans*. During this period, 16 individual turtles were directly sighted or encountered through visual encounter surveys and rescue operations. Based on these observations, the Sighting Per Unit Effort (SPUE) was calculated to be approximately 0.066 individuals per hour (95% CI: 0.033 - 0.098), indicating an average of one turtle observed every 15 hours of survey effort. Our direct field observations have confirmed the presence of *Nilssonina nigricans* populations within Kaziranga and Orang NPs, indicating potentially stable populations and suitable habitat conditions for softshell turtles. In Kaziranga NP, 13 individuals comprising subadults and adults were positively identified as *N. nigricans*. Additionally, eight *Nilssonina* softshell turtles were encountered during visual surveys but were excluded from analysis as species identification could not be conclusively determined. Similarly, in Orang NP, three subadult and adult *N. nigricans* were observed, along with three unidentified *Nilssonina* softshell turtle individuals.

### *Distribution*

Between July 2019 and March 2021, extensive field surveys were conducted across 72 sites within four NPs and adjacent areas in Assam to assess the presence of *N. nigricans*. A total of 16 confirmed records of wild individuals were documented through direct visual encounters and rescue operations within protected areas (Appendix 1). In addition to these field-based observations, 27 confirmed records of wild *N. nigricans* from Assam were compiled from a combination of published literature, social media platforms, citizen science databases, and information shared through collaborative networks and messaging groups with forest department personnel, local fishers, and community members, dating from 2010–2023. Collectively, these efforts yielded 43 confirmed records of wild *N. nigricans* across protected and non-protected areas of Assam. Furthermore, all verified records of the species were compiled to delineate the current known distribution of *N. nigricans* across a total of 8 states across Northeast India (Assam, Nagaland, Arunachal Pradesh, Tripura, Mizoram, West Bengal), Nepal (Koshi), and Bangladesh (Chittagong) (Figure 3). A total of 73 records were collated from 2002-2024, and categorized by population origin, distinguishing between wild populations (n = 51) and those inhabiting temple ponds (n = 22). Duplicate records of turtles from temple ponds were omitted. However, several temple ponds across northeast India may host unreported populations of *N. nigricans* that are not captured in news reports, citizen science databases, or the literature; these were not included, as confirmation of species identity is required.

### *Natural history and behaviour*

Recent baseline habitat surveys aimed at understanding the distribution and ecology of *N. nigricans* reveal distinct seasonal patterns in habitat utilization. Adult individuals were predominantly observed in the main channel of the Brahmaputra River and its tributaries during the post-monsoon season (October–December), where they were seen basking on sandbanks and emergent logs. In contrast, during the pre-monsoon period (January–May), preceding the annual floods, the species was primarily encountered in lentic water bodies such as wetlands, beels, and lakes. Additionally, individuals were observed traversing forest trails and agricultural landscapes across the floodplain, presumably in search of suitable habitats, foraging grounds, and nesting sites.

Through our survey effort of 244 h during the given study period, a total of 16 direct sightings of *N. nigricans* were recorded from the study area. Approximately 90 percent of the sightings were recorded in the afternoon from 1200 h to 1500 h. Pre-monsoon seasons (February–May) provided the highest number of sightings ( $n = 11$ ), and post-monsoon season (October–January) provided the lowest ( $n = 4$ ). There was one *N. nigricans* adult encountered during the monsoon season that was rescued from the buffer of Kaziranga NP (north bank). We also classified the seasonal occurrence of wild *N. nigricans* sightings from our survey efforts and from citizen science records ( $n = 36$ ) in Assam, from their date of sighting metadata (Figure 4). A one-way ANOVA test suggested there was no significant variation in the encounter rates of *N. nigricans* across seasons in Assam. Although pre-monsoon records ( $n = 18$ ) made up 50% of the observations, statistical analysis revealed no significant seasonal variation in occurrence frequency ( $F(2,33) = 0.485$ ,  $p = 0.620$ ), also indicating no substantial seasonal bias in reporting patterns. Analysing the Habitat Preference Rating Index (HPRI) revealed significant non-random habitat use by *N. nigricans*, with selection strongly favouring tributaries ( $\chi^2 = 18.24$ ,  $df = 3$ ,  $p < 0.001$ ). Despite representing only 7.9% of the total sampling effort (34 out of 432 h), tributaries accounted for 43.8% of all turtle sightings (7 of 16 observations), resulting in a strong positive selection (HPRI = 5.56, 95% CI: 3.21-7.90\*). In contrast, wetlands were the most extensively surveyed habitat representing 60.2% of the total sampling effort but were used less than expected given their availability (HPRI = 0.62) (Table 2).

Scavenging behaviour in *N. nigricans* has been previously documented in the wild from Kaziranga NP where an individual was observed feeding on the partially submerged carcass of a Hog deer (Sharma et al. 2020). During our field surveys along the Mora-Diffloo River in the Kohora range of Kaziranga NP, we recorded a notable instance of hunting/feeding, involving what was likely the largest adult *N. nigricans* observed during our study. The individual had a straight carapace length over 70 cm, as estimated from photographs taken, and was seen actively feeding on a large fish, tentatively identified as *Wallago attu* based on visible morphological features of the catfish head. The turtle was observed repeatedly thrashing the fish on the water surface, exposing the skeletal structure, while consuming substantial portions of the midsection. The feeding bouts of the turtle involved short submergence intervals of several seconds, and it

remained in the shallow margins of the river for approximately two minutes before submerging with the remaining carcass.

No evidence of breeding or nesting behaviour of *N. nigricans* was recorded during the study period, and no nests were encountered during transect surveys of riverbanks and sand islands. Anecdotal information regarding nesting behaviour was obtained from interviews with a forest staff member from Orang NP, who has over 30 years of field experience. According to this account, female *N. nigricans* are reported to nest on sandy shores with sparse emergent vegetation, typically located approximately 10 meters from the water's edge of tributaries like the Pachnoi or Dhansiri River. Hatchlings are said to emerge with the early onset of the monsoon season (Tilak Boro, personal communication). While this observation offers valuable insight, it underscores the need for systematic studies to verify and document nesting ecology in wild populations.

### *Threats*

Cumulative threat scores varied across habitat types where *N. nigricans* were sighted in Kaziranga NP (south and north bank) and Orang NP. These differences were not statistically significant (Kruskal-Wallis  $\chi^2 = 3.86$ ,  $df = 3$ ,  $p = 0.27$ ). Mean threat scores were highest in riverine habitats ( $\bar{x} = 3.0$ ), followed by tributaries ( $\bar{x} = 1.0$ ), other habitats like forested trails and grasslands ( $\bar{x} = 0.57$ ), and wetlands ( $\bar{x} = 0.33$ ) (Figure 5). Lesser-used habitats like the main channel of the Brahmaputra River and other forested areas and grasslands showed higher threat scores, such as presence of invasive species, like water hyacinth (*Eichhornia crassipes*) and parthenium spp., riverbed agriculture, and occasional fishing pressures. The overall pattern suggests potential habitat-specific threat profiles, though limited sample sizes constrain statistical power.

## **Discussion**

### *Importance of a freshwater protected area network for endangered turtles*

This study assessed the current distribution and ecology of *N. nigricans* across the Brahmaputra River floodplains in Assam, with the broader objective of informing long-term conservation strategies. We confirmed populations of *N. nigricans* within Kaziranga and Orang NPs, with additional photographic records from the peripheries of Nameri NP, upstream of the Jia Bhoreli River in Pakke Wildlife Sanctuary in Arunachal Pradesh. This highlights the importance of maintaining ecological connectivity across the Brahmaputra and Jia Bhoreli River systems. The 31 records of wild *N. nigricans* clustered in the four protected areas in Assam, suggest that these NPs function not as isolated refuges, but as nodes within a broader landscape network that may facilitate movement, gene flow, and seasonal habitat use. Additional

records collated from citizen science and communities confirm that the distribution range of *N. nigricans* is more extensive than previously documented, outside the protected area network. This study provides a comprehensive collation of all known occurrence records, integrating information scattered across published literature, news reports, citizen science platforms, and informal messaging networks. This updated distribution emphasizes the importance of both protected areas and non-protected habitats, including community-managed ponds and temple ponds, in supporting the persistence of this critically endangered species. A critical step in reducing biodiversity loss involves understanding what constitutes suitable habitat across the range of a species and how these habitats may shift under future environmental pressures. As demonstrated by research on similar large softshell turtles in Asia, large, interconnected freshwater habitats are essential for sustaining viable populations (Ghaffari et al. 2014; Ihlow et al. 2014, Jain et al. 2021). These studies show that wide-ranging softshell species depend on extensive river networks, seasonal floodplain connectivity, and access to undisturbed nesting and basking sites, thus highlighting the importance of maintaining habitat continuity. However, designated protection for such critical habitats remains limited, and extensive fragmentation due to infrastructure such as dams poses significant challenges (Bárcenas-García et al. 2022). Similar insights are relevant to the Brahmaputra floodplain, where hydrological alteration and habitat fragmentation could severely impact the long-term persistence of *N. nigricans*. The relatively low detection rate of *N. nigricans* in our study likely reflects both the cryptic, elusive nature of the species, and the inherent difficulty of surveying freshwater turtles in large, dynamic river systems. Given the well-documented decline of several freshwater turtle species in the region due to anthropogenic pressures such as subsistence hunting, agricultural encroachment, habitat degradation, and modification of nesting areas (Turtle Conservation Coalition 2018), it is essential to adopt a landscape-level approach to conservation that incorporates both *in-situ* protection within protected areas, with strong community engagement across non-protected habitats.

#### *Filling in the life history lacunae on N. nigricans*

In India, most freshwater turtle studies have traditionally focused on species diversity and distribution, while ecological research, particularly on behaviour, reproduction, and long-term population dynamics remains limited (Mital 2016). Freshwater turtles, including *N. nigricans*, exhibit life history traits such as delayed sexual maturity, long lifespans, and low reproductive rates, which make them particularly vulnerable to increased adult mortality (Lovich et al. 2018). In our study, the predominance of subadult encounters, even within a limited sample size, raises concerns because modest reductions in adult survival can disproportionately affect long-term population persistence in long-lived turtle species. When restricted to small or degraded habitats, turtles may experience stress, compromised health, and reduced reproductive output (Browne and Hecner 2007; Butler 2019). Resource limitations along with the absence of key

microhabitats such as basking sites and suitable nesting areas further undermines population viability. India's freshwater turtles also face a multitude of anthropogenic threats such as pollution, sand mining, riverbed agriculture, accidental drownings in fishing nets and the effects of a warming climate (Moll and Moll 2004; Ahmad and Das 2010; Mital and Kumar 2019; Jain et al. 2021). Market surveys conducted in Assam by Das and Gupta (2004) revealed the active exploitation and trade of several softshell species, including *N. gangetica*, *N. hurum*, and *Chitra indica*. Further, Praschag and Gemel (2002), reported the targeted killing and commercial sale of softshell turtles including *N. nigricans* in local markets near the periphery of Kaziranga NP. The widespread collection of eggs from sandbanks and riverine islands represents an additional, significant threat to turtle populations across the Brahmaputra floodplain (Praschag and Gemel 2002).

Assessing population density and abundance is critical for monitoring species status and developing effective conservation strategies. However, estimating these parameters in freshwater turtles, especially softshell turtles, presents significant challenges due to their predominantly aquatic lifestyles, secretive behaviour, and tendency to inhabit areas with minimal human disturbance (Lovich et al. 2018; Luiselli 2009). Although *N. nigricans* has been downlisted to 'Critically Endangered' (IUCN 2025), the full extent of the projected declines and associated ecological impacts has yet to be systematically studied, as comprehensive scientific data on its population size, behavioural ecology, and habitat preferences remain limited. The conservation of *N. nigricans* populations outside traditional protected areas will be crucial, especially in the Brahmaputra floodplains, where human-wildlife interfaces are pronounced.

Our study contributes to the start of filling this knowledge gap by providing the first detailed morphometrics for wild *N. nigricans* individuals, as well as baseline ecological and threat assessment data specific to *N. nigricans*. Our findings also show that tributary habitats of the Brahmaputra floodplains are used by *N. nigricans* more frequently than other habitats, relative to their availability. This suggests that tributary habitats provide unique habitat features that cannot be compensated for by more abundant wetland habitats, and these areas must be prioritised for protection. While our small sample size limited statistical power, the significant preference for tributary habitats provides preliminary evidence for habitat specialisation that warrants further investigation with larger sample sizes. These findings underscore the importance of continued monitoring and habitat management in protected areas to ensure the long-term conservation of this critically endangered species. The distribution records and associated data gathered can be utilized to develop species distribution models and suitability maps, which can directly inform park management plans by identifying high-value habitats for protection. These outputs can also guide patrolling and monitoring efforts, and support evidence-based decisions on habitat restoration, and future release sites. The threat assessment in protected areas also revealed anthropogenic pressures including habitat pollution from floating solid waste and the presence of aquatic invasive species. The threat scoring matrix can be

systematically replicated outside protected areas where there are more intense anthropogenic pressures to gain a better understanding of which threats need to be proactively mitigated. Identifying these localized stressors can help managers prioritise targeted interventions such as waste reduction measures and invasive species control, to maintain or improve habitat quality for remaining populations.

#### *Strategies for conservation of Nilssonina softshell turtles in India*

Community involvement has emerged as a powerful tool in turtle conservation, particularly in areas where conservation conflicts arise due to overlapping turtle nesting and agricultural cycles. Our study shows that older fishers, farmers, and long-serving forest staff possess extensive ecological knowledge of turtle natural history, including local names, behaviour, and long-term population changes. Their observations consistently reflected an awareness of population declines over the years, and all respondents expressed positive perceptions of turtles along with a clear understanding of the factors driving these declines. These locally grounded insights underscore the value of participatory approaches that place community knowledge at the centre of conservation planning. Community-led initiatives such as those implemented in Hastinapur Wildlife Sanctuary along the Ganges River floodplains have demonstrated the potential for effective conservation through riparian farmer engagement, nest monitoring, and habitat protection (Dubey et al. 2025). By encouraging stewardship and capitalizing on the cultural and religious significance of turtles and rivers, local communities can be encouraged to actively participate in conservation (Sarkar et al. 2019), and this effort can be extended to other aquatic species, such as the Ganges River Dolphin (*Platanista gangetica*), through citizen science monitoring programs. In Assam, temple ponds serve as important refugia for several endangered turtle species, including *N. nigricans*. However, these *ex-situ* populations are often unmanaged, and individuals may be released without consideration of genetic or ecological suitability. Moreover, post-release survival and movement are seldom monitored, even though such information is critical for evaluating the effectiveness and long-term viability of release efforts. Therefore, moving beyond hatchery-based conservation and towards habitat protection and restoration is critical for the long-term survival of the species. The success of any conservation intervention for an endangered species like freshwater turtles depends on sustained community engagement and awareness-building. Training riparian communities, involving them in nest protection and rescue methods, and fostering a sense of ownership can ensure long-term success. Continued data collection, ecological monitoring, and community science are essential for refining research and conservation priorities for *N. nigricans* and other freshwater turtle species in the region.

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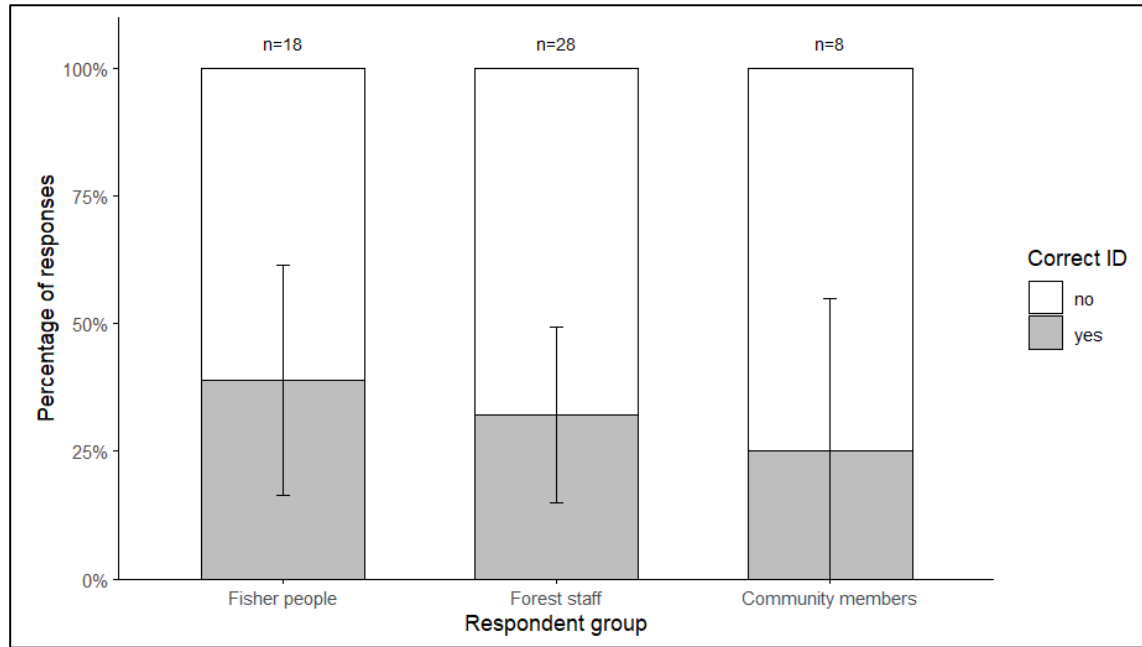
**Table 1.** Morphometric measurements of *N. nigricans* individuals encountered during field surveys (KZ SB: Kaziranga NP Southbank; KZNB: Kaziranga NP Northbank; OR: Orang NP; F: Female; M: Male; SCL: Straight Carapace Length, SCW: Straight Carapace Width, PL: Plastron Length; WT: Weight)

Date	Site	Sex	Dead/ Live	Age class	SCL (cm)	SCW (cm)	PL (cm)	WT (kg)
28/09/2020	KZ SB	F	Live	Sub Adult	20.29	16.81	15.58	11.30
27/11/2019	OR	M	Live	Sub Adult	20.66	16.98	16.71	12.6.0
10/12/2020	KZ SB	F	Dead	Sub Adult	24.20	18.30	-	-
27/03/2021	KZ NB	M	Live	Sub Adult	26.10	21.40	21.10	18.00
20/09/2019	KZ SB	F	Dead	Sub Adult	27.50	22.00	-	-
				Sub Adult (Mean $\pm$ SD)	23.75 $\pm$ 2.86	19.10 $\pm$ 2.26	17.80 $\pm$ 2.90	14.0 $\pm$ 3.20
01/03/2020	KZ NB	F	Live	Adult	72.00	51.00	53.00	44.00

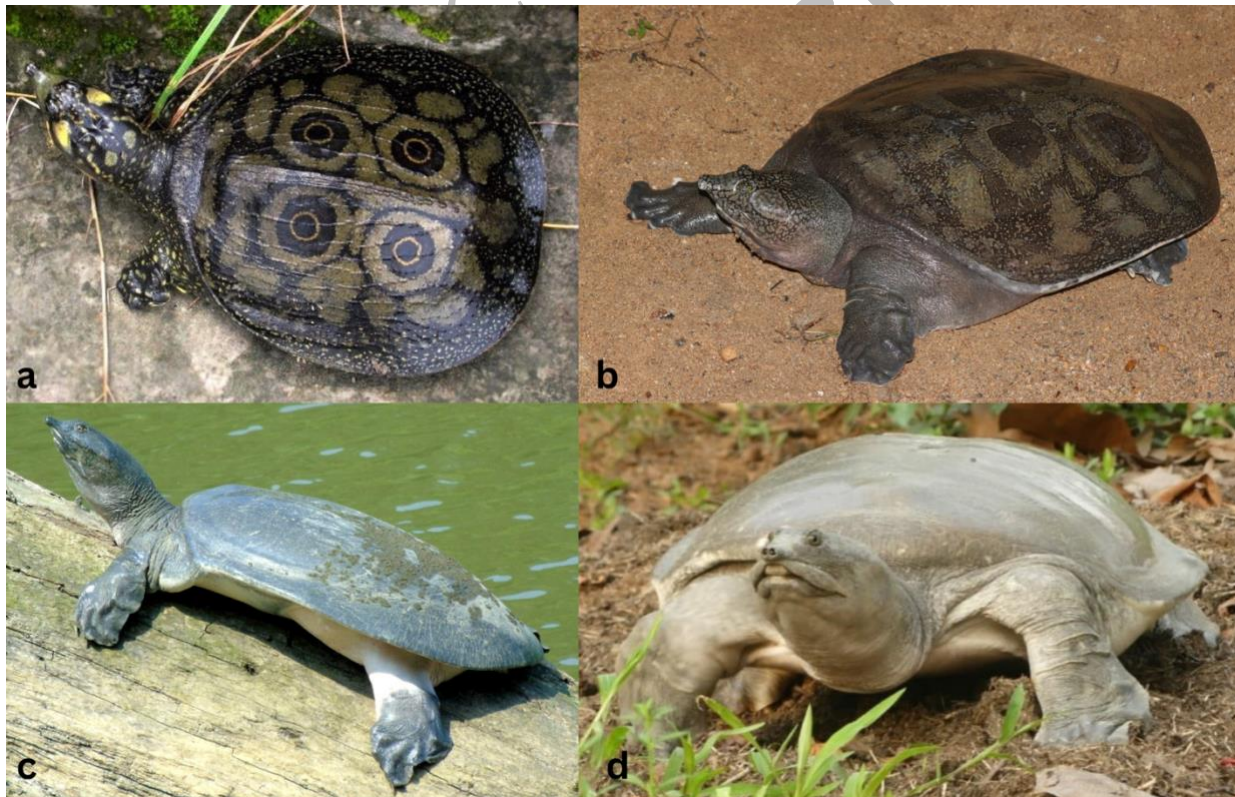
**Table 2.** Pooled Habitat Preference Rating Index (HPRI) calculated for turtle occurrence across four habitat categories in Kaziranga and Orang NPs. Other = trails, forested areas and grasslands. (\*indicates significance,  $\chi^2 = 18.24$ ,  $df = 3$ ,  $p < 0.001$ )

Habitat type	No. Sightings (% use)	Sampling effort hours (% available)	HPRI	95% CI
Tributary	7 (43.8%)	34 (7.9%)	5.559*	(3.214–7.904)
Wetland	6 (37.5%)	260 (60.2%)	0.623	(0.321–0.925)
Other	2 (12.5%)	92 (21.3%)	0.587	(0.234–0.940)
River	1 (6.3%)	46 (10.7%)	0.587	(0.012–1.162)

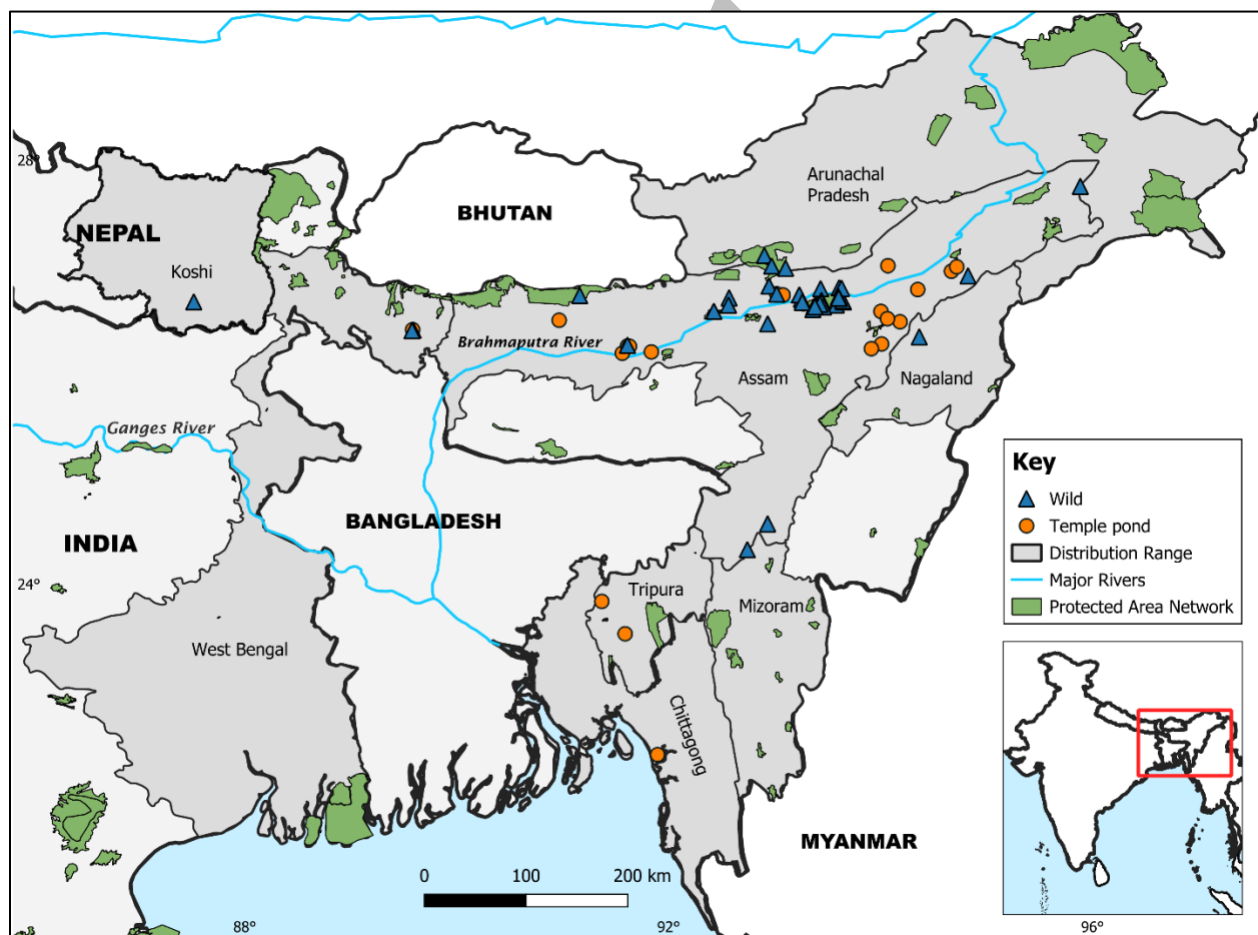
Note: Total turtle sightings (n = 16); Total sampling effort = 432 hours.



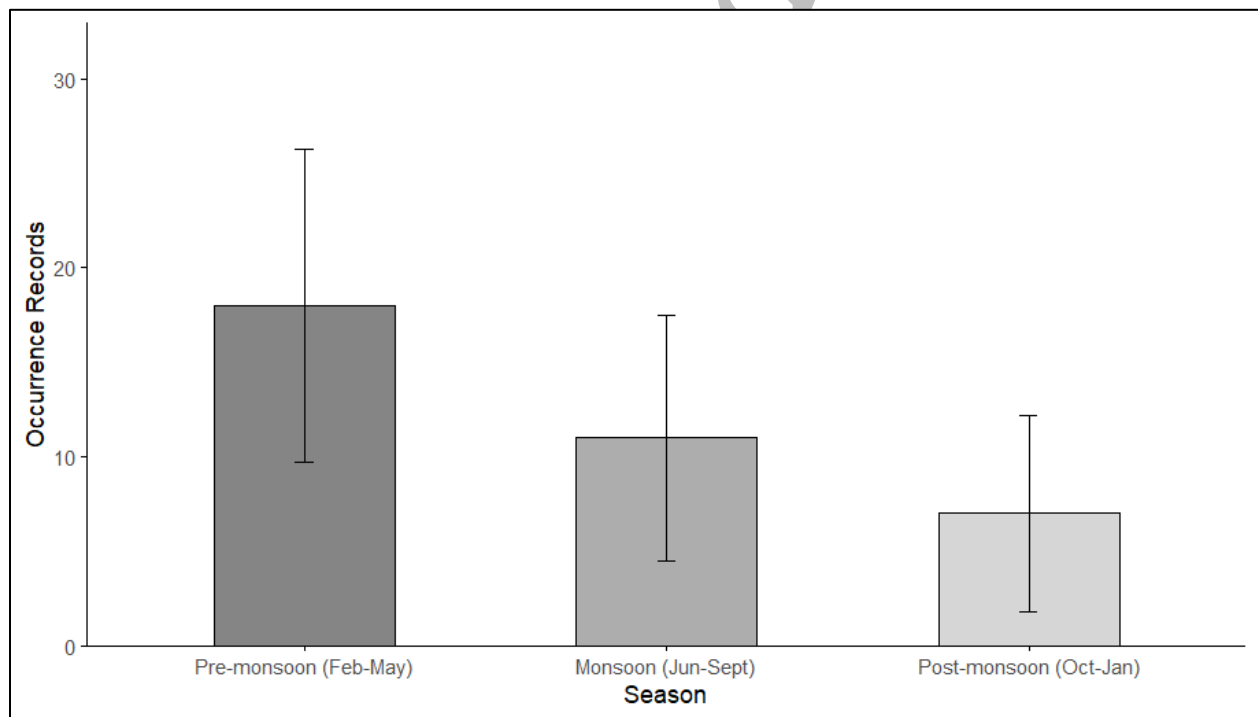
**Figure 1.** Percentage of respondents across three stakeholder groups that correctly identified *N. nigricans* from photographs during questionnaire surveys. Error bars show 95% confidence intervals. No significant difference was observed among stakeholder groups ( $\chi^2 = 0.517$ ,  $df = 2$ ,  $p\text{-value} > 0.05$ ).



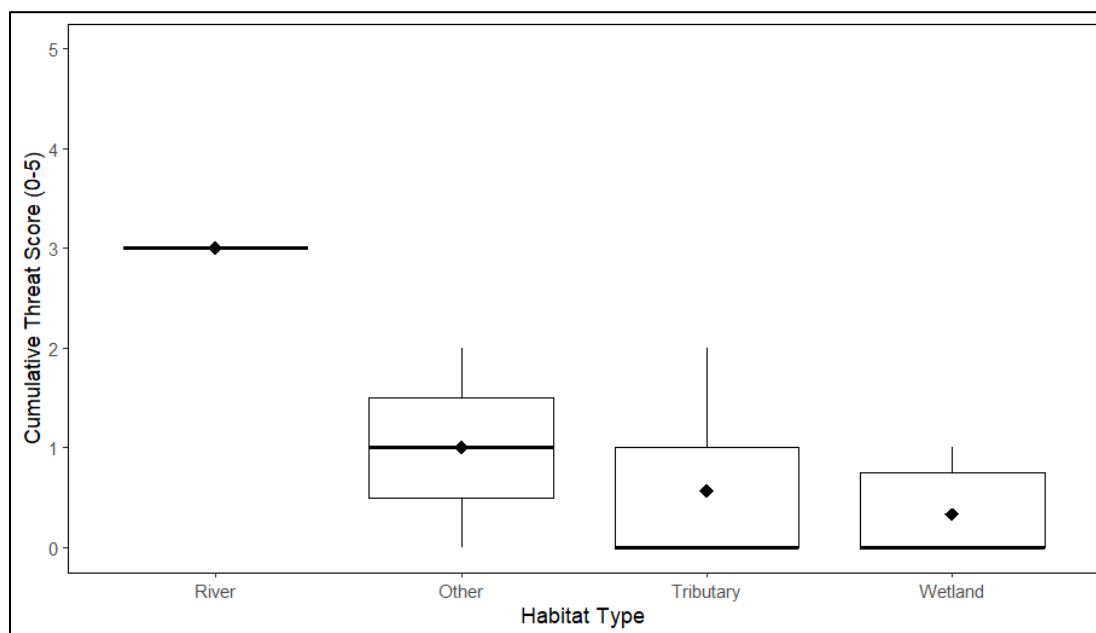
**Figure 2.** Ontogenetic morphological changes in *N. nigricans*. a. Juvenile (photo: Sadananda Bhuti); b. Sub-adult (photo: Abhijit Das); c. Adult (photo: Anuja Mital); d. Adult- with mandibular symphysis visible (photo: Kapish Rai)



**Figure 3:** *Nilssonina nigricans* occurrence in the Brahmaputra River basin in India (Assam, Nagaland, Arunachal Pradesh, Tripura, Mizoram, West Bengal), Nepal (Koshi), and Bangladesh (Chittagong), compiled from field surveys, literature, and citizen science. Map prepared in QGIS v3.36.1.



**Figure 4:** Seasonal occurrence of *N. nigricans* across Assam ( $F(2,33) = 0.485$ ,  $p = 0.620$ ), from records collated from field surveys and citizen science ( $n = 36$ ). Error bars show 95% confidence intervals.



**Figure 5:** Boxplot of cumulative threat scores (0–5; sum of presence/absence across five threat categories) for sites where *N. nigricans* was recorded in protected areas of Assam, shown by habitat type. Diamonds indicate mean threat scores. Differences among habitat types were not significant (Kruskal-Wallis  $\chi^2 = 3.86$ ,  $df = 3$ ,  $p = 0.277$ ) Other = trails, forested areas and grasslands (n = 6 sites).

**Appendix 1.** Occurrence records of *N. nigricans* across protected areas of Assam from field surveys from 2019–2021.

SN	Date	Site Locality	District	Protected Area
1	04/08/2019	Dipara pukhurim, Gameri	Biswanath	Kaziranga NP, north bank
2	14/09/2019	Roumari beel	Darrang	Orang NP
3	20/09/2019	Donga beel, Bagori	Nagaon	Kaziranga NP, south bank
4	27/11/2019	Silbori	Darrang	Orang NP
5	15/01/2020	Forested Trail near Pachnoi river	Darrang	Orang NP
6	29/02/2020	No. 1 Bolakhata, Biswanath Ghat	Biswanath	Kaziranga NP, north bank
7	02/03/2020	Bhorontika beel, Kohora	Golaghat	Kaziranga NP, south bank

8	02/03/2020	Kawaimari, Kohora	Golaghat	Kaziranga NP, south bank
9	28/09/2020	Dighali beel, Kohora	Golaghat	Kaziranga NP, south bank
10	10/12/2020	Bhorontika beel, Kohora	Golaghat	Kaziranga NP, south bank
11	11/03/2021	Diffloo, Kohora	Golaghat	Kaziranga NP, south bank
12	15/03/2021	Kawaimari, Kohora	Golaghat	Kaziranga NP, south bank
13	16/03/2021	Hollopath, Kohora	Golaghat	Kaziranga NP, south bank
14	16/03/2021	Kawaimari, Kohora	Golaghat	Kaziranga NP, south bank
15	27/03/2021	Umatumuni, Biswanath Ghat	Biswanath	Kaziranga NP, north bank
16	16/04/2021	Kawaimari, Kohora	Golaghat	Kaziranga NP, south bank

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