Shared Spaces, Shared Challenges: Assessing Habitat and Resource Sharing Between the Greater One-Horned Rhinoceros and Livestock in Pobitora Wildlife Sanctuary, Assam

By

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in

Wildlife Science

Under the supervision of

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DECLARATION

I hereby declare that the work conducted under the thesis entitled "**Shared Spaces, Shared Challenges: Assessing Habitat and Resource Sharing Between the Greater One-Horned Rhinoceros and Livestock in Pobitora Wildlife Sanctuary, Assam",** is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master's in Wildlife Science** at the **Academy of Scientific and Innovative Research (AcSIR).** This research work has been carried out under the guidance and supervision of Dr Samrat Mondol, with co-supervision by Dr S. P. Goyal of the Wildlife Institute of India, Dehradun, and Mr Amit Sharma of WWF-India. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding, and the particulars given in it are true to the best of my knowledge.

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This is to certify that the thesis by **Kiruthika S M** entitled "**Shared Spaces, Shared Challenges: Assessing Habitat and Resource Sharing Between the Greater One-Horned Rhinoceros and Livestock in Pobitora Wildlife Sanctuary, Assam**", is an original work submitted to the **Academy of Scientific and Innovative Research,** for the award of the degree of **Master's in Wildlife Science.**

Kiruhtika S M has completed one semester of research work, embodied in this thesis, under my guidance and supervision. The work presented in this thesis has not been submitted to any other university or Institute for the award of any degree, diploma or distinction.

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List of Appendices

- Photographs of the study area
- Photographs of wildlife in PWLS
- Photographs of rhinos and livestock interaction in PWLS
- Photographs of field surveys
- Photographs of vegetation sampling and dung sample collection
- Photographs of laboratory methods

List of Tables

List of Figures

Table of Contents

Abstract

The Greater One-Horned Rhinoceros (GoH rhino) is a keystone species of the alluvial grasslands and riverine forests. Despite conservation successes, its long-term survival is threatened by population fragmentation, habitat degradation, and intense competition for resources with sympatric herbivores. Pobitora Wildlife Sanctuary (PWLS), Assam, feature a habitat mosaic embedded within a largely human-dominated landscape, yet supports the highest density of rhinos and a large number of livestock from surrounding villages. This makes it an ideal site to investigate the spatial use and nutritional ecology of the rhino during the dry winter season. The aim is to clarify whether high rhino density pressures force rhinos to utilise habitats non-selectively and how livestock encroachment influences their nutritional status. Spatial distribution patterns at the larger and finer scales, spatial overlaps between species, and the dietary quality of rhinos in relation to environmental variables and livestock pressure were assessed through systematic animal and vegetation surveys and analysis of dung samples for nutritional parameters. Habitat use by rhinos was concentrated in mosaics of tall grassland, wet short grassland, and marshy habitats; these overlapped with those of buffalo but not with those of cattle, even though cattle were dispersed throughout the study area. Habitat selection was shown to reflect a complex trade-off among nutritional quality, physiological requirements, and the energetics involved, even at such high densities. The results also suggest that cattle could be indirectly affecting spatial use, though additional research is needed to confirm this effect.

1 Introduction and Literature Review

1.1 Introduction to the species

The Greater One-Horned Rhinoceros (*Rhinoceros unicornis*), also commonly referred to as the Indian rhinoceros or GoH rhino, is one of the world's most threatened megaherbivores and the only rhinoceros species found in the Indian subcontinent. First scientifically described by Linnaeus in 1758, it is the largest of the three extant Asian Rhinoceros species. Taxonomically, the species belongs to the family Rhinocerotidae, which comprises four genera and five extant species globally: white rhinoceros, black rhinoceros, Indian rhinoceros, Javan rhinoceros, and Sumatran rhinoceros. The family Rhinocerotidae emerged in the late Eocene in Eurasia and diversified in the Oligocene. Phylogenetic studies indicate that Asian rhinos diversified earlier than African counterparts, positioning the Indian rhinoceros as the basal extant lineage. Over time, modern rhinos have evolved anatomical and physiological features such as a boneless horn, broad three-toed feet and modified dentition to adapt to marshy floodplains and graze on coarse fibrous forage (Johnsingh & Manjrekar, 2016).

Morphologically, the GoH rhino is characterised by a deep slate-grey, almost hairless skin marked by prominent tubercles and large folds across the flank, giving it a distinct armour-plated appearance. It bears a single, boneless horn. As the second-largest terrestrial mammal in India, adults can weigh from 1,500 (females) to 2,000 kg (males), with a shoulder height of 1.75 - 2 m (Menon, 2023). Physiologically, as an odd-toed ungulate (perissodactyl), the species possesses a hindgut fermentation system with a simple stomach and enlarged caecum. This non-ruminant digestive tract places them among the 'bulk and roughage' feeders, a trait with a major role in their forage selection strategy and nutritional ecology.

The GoH rhino is widely recognised as a keystone species within the Indian subcontinent's alluvial grasslands and riverine forests. Its ecological impact extends beyond simple biomass

consumption. Through frequent grazing and trampling, it places strong selective pressure on vegetation, especially by inhibiting the vertical growth of seedlings and saplings (Dinerstein, 1992). Furthermore, GoH rhinos play a vital role in riverine forest regeneration by dispersing seeds of numerous herbaceous and woody plant species (Dinerstein, 1991). Research shows that GoH rhinos can disperse seeds over long distances, aiding gene flow and floodplain habitat restoration (Awasthi, McConkey, Subedi, et al., 2024). Even at low population densities, rhino reintroductions can mitigate ecosystem degradation and benefit other species. Seeds dispersed by rhinos have similar or higher germination rates than those dispersed by cattle and buffalo. While domestic bovids can partly replace rhinos in seed dispersal roles, they cannot fully compensate for the loss caused by rhino declines (Awasthi, McConkey, Aluthwattha, et al., 2024), highlighting the rhino's key role as a keystone species in maintaining vegetation diversity and ecosystem health. Thus, the ecological functions performed by the GoH rhino extend far beyond its individual conservation value, acting as a pillar for ecosystem health and broader biodiversity of the landscapes it inhabits.

1.2 Population status

Historically, the GoH rhinos roamed widely across the Indo-Gangetic plains, covering parts of Bangladesh, India, Myanmar, Nepal and Pakistan (Talukdar et al., 2025). Due to persistent hunting pressure and habitat destruction, their numbers declined drastically, and by the early 20th century, only about 200 individuals survived in the wild (Rookmaaker et al., 2016). However, effective protection and conservation measures, along with active population management, including translocation and range expansion programmes, have helped the species recover to its present status.

Despite these achievements, the species remains classified as Vulnerable on the IUCN Red List, with its population scattered in isolated pockets across Nepal and India. Hence, to ensure

consistent monitoring, India's Ministry of Environment, Forests, and Climate Change (MoEF&CC) established a standard operating protocol (SoP) for monitoring the GoH rhino population in 2020. According to the 2022 survey, there were 3,282 GoH rhinos in India (MoEFCC, WII and WWF, 2020), while Nepal's 2021 assessment recorded 752 animals (NTNC, 2021), indicating a total of about 4,034 individuals, all confined to a handful of protected areas (Sharma, 2022). More recently, the State of the Rhino 2025 reported slightly higher numbers (4,075). Although this recovery is highly encouraging, it masks vulnerabilities such as the species' presence in small, geographically isolated protected areas in India and Nepal with limited genetic exchange, each embedded within landscapes subjected to intense human pressure (Jhala et al., 2021). Within India, the major populations are found in Kaziranga, Orang, Pobitora, Manas, and Laokhowa-Burachapori in Assam; Jaldapara and Gorumara in West Bengal; Valmiki Tiger Reserve in Bihar; and Dudhwa National Park in Uttar Pradesh. The state of Assam accounts for the largest share of the global population, with Kaziranga National Park (KNP) supporting more than 75% of the Indian population (Sharma, 2022). All these populations face threats such as poaching, habitat degradation, invasive species, livestock grazing, tourism pressure, and loss of genetic diversity; however, the severity of these threats varies across protected areas. Therefore, each protected area requires site-specific management strategies to address its unique challenges effectively. Hence, the future survival of the GoH rhino thus depends critically on the ecological health and management of individual protected areas and connectivity between them, which presents a distinct set of threats and opportunities.

1.3 Studies on habitat use and nutrition

Understanding how the GoH rhino uses its environment is important for its management. The GoH rhino habitat use has been studied for decades across the species' range. One of the earliest studies in Royal Chitwan National Park, Nepal, suggested that rhino densities peaked in areas of high habitat diversity, with individual home ranges as small as 3.26 km² (Laurie, 1978). In

contrast, a subsequent work by Dinnerstein and Price showed that the GoH rhino density was positively related to the abundance of *Saccharum spontaneum* rather than habitat diversity, with the species reaching densities of 13.3/km^2 in such suitable habitats (Dinerstein & Price, 1991). A study in Manas National Park with radio-collared GoH rhino individuals showed a preference for tall grassland, and also for short grasslands near water bodies. This reliance on grassland habitat has been shown by multiple studies across the landscape. These studies showed that GoH rhinos preferred tall grasslands and riverine forests, while avoiding forests (Dutta et al., 2012; Ranabhat et al., 2026). These habitat preferences are very dynamic, with a clear seasonal shift. During the monsoon, GoH rhinos disperse into higher-elevation habitats to escape flooding (Konwar et al., 2009). A study in Nepal showed that GoH rhinos preferred grasslands and riverbed forests in the winter, and forest habitat in the summer (Gurung & Chalise, 2015), probably to meet foraging and thermoregulatory needs.

These seasonal movements are tied to forage availability and the species's requirements. According to Laurie (1978), GoH rhinos fed on 183 species of plants, with grass species making up the bulk of their diet, with slight seasonal variation (Laurie, 1978). A similar grass-dominant diet pattern has been confirmed by subsequent studies across multiple protected areas. When preferred grass sources become scarce, GoH rhinos display dietary flexibility, browsing on woody plants and feeding on aquatic vegetation (Hazarika & Saikia, 2012; Konwar et al., 2009; Steinheim et al., 2005). Since food availability varies with the season, GoH rhinos exhibit seasonal changes in habitat use, feeding behaviour and movement. The spatial use might also be influenced by environmental and anthropogenic factors such as distance to human settlements and waterbodies (Borkowski et al., 2019).

As a large-bodied hind-gut fermenter, their digestive physiology can be closely modelled by that of domestic horses. While their large bodies impose certain digestive limitations, GoH rhinos compensate by increasing their gastrointestinal retention time to extract the nutrients

efficiently (Clauss et al., 2005). A study on the nutritional dimension of the GoH rhino foraging strategy revealed a preference for short grasslands with high crude protein and low silica content, leading to seasonal adjustments in habitat use (Banerjee, 2011). This suggests that GoH rhinos are not simply bulk feeders but actively select for high-quality forage. To understand this aspect of habitat use, nutritional analysis of faecal samples emerged as a robust, non-invasive method for assessing the diet quality of herbivores. Studies across diverse species and landscapes have used faecal nutritional parameters such as ash content (mostly silica, reflecting the inorganic part of the diet), crude protein (CP; reflecting dietary protein and essential amino acids), acid detergent fibre (ADF; representing structural fibre of the diet), and acid detergent lignin (ADL) to assess animal diets. Higher ash, ADF, and ADL values indicate lower quality diets, and higher CP values indicate better diet quality. Among these parameters, the ratio of crude protein to lignin (CP: ADL) acts as the strongest indicator of diet quality, as it represents crude protein gained relative to lignin, which hinders the digestion of other structural carbohydrates (Green M. J. B, 1985; Manjrekar, 1998). All these studies demonstrate the complex interplay between seasonal resource availability and the shaping of the GoH rhino habitat use and nutrition.

1.4 Studies on competition interactions of GoH rhinos

Along with seasonal fluctuations, competitive interactions can also drive spatial ecology. Competition can manifest as intraspecific (within species) or interspecific (between species). In intraspecific competition, weaker/subordinate individuals are often displaced from prime foraging areas by dominant bulls, a pattern that intensifies with increasing density (Dutta, 2023; Johnsingh & Manjrekar, 2016). Megaherbivores exhibit considerable dietary plasticity in the presence of competition. For example, studies on black rhinoceroses in South Africa have shown dietary flexibility in response to interspecific competition with African elephants, wherein rhinos expanded their diet breadth (Landman et al., 2013). This ecological plasticity

enables rhinoceroses to adapt to short-term resource limitations or competition. However, such conditions over the long term may not only alter habitat use and diet but also degrade body condition, increase competition for limited nutrients, and elevate stress levels, which can influence disease susceptibility and reproductive success by affecting reproductive behaviour and physiology (Kiambi et al., 2020; Suvorov, 2021).

Crucially, in modern landscapes, Interspecific competition is not limited to wild species; it can also be with livestock. Intensive livestock grazing is known to affect habitats by depleting palatable grasses, reducing forage quality, promoting the expansion of unpalatable vegetation, and lowering the carrying capacity for wild herbivores (Dahal et al., 2023; Tian et al., 2025). Long-term livestock grazing alters the abiotic components of ecosystems by modifying soil nutrient availability and increasing soil compaction (Proesmans et al., 2022). These can further shift vegetation structure, primary productivity and hydrology. The response of wild species to competition varies with ecological context. For example, a study on wild ungulates and cattle in Kenya showed that whether they avoid or coexist with cattle also depends on the habitat they occupy (Kinga et al., 2018) Though both tend to concentrate in nutrient-rich grassland patches. In some cases, species may coexist by spatial or temporal partitioning of resources. A study showed high dietary overlap between the GoH rhinos and elephants in the high-resource period, with resource partitioning in the scarce period (Pradhan et al., 2008). However, at higher competition intensity, one species may competitively exclude the other from preferred habitats, leading to spatial displacement, or both species may suffer from reduced nutritional condition and population performance. In summary, for megaherbivores that lack natural apex predators, food and space become the limiting factors for the population

1.5 Research gap

Although numerous studies have examined GoH rhino ecology, diet, and habitat use across their range, site-specific information, particularly regarding competition among rhino populations in India, remains limited. A prime example is the subpopulation of the GoH rhino in the Pobitora Wildlife Sanctuary (hereafter, PWLS). This sanctuary presents a striking paradox; it is one of the most successful but also one of the most fragile rhino habitats in the world. In Pobitora, high densities of both GoH rhinos and livestock indicate they may be competing for scarce resources. Existing studies have documented general patterns of seasonal habitat use and dietary composition (Deka & Sarma, 2015; Konwar et al., 2009), but the spatial distribution of GoH rhinos within PWLS, or how much they overlap with other species, has not been formally quantified or analysed. It is also unknown whether, given the sanctuary's small area and habitat structure, GoH rhinos still exhibit meaningful habitat preferences during the winter season, or whether they are forced to use all available areas non-selectively under the pressure of high density and competition from livestock. From a nutritional perspective, no study has systematically compared the diet quality of GoH rhinos with that of cattle in PWLS, nor has it examined how habitat selection during winter influences nutritional condition. Addressing these knowledge gaps is essential for developing evidence-based, site-specific management measures for PWLS.

1.6 Objectives and research questions

The study was limited to the winter season (January - February, 2026) due to time constraints.

The primary objective was to assess spatial distribution patterns and key factors shaping the distribution of the GoH rhino (hereafter rhino). Specific research questions included:

- What is the spatial distribution pattern of major herbivores within the study area?
- What is the spatial overlap between rhino and other sympatric herbivores and livestock?

- What are the main drivers of rhino spatial distribution?
- Given the competitive pressures, do species still exhibit habitat preferences?

The secondary objective was to assess the nutritional status of rhinos. Specific research questions included:

- How does the rhino diet quality differ from that of cattle?
- Does habitat selection influence the nutritional condition of rhinos within PWLS?

1.7 Hypotheses and predictions

Hypothesis 1:

Based on the literature and prior knowledge of the species, rhinos will primarily prefer grassland habitats and avoid woodland during the winter season, and are likely to show a clustered distribution concentrated in grassland habitats. However, an alternative scenario could be a preference for short grassland driven by nutritional quality or due to competition with livestock; rhinos might be pushed into low-quality forage patches.

Hypothesis 2:

Wild ungulates and livestock often share similar resources; this might result in high overlap in their spatial distribution. Given the prior knowledge of the species, rhino distribution is likely to be positively influenced by proximity to forage and water sources availability, but negatively affected by livestock numbers and proximity to human settlements.

Hypothesis 3:

Rhino and cattle will occupy distinct nutritional spaces, reflecting species-specific dietary adaptation and digestive physiology. Under the present conditions of intra- and interspecific competition within the sanctuary, the ratio of crude protein to acid detergent lignin (CP: ADL) will be lower in rhinos compared to cattle.

2 Study Area

2.1 Location and extent

Pobitora Wildlife Sanctuary (PWLS) is located in Morigaon District, Assam, on the southern floodplains of the Brahmaputra River. It covers approximately 38.81 km², lying from 26°12′N to 26°15′N and 91°59′E to 92°05′E. The sanctuary is divided into three parts:

- The eastern part (15.85 km²) comprises the sanctuary's core protected zone.
- The central part (11 km²) consists mainly of government khas land.
- The western part (12 km²) corresponds to the Raja Mayong Reserve Forest.

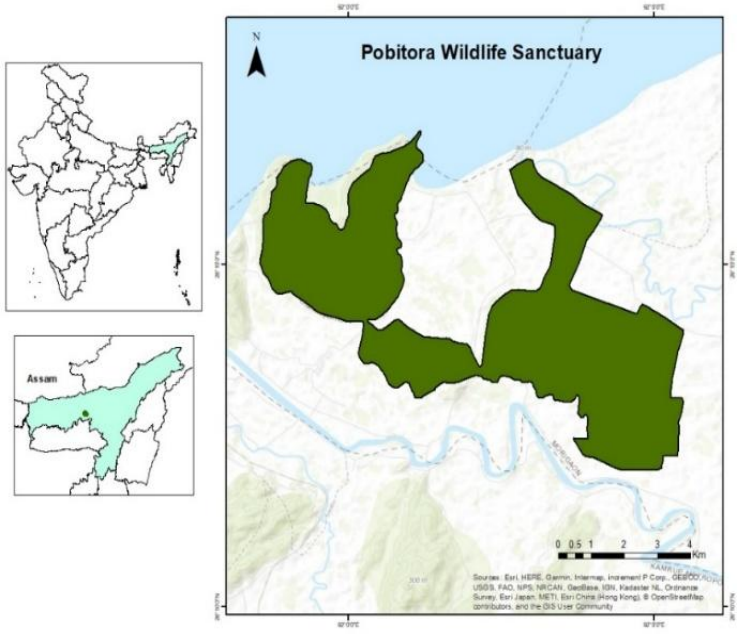

Figure 1 Map depicting the location of Pobitora Wildlife Sanctuary (PWLS)

2.2 Habitat and Wildlife

Topographically, the area is predominantly flat, with a gradual east-to-west slope except around the Burh Mayong Hillock (Choudhury, 2005). The eastern part of PWLS represents a dynamic landscape of natural floodplain ecosystems interspersed with human-modified grasslands and surrounded by dense human settlements on all sides. The central part is majorly agriculture

fields. In contrast, the western part is characterised by hilly terrain. The study was confined to the core protected zone (the eastern part) of the sanctuary, which was confirmed to be the primary area used by rhinos during the daytime. The focused study area, covering approximately 15.8 km², was characterised into six habitat types using the Google Earth Engine platform, with training locations collected in the field.

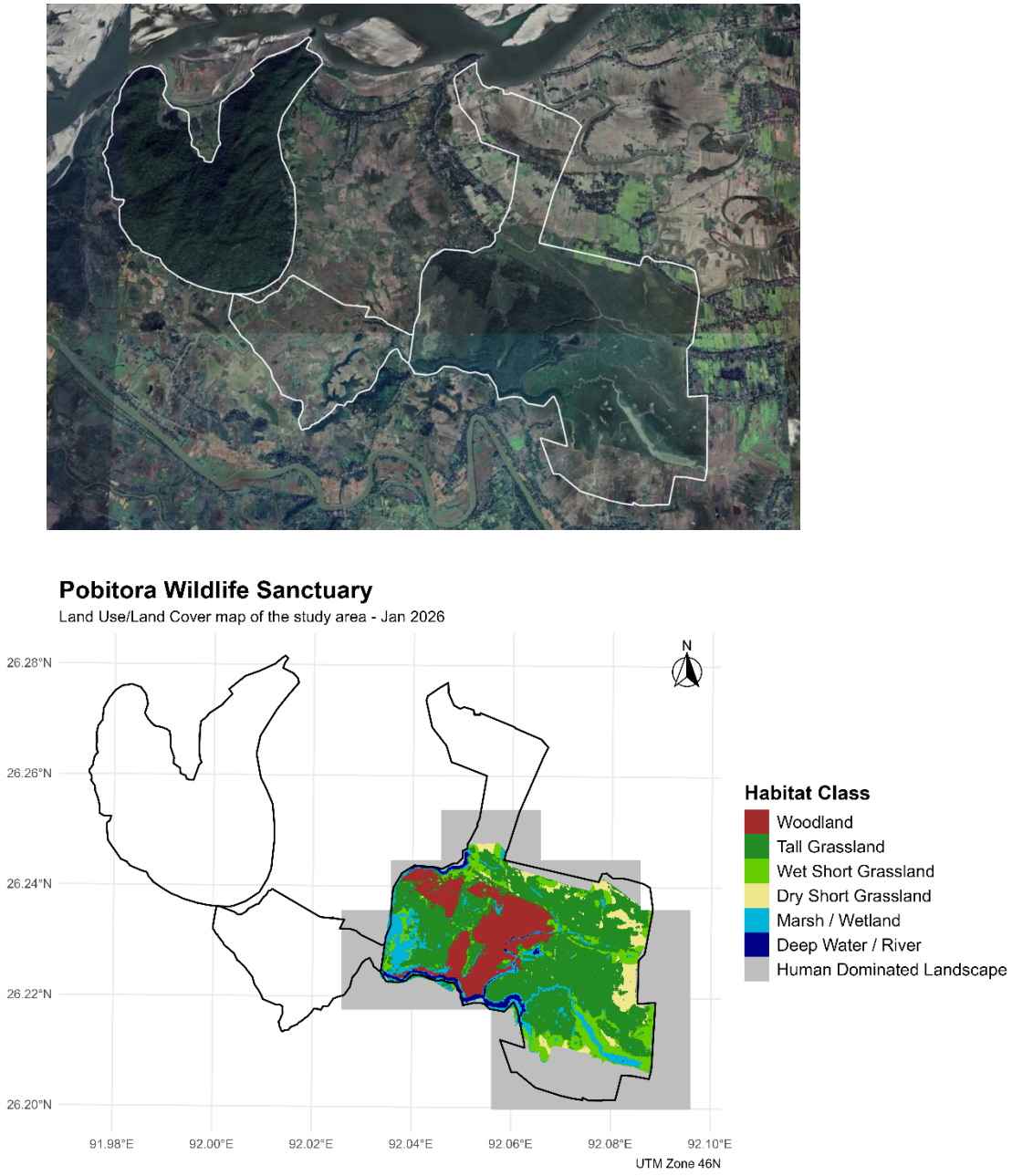

Figure 2 Land-use/land cover (LULC) map of the study area (Satellite imagery of the sanctuary – top, LULC of the focused study area - bottom)

Habitat type	Area cover (km²)	percentage
Tall grassland	7.97	50.5%
woodland	2.83	18%
Wet short grassland	2.06	13.1%
Dry short grassland	0.93	5.9%
Marsh/Wetland	1.6	10.1%
Deeper water bodies/ River	0.38	2.4%

Table 1 Habitat types in PWLS, with area (sq. km) and percentage cover

Major wildlife in the sanctuary is typically concentrated in the plains. However, the western hilly terrain may serve as an important refuge during severe floods. Wetland and marshy habitats, together with the microclimate, create suitable conditions for birds. The sanctuary supports a rich avifauna, including both resident and migratory species. The mosaic of grassland and woodland further enhances bird diversity, attracting naturalists and tourists during the winter months. The sanctuary contains a high density of rhinos and a population of water buffalo. In addition, wild pigs, the fishing cat, and the jungle cat inhabit the area. A variety of reptiles, fish, insects, and butterflies further contribute to the area's biodiversity.

2.3 History of PWLS and Rhino

Despite its modest size, the sanctuary supports approximately 107 rhinos, concentrated mainly within a core rhino-bearing area of about 16 km², giving a density of 6 to 7 individuals per km² - the highest of any rhino habitat globally (Talukdar et al., 2025). This extraordinary density is a direct outcome of decades of effective anti-poaching enforcement, yet this very success has created new ecological and management challenges that require scientific attention. The sanctuary is surrounded by dense human settlements, agricultural lands, and livestock-

dependent communities. Over 3,000 livestock (cattle and buffalo) enter and graze within the sanctuary daily (MICRO-PLAN, 2016), creating intense competition for the grassland resources used by both rhinos and cattle. These conditions make PWLS an ideal natural laboratory for examining patterns of resource use and potential competitive interactions between rhinos and livestock.

PWLS records the lowest annual rhino population growth rate in India at just 1.5%, compared to 7.7% at Jaldapara National Park, West Bengal (Sharma, 2022; Suvorov, 2021). This reduced demographic performance might result from the combined pressures of extreme rhino density and chronic livestock encroachment. Resource shortages force an estimated 20 - 30 rhinos to leave the sanctuary each winter (Talukdar et al., 2007). Rhino-human conflicts are also reported in the surrounding agricultural matrix, with crop depredation most frequent near sanctuary borders and during paddy cultivation seasons (MICRO-PLAN, 2016). These patterns indicate that PWLS's carrying capacity is under severe stress, with both intraspecific competition at high rhino densities and interspecific competition with livestock likely acting as primary limiting factors. However, the actual magnitude and ecological consequences of this competition remain poorly understood. Against this background, the present study aims to examine the spatial distribution patterns and degree of habitat overlap between rhinos and other ungulates, particularly livestock and to assess the consequences of this overlap for rhino nutritional status within PWLS.

3 Methods

3.1 Field methods

The focused study area was divided into 1 × 1 km grid cells, considering their small home ranges in high-density areas (Laurie, 1978). The initial days of fieldwork were used to understand the landscape and finalise survey routes and optimal survey times.

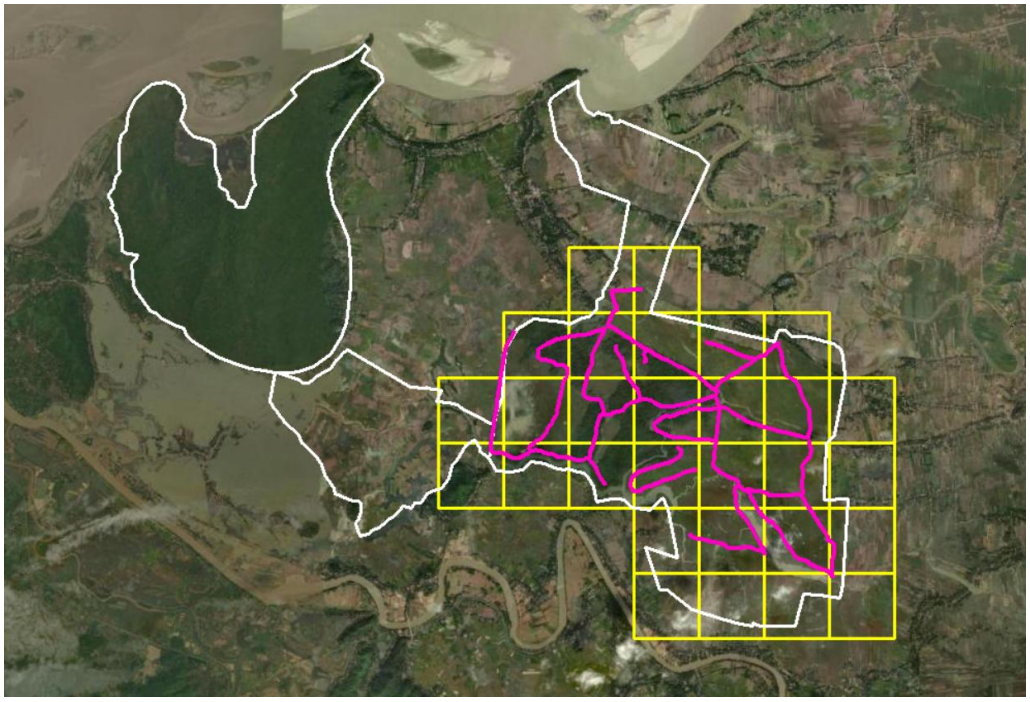

Figure 3 Grids and survey routes within the study area (white - sanctuary boundary, Yellow - grids, pink - survey routes)

Animal surveys: Systematic surveys were conducted along all available routes in two daily time blocks: morning (08:30–10:00) and afternoon (13:30–15:00), with three replicate surveys. Observations were made from vehicles (Gypsy) or from elephant-back to maximise detectability (MacKenzie et al., 2017). Target species were rhino, cattle, and buffalo (including wild water buffalo, domestic buffalo, feral buffalo, and potential hybrids to avoid misrepresentation); opportunistic records of other species were also collected. At each animal sighting, the observer's GPS location, bearing, and distance to the animal; the number of

individuals; the animal's activity (grazing, resting, moving, fighting, wallowing), and the habitat type were recorded.

Vegetation surveys: Vegetation sampling was conducted at randomly generated points, stratified by the proportional area of each habitat type within each grid. Five nested plots were sampled per grid to characterise the habitat: 10 × 10 m quadrats for trees, 5 × 5 m quadrats for shrubs and 2 × 2 m quadrats for herbs and grasses (Higgins et al., 1996; Krebs, 1999). At each plot, data collected were: Species composition with abundance (number of individuals for trees, shrubs and herbs; percentage cover for grasses) estimated ocularly; Species phenology as categories like presence of old inflorescence, flowering, presence of fruits, presence of fresh shoots and mostly dry (Banerjee, 2001); Forage volume was calculated for grasses and forbs/herbs as the quadrat area occupied (percentage cover) multiplied by mean species height.

Samples collected: Plant specimens were collected for laboratory identification and further analysis. Dung samples of both cattle and rhinos were collected across the sanctuary, sampling all study-area grids (cattle n = 56; rhino n = 67). Fresh dung samples were preferentially collected during the last week of fieldwork to minimise contamination and fungal growth before laboratory analysis.

3.2 Laboratory methods

Dung samples were oven-dried at 55°C for 24-48 hours to remove moisture. Dried samples were ground using a grinder and sieved to homogenise particle size. The resulting powder was stored in airtight containers until analysis. The same processing methods were applied to plant specimens collected.

Ash content:

- A sample of known weight (0.5 g) was placed in a pre-weighed silica crucible.
- The crucible with the sample was combusted in a muffle furnace at 550°C for 4 hours.

- The residue remaining after combustion was recorded as ash (Manjrekar, 1998).

Crude protein (%):

- A sample of known weight (1 g) was taken in kjeltec tube with approximately 10 ml concentrated sulphuric acid and a catalyst (potassium sulphate and copper sulphate, 10:1 by mass).
- Samples were digested at 360°C for 3-4 hours with a blank (tube without sample) in each batch.
- The digested samples were analysed using a fully automated nitrogen analyser (Kjeltec^{TM} 8400) standardised with ammonium sulphate; it integrates distillation, colourimetric titration, and calculation of nitrogen percentage from ammonia by the Kjeldahl method.
- Crude protein was calculated from the measured nitrogen using the factor 6.25 (Green M. J. B, 1985).

Acid detergent fibre (ADF):

- A sample of known weight (0.5 g) was refluxed (slow boiled) for 1 hour in Acid detergent solution (prepared by dissolving 20 g of Cetyl tri-methyl ammonium bromide (CTAB) in 1 N sulphuric acid) in a spoutless beaker with a manually managed condensation setup.
- The refluxed sample was filtered through a pre-weighed sintered-glass crucible and washed with hot water, followed by acetone (3 to 5 rinses) under low vacuum.
- Samples were then oven-dried at 100°C overnight.
- The dried residue was recorded as acid detergent fibre.

Acid detergent lignin (ADL):

- The ADF residue was further treated with 72% sulphuric acid for 3 hours, then washed with hot water under low vacuum.
- Samples were then oven-dried at 100°C overnight.
- The dried residue was combusted in a muffle furnace at 500°C for 4 hours.
- The weight loss from the dried residue upon combustion is recorded as ADL (Goering & Soest, 1970).

Ratios of crude protein to ADF and to ADL, as well as the ADF:ADL ratio, were calculated and used, along with the above parameters, as indicators of diet quality.

3.3 Analytical methods

3.3.1 Spatial distribution and overlap

Animal locations were obtained from observer positions using recorded bearing and distance. Kernel density estimation (KDE) is widely used to estimate animal space use and identify high-use "hotspots" or aggregations from point data. To characterise spatial use, a KDE of a utilisation distribution (UD) was fitted separately for each species and time period. Standard (unweighted) KDE would under-represent areas where large herds were recorded and over-represent areas with small groups or solitary animals (Fieberg, 2007). Since animals were frequently observed in herds of varying sizes, an abundance-weighted KDE was used. KDE was implemented separately for each species and time period using their respective bandwidths. The resulting 95% and 50% isopleths (UD95, UD50), which are analogous to overall and core use areas, were clipped to the study area to calculate utilisation areas.

Spatial overlap between species was quantified using the Utilisation Distribution Overlap Index (UDOI) and Bhattacharyya's Affinity (BA), derived from abundance-weighted kernel density estimates (Fieberg & Kochanny, 2005). BA ranges from 0 to 1, where values closer to 0 indicate no overlap and closer to 1 indicate high overlap. Meanwhile, UDOI can go beyond

1 as it emphasises the shared intensity of use, rather than just the shared area. UDOI values close to 0 indicate no overlap, closer to 1 indicate overlap, and more than 1 indicate overlap in high-use (core) areas. Having both indices allows comparison not just of the area but also of the shape and position of the distributions. All analyses were performed in the RStudio environment using the adehabitatHR package with appropriate functions such as kernelUD and kerneloverlaphr (Calenge, 2011). As all species were surveyed simultaneously along identical routes, detection biases are shared across species, making relative distributional comparisons valid without effort correction.

3.3.2 Drivers of rhino spatial distribution

Rhino counts from six replicates per grid across 19 grids were analysed to assess habitat use at a 1 x 1 km scale. Because the counts exhibited overdispersion (variance >> mean), a Generalised Linear Mixed Model (GLMM) (Mauguière, 2022) with negative binomial distribution was used. Grid ID was included as a random effect to account for the replicate structure. Sampling effort was controlled by including the natural log of survey length as an offset, ensuring the model estimated encounter rate (rhinos per km) rather than raw counts. Predictor variables included proportion of each habitat type per grid, forage volume (derived from vegetation sampling), grid area (to account for unequal boundary grid sizes), and counts of cattle and buffalo within each grid at each replicate. Grids were also categorised by their level of continuity with the human-dominated landscape – low (no continuity), medium (partial connectivity with impediments such as elevated roads or fences) or high (direct continuity) – with higher continuity indicating greater facilitation of movement for both animals and people. All numerical predictors were standardised (z-scaled) to allow direct comparison of effect sizes. Correlations among predictors were checked, and forage volume was removed because it correlated strongly with the proportion of tall grassland in a grid ($r = 0.79$). The full model was validated using simulated residuals with the DHARMa package in R to ensure that model

assumptions were not violated. Spatial autocorrelation was ruled out with Moran's I test (Getis, 2010). All ecologically meaningful additive and interactive models incorporating habitat and competition factors were inspected. Model selection was done by ranking all sub-models according to Akaike Information Criterion (AIC & AICc).

3.3.3 Habitat selection

At a finer scale, Habitat use by each species (Rhino, cattle, and buffalo) was evaluated using a point-based approach with a use-availability framework. Habitat availability was defined as the proportional coverage of each LULC class across the study area during January 2026 *(Figure 2)*. For each species and time block, the number of animals recorded in each habitat was summed across all sightings to produce abundance-weighted use frequencies. This accounts for variation in group size and provides a population-level measure of habitat use. The selection ratios for each habitat were calculated as the proportion used divided by the proportion available, following Savage (1931) (Manly et al., 2002). Ratios above 1 indicate high use (selection), while ratios below 1 indicate that use is disproportionate to availability. Selection ratios were calculated for the overall dataset and separately for morning and noon observation periods to assess temporal shift in habitat use.

To model habitat selection formally and assess the effect of competition for rhinos at finer scale, binomial generalised linear models (GLMs) were fitted (Boyce et al., 2002). For each rhino-used location (n = 252) recorded during surveys, four random points were generated within the study area. Predictor variables included habitat type, time of day, and cattle count within 300m buffers around each location. Ecologically meaningful additive and interactive models were compared using AIC.

3.3.4 Activity pattern

The activity pattern of rhinos was analysed using activity data recorded during surveys, and the number of animals performing each activity was summarised by time block and habitat. Activity composition within each time block was calculated as the number of animals in each activity divided by the total number of animals recorded in that time block (for example, Number of animals grazing in the morning / Total number of animals sighted in the morning). Temporal distribution of each activity was calculated as the number of animals performing that activity within each time block divided by the total number of animals recorded performing that activity (for example, Number of animals grazing in the morning / Total number of animals recorded as grazing). The same two-way approach was applied to habitat type: activity composition (for example, Number of animals grazing in tall grassland / Total number of animals sighted in tall grassland) and habitat distribution (for example, Number of animals grazing in tall grassland / Total number of animals recorded as grazing). Combined with habitat selection data, these will describe not only where and when the species occurred but also what it was doing in each habitat and at each time of day, and how each activity was distributed across habitats and time blocks.

3.3.5 Nutritional differences

Dung samples were processed and analysed for Ash%, CP%, ADF%, and ADL%, and the derived ratio indices (CP:ADF, CP:ADL, and ADF:ADL) were summarised by species using descriptive statistics (mean ± SD, median, range) to assess nutritional differences. Distributional assumptions for parametric tests were examined with the Shapiro-Wilk test for normality and Levene's test for homogeneity of variances. Because one or more parameters violated these assumptions, parameters were tested using the nonparametric Mann–Whitney U (Wilcoxon rank-sum) test with effect sizes reported as Cliff's delta. It is an approach previously

applied to species-level comparisons of faecal/dung parameters under non-normality (Otte et al., 2025). To account for comparisons across the parameters, p-values were adjusted using Bonferroni and Benjamini-Hochberg corrections. Nutritional parameters were also analysed using Generalised Linear Mixed Models (GLMMs), with Grid ID included as a random effect to account for the structure of sample collection. Residual normality and homogeneity were inspected to validate the models.

To examine multivariate differences in dung chemistry between rhino and cattle, pairwise correlations among variables were inspected and strongly intercorrelated variables (including ADL and the ratio indices) were removed. The three retained variables (Ash%, CP% and ADF%) were standardised to z-scores, and a Euclidean distance matrix was computed. Differences in overall dung chemical composition between species were tested using PERMANOVA with the adonis2 function in the R package vegan (Anderson, 2006). Because significant PERMANOVA results can arise from differences in group centroids, within-group dispersion, or both, homogeneity of dispersion was assessed using betadisper function, followed by ANOVA and a permutation test (Bergo et al., 2022). Principal Coordinates Analysis (PCoA) was performed on the distance matrix of standardised dung-chemistry variables to visualise differences in chemical composition among species.

3.3.6 Influence of habitat selection on rhino nutrition

Nutritional consequences of habitat selection for rhinos were evaluated by relating grid-level metrics to faecal nutritional parameters. Dung samples of rhinos (n=67) were categorised by collection location. Quality Score for each grid was derived from the top-performing driver distribution model by predicting response. Mixed effect models (LMMs & GLMMs) were fitted depending on the response variable (Bates et al., 2015), with Grid ID included as a random effect to account for multiple samples collected within the same grid.

4 Results

4.1 Spatial distribution and overlap

A total of 332 GPS animal points for rhino, 15,223 for cattle, and 959 for buffalo were used in the analysis. Bandwidth values were 416.1 m (rhino), 291.2 m (cattle), and 491.4 m (buffalo). Utilisation areas were broadly similar across the three herbivore species (13 – 13.9 sq.km). Morning and noon Utilisation distributions (UDs) *(Table 2)* were also comparable within each species, with only modest shifts in core areas. Visual inspection of the density surfaces *(Figure 5,6 & 7)* revealed that rhino and buffalo core hotspots were concentrated around marshy and grassland mosaic areas within the study site. In contrast, cattle hotspots were concentrated along the study area boundary, particularly near accessible points from villages.

	UD95 (km^2) **Overall use area**	**UD50 (km^2)** **Core use area**
Rhino	13.07	3.60
Cattle	13.43	3.39
Buffalo	13.92	3.71
Rhino Morning	13.85	4.47
Rhino Noon	12.99	3.42
Cattle Morning	14.17	4.24
Cattle Noon	12.46	2.70
Buffalo Morning	14.72	4.94
Buffalo Noon	12.74	3.31

Table 2 Utilisation distribution areas estimated from abundance-weighted kernel density analysis

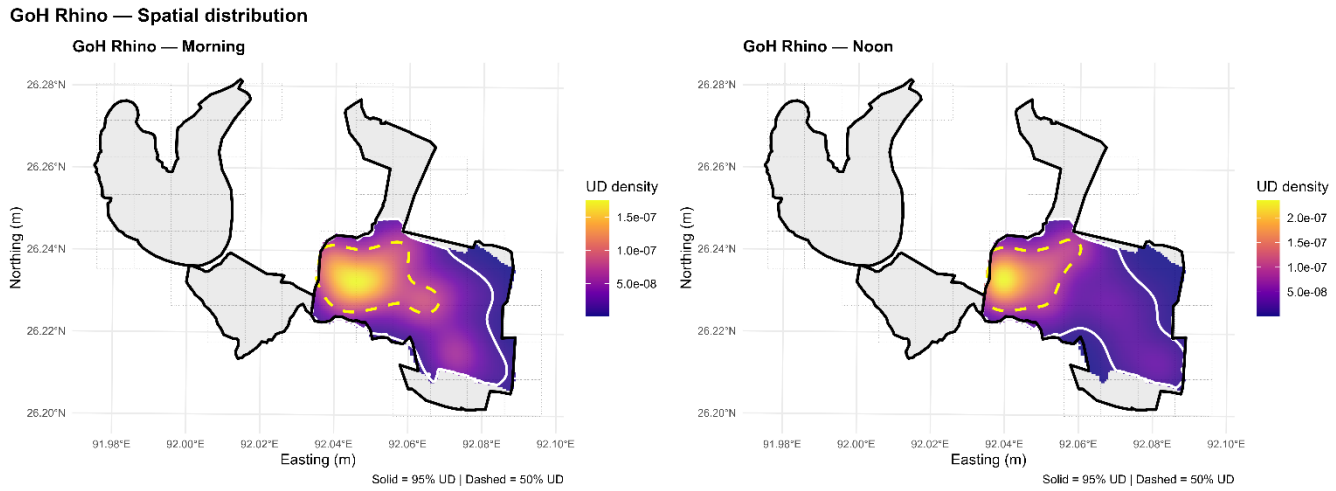

Figure 4 Spatial distribution of rhinos by time block, morning (left) and noon (right)

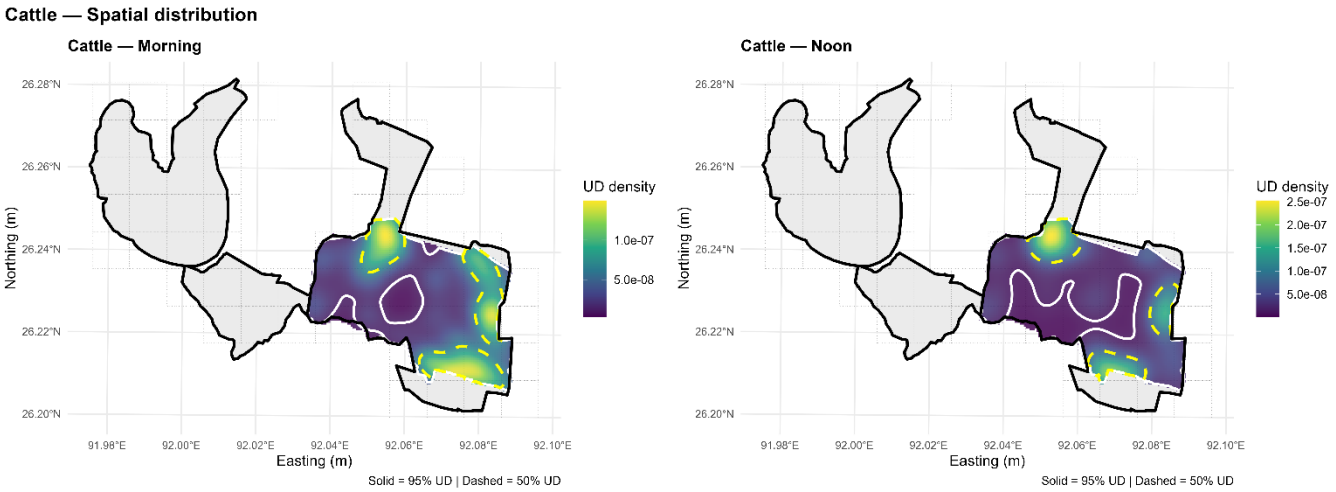

Figure 5 Spatial distribution of cattle by time block, morning (left) and noon (right)

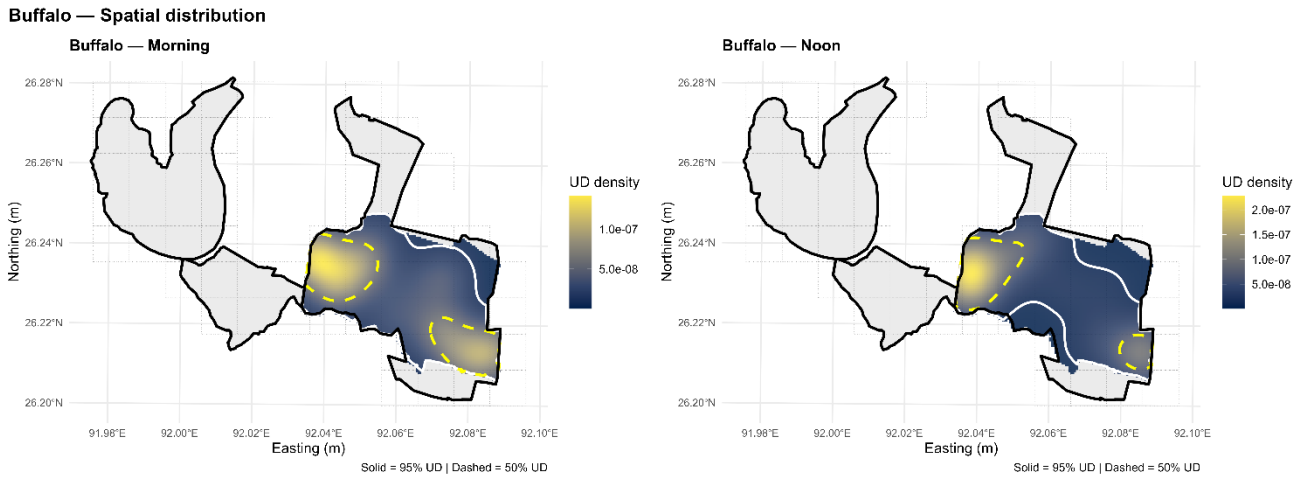

Figure 6 Spatial distribution of buffalo by time block, morning (left) and noon (right)

Overlap indices	UDOI	BA
Rhino vs Cattle	0.44	0.73
Rhino vs Buffalo	1.15	0.93
Cattle vs Buffalo	0.54	0.77
Rhino: Morning vs Noon	1.27	0.97
Cattle: Morning vs Noon	1.20	0.96
Buffalo: Morning vs Noon	1.21	0.95
Rhino Morn vs Cattle Morn	0.51	0.77
Rhino Morn vs Buffalo Morn	0.99	0.92
Cattle Morn vs Buffalo Morn	0.65	0.83
Rhino Noon vs Cattle Noon	0.41	0.69
Rhino Noon vs Buffalo Noon	1.26	0.93
Cattle Noon vs Buffalo Noon	0.46	0.72

Table 3 Overlap indices for species-time block combinations

(UDOI – Utilisation Distribution Overlap Index, BA – Bhattacharyya's Affinity)

Overlap metrics *(Table 3)* revealed high spatial overlap between rhino and buffalo (UDOI = 1.1503, BA = 0.9296), lower overlap between rhino and cattle (UDOI = 0.4442, BA = 0.73), and lower overlap between cattle and buffalo (UDOI = 0.541, BA = 0.7708). These patterns align with the visual segregation of cattle toward the edges, rather than in the marsh-centred rhino-buffalo hotspots.

Within-species temporal overlap (morning vs. noon) was consistently high across all three species. Time-specific inter-species overlaps followed similar patterns, with rhino-buffalo overlap remaining strong in both the morning (UDOI = 0.992, BA = 0.9236) and noon (UDOI = 1.2547, BA = 0.9317) periods, with slightly higher core overlap in the noon period, while rhino-cattle overlap was lower in both periods. These results suggest substantial spatial overlap between the rhino and buffalo, with cattle exhibiting more peripheral and boundary-associated space use despite having similar total utilisation areas.

4.2 Drivers of rhino spatial distribution

Models	npar	LogLik	AIC	AICc
rhino ~ cont + dry_short_s + habitat_s + time_block + (1 | Grid_id) + offset(log(effort_km))	8	-198.445	412.8893	414.2607
rhino ~ cont + dry_short_s + habitat_s + (1 | Grid_id) + offset(log(effort_km))	7	-200.361	414.7223	415.7789
rhino ~ dry_short_s + habitat_s + cont * cattle_s + time_block + (1 | Grid_id) + offset(log(effort_km))	11	-197.442	416.8844	419.4726
rhino ~ cont + cattle_s + buffalo_s + grass_s + marsh_s + wet_short_s + dry_short_s + habitat_s + time_block + offset(log(effort_km)) + (1 | Grid_id)	13	-196.16	418.3199	421.9599
rhino ~ dry_short_s + habitat_s + time_block + offset(log(effort_km)) + (1 | Grid_id)	6	-205.378	422.7565	423.5416
rhino ~ dry_short_s + habitat_s + buffalo_s + time_block + (1 | Grid_id) + offset(log(effort_km))	7	-204.579	423.158	424.2146

rhino ~ dry_short_s + habitat_s + (1 | Grid_id) + offset(log(effort_km))	5	-207.275	424.5508	425.1064
rhino ~ dry_short_s + habitat_s * cattle_s + time_block + (1 | Grid_id) + offset(log(effort_km))	8	-203.871	423.7415	425.113
rhino ~ dry_short_s + habitat_s + grass_s + time_block + offset(log(effort_km)) + (1 | Grid_id)	7	-205.144	424.2873	425.3439
rhino ~ dry_short_s + habitat_s + cattle_s + time_block + (1 | Grid_id) + offset(log(effort_km))	7	-205.378	424.7565	425.8131
rhino ~ woodland_s + marsh_s + water_s + dry_short_s + habitat_s + time_block + offset(log(effort_km)) + (1 | Grid_id)	9	-203.06	424.1206	425.8513
rhino ~ woodland_s + marsh_s + wet_short_s + dry_short_s + habitat_s + time_block + offset(log(effort_km)) + (1 | Grid_id)	9	-203.852	425.7044	427.4351
rhino ~ grass_s + marsh_s + wet_short_s + dry_short_s + habitat_s + time_block + offset(log(effort_km)) + (1 | Grid_id)	9	-204.036	426.0718	427.8026
rhino ~ dry_short_s * cattle_s + habitat_s + time_block + (1 | Grid_id) + offset(log(effort_km))	8	-205.375	426.7507	428.1221
rhino ~ buffalo_s + cattle_s + dry_short_s + grass_s + habitat_s + marsh_s + time_block + (1 | Grid_id) + offset(log(effort_km))	10	-203.838	427.6762	429.8121
rhino ~ buffalo_s + cattle_s + dry_short_s + grass_s + habitat_s + marsh_s + time_block + (1 | Grid_id) + offset(log(effort_km))	10	-203.838	427.6762	429.8121
rhino ~ time_block + offset(log(effort_km)) + (1 | Grid_id)	4	-213.124	434.2473	434.6143

Table 4 Comparison of candidate models with the best-fitted model for rhino encounter rate at 1km grid scale, arranged in increasing order of AICc

The top-ranked model *(Table 4)* identified four significant predictors of rhino encounter rates: continuity class, proportion of dry short grassland within a grid, grid area, and time of day. Rhino encounter rates decreased significantly with the proportion of dry short grassland (Estimate = -0.98 ± 0.33 SE, p = 0.003). Meanwhile, encounter rates were higher in larger grids (Estimate = 0.88 ± 0.24 SE, p = 0.001). Time of the day also influenced encounter rate, with significantly higher encounter rates during the noon period (Estimate = 0.36 ± 0.18 SE, p = 0.04) compared to morning, possibly reflecting shifts in habitat use and activity between morning and noon. In addition, continuity had a strong effect: compared with grids categorised as high continuity, encounter rates were higher in medium-continuity grids (Estimate = 1.54 ± 0.45 SE, p = 0.001). Neither cattle nor buffalo appeared in the best model, suggesting they were not the best predictors of rhino distribution in PWLS. In Summary, rhino space use was negatively associated with dry short grassland proportion and positively associated with grid area, medium landscape continuity, and noon observations.

Predictors	**Estimate**	**Std. Error**	**Z value**	**Pr(>|z|)**
Continuity high, Time morning (Intercept)	-0.93	0.33	-2.857	0.004 **
Continuity low	-0.12	0.44	-0.28	0.78
Continuity medium	1.54	0.45	3.40	0.001 ***
Dry short grassland proportion	-0.98	0.33	-2.99	0.003 **
Grid area	0.88	0.24	3.63	0.001 ***
Time - noon	0.36	0.18	1.97	0.04 *

Table 5 Coefficients of the best-fitted model for rhino encounter rate

4.3 Habitat selection

Analysing all candidate point-based models for rhino habitat use revealed that the habitat-only GLM received the strongest support (lowest AIC) *(Table 7)*. Including cattle and time block did not improve model fit, indicating that habitat type is the primary driver of rhino space use even at the finer scale. Competitive effects from cattle or temporal shifts do not independently explain additional variation beyond that explained by habitat.

Rhinos showed strong selection for tall grassland in both time blocks (SR = 1.41 morning, 1.21 noon) *(Table 6)*; tall grassland was the most used habitat overall, accounting for 65.4% of rhino observations. The GLM confirmed significantly greater use of tall grassland compared to dry short grassland ($p = 0.002$) *(Table 8)*. The selection for the marsh/wetland increased from neutral in the morning (SR = 0.97) to strongly positive at noon (SR = 1.59); the marsh/wetland also showed the strongest positive selection of any habitat by rhinos in the noon block, further confirmed by the GLM ($p < 0.001$). Wet short grassland showed moderate use, with selection ratios increasing from lower in the morning (SR = 0.75) to higher at noon (SR = 1.15). The GLM also indicated significant positive selection of wet short grassland relative to dry short grassland ($p = 0.008$). Woodland, dry short grassland, and deeper water bodies were consistently used less than their availability, based on both selection ratio and GLM.

Cattle exhibited the highest selection ratios for dry short grassland among all species–habitat combinations, with selection intensifying at noon (SR = 3.67 morning, 6.64 noon, 5.01 overall) *(Table 6)*. They also showed a strong and consistent preference for wet short grassland. Despite the high availability of tall grassland, cattle used it less (SR = 0.65 overall). Marsh/wetland, deeper water bodies, and woodland were consistently underused by cattle.

Buffalo consistently selected wet short grassland across time blocks, making it their most preferred habitat (SR = 2.44 overall; 2.18 in the morning; 2.69 at noon) *(Table 6)*. They

preferred tall grassland in the morning (SR = 1.24 morning, 0.63 noon) but shifted to strong selection for marsh/wetland at noon (SR = 0.73 morning, 2.80 noon). Woodland, deeper water, and dry short grassland were consistently used less than their availability. The buffalo pattern parallels that of the rhino, suggesting overlapping habitat preferences and shared midday use of marsh/wetland habitats.

Species	Time	Habitat	No.of animals	Used proportion	Available proportion	Selection ratio
Rhino	Morning	Dry short grassland	2	0.02	0.06	0.26
Rhino	Morning	Tall grassland	95	0.71	0.51	1.41
Rhino	Morning	Marsh/ Wetland	13	0.10	0.10	0.96
Rhino	Morning	Deep water/ River	1	0.01	0.02	0.31
Rhino	Morning	Wet short grassland	13	0.10	0.13	0.75
Rhino	Morning	Woodland	9	0.07	0.18	0.38
Rhino	Noon	Dry short grassland	2	0.01	0.06	0.17
Rhino	Noon	Tall grassland	122	0.61	0.51	1.21
Rhino	Noon	Marsh/ Wetland	32	0.16	0.10	1.59
Rhino	Noon	Deep water/ River	0	0.00	0.02	0.00
Rhino	Noon	Wet short grassland	30	0.15	0.13	1.15
Rhino	Noon	Woodland	13	0.07	0.18	0.36
Rhino	Overall	Dry short grassland	4	0.01	0.06	0.20
Rhino	Overall	Tall grassland	217	0.65	0.51	1.29
Rhino	Overall	Marsh/ Wetland	45	0.14	0.10	1.34
Rhino	Overall	Deep water/ River	1	0.00	0.02	0.12
Rhino	Overall	Wet short grassland	43	0.13	0.13	0.99
Rhino	Overall	Woodland	22	0.07	0.18	0.37
Cattle	Morning	Dry short grassland	1674	0.22	0.06	3.67
Cattle	Morning	Tall grassland	3036	0.39	0.51	0.78
Cattle	Morning	Marsh/ Wetland	393	0.05	0.10	0.50
Cattle	Morning	Deep water/ River	42	0.01	0.02	0.22
Cattle	Morning	Wet short grassland	2148	0.28	0.13	2.12
Cattle	Morning	Woodland	457	0.06	0.18	0.33

Cattle	Noon	Dry short grassland	2493	0.39	0.06	6.64
Cattle	Noon	Tall grassland	1588	0.25	0.51	0.49
Cattle	Noon	Marsh/ Wetland	171	0.03	0.10	0.26
Cattle	Noon	Deep water/ River	0	0.00	0.02	0.00
Cattle	Noon	Wet short grassland	2004	0.31	0.13	2.40
Cattle	Noon	Woodland	124	0.02	0.18	0.11
Cattle	Overall	Dry short grassland	4167	0.29	0.06	5.01
Cattle	Overall	Tall grassland	4624	0.33	0.51	0.65
Cattle	Overall	Marsh/ Wetland	564	0.04	0.10	0.39
Cattle	Overall	Deep water/ River	42	0.00	0.02	0.12
Cattle	Overall	Wet short grassland	4152	0.29	0.13	2.24
Cattle	Overall	Woodland	581	0.04	0.18	0.23
Buffalo	Morning	Dry short grassland	0	0.00	0.06	0.00
Buffalo	Morning	Tall grassland	288	0.63	0.51	1.24
Buffalo	Morning	Marsh/ Wetland	34	0.07	0.10	0.73
Buffalo	Morning	Deep water/ River	0	0.00	0.02	0.00
Buffalo	Morning	Wet short grassland	131	0.29	0.13	2.18
Buffalo	Morning	Woodland	6	0.01	0.18	0.07
Buffalo	Noon	Dry short grassland	4	0.01	0.06	0.14
Buffalo	Noon	Tall grassland	159	0.32	0.51	0.63
Buffalo	Noon	Marsh/ Wetland	142	0.28	0.10	2.80
Buffalo	Noon	Deep water/ River	0	0.00	0.02	0.00
Buffalo	Noon	Wet short grassland	176	0.35	0.13	2.69
Buffalo	Noon	Woodland	19	0.04	0.18	0.21
Buffalo	Overall	Dry short grassland	4	0.00	0.06	0.07
Buffalo	Overall	Tall grassland	447	0.47	0.51	0.92
Buffalo	Overall	Marsh/ Wetland	176	0.18	0.10	1.81
Buffalo	Overall	Deep water/ River	0	0.00	0.02	0.00
Buffalo	Overall	Wet short grassland	307	0.32	0.13	2.44
Buffalo	Overall	Woodland	25	0.03	0.18	0.15

Table 6 Selection ratios of species for different habitat types across time blocks

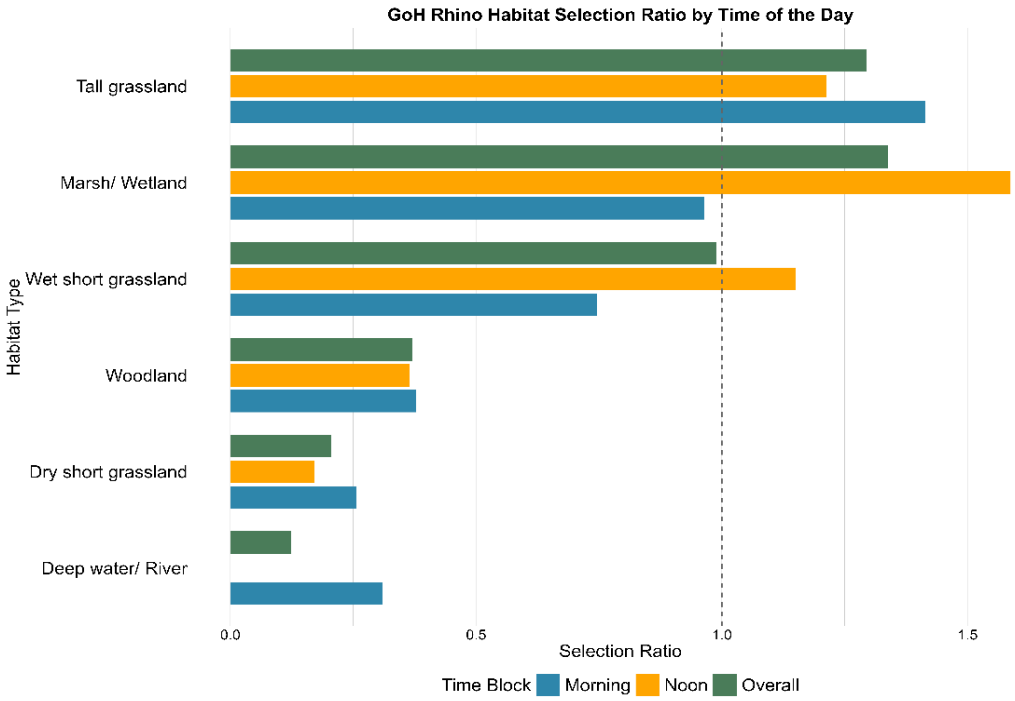

Figure 7 Selection ratios of rhinos for different habitat types by time blocks (selection ratio 1 represented by dashed line)

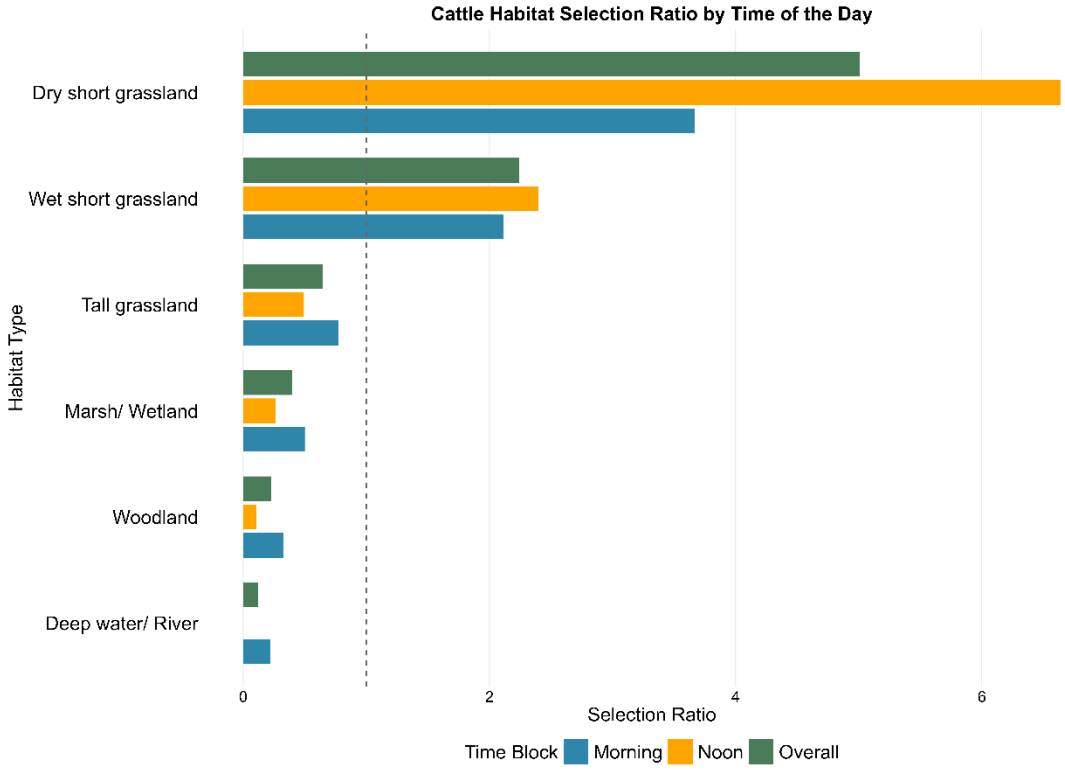

Figure 8 Selection ratio of cattle for different habitat types by time blocks (selection ratio 1 represented by dashed line)

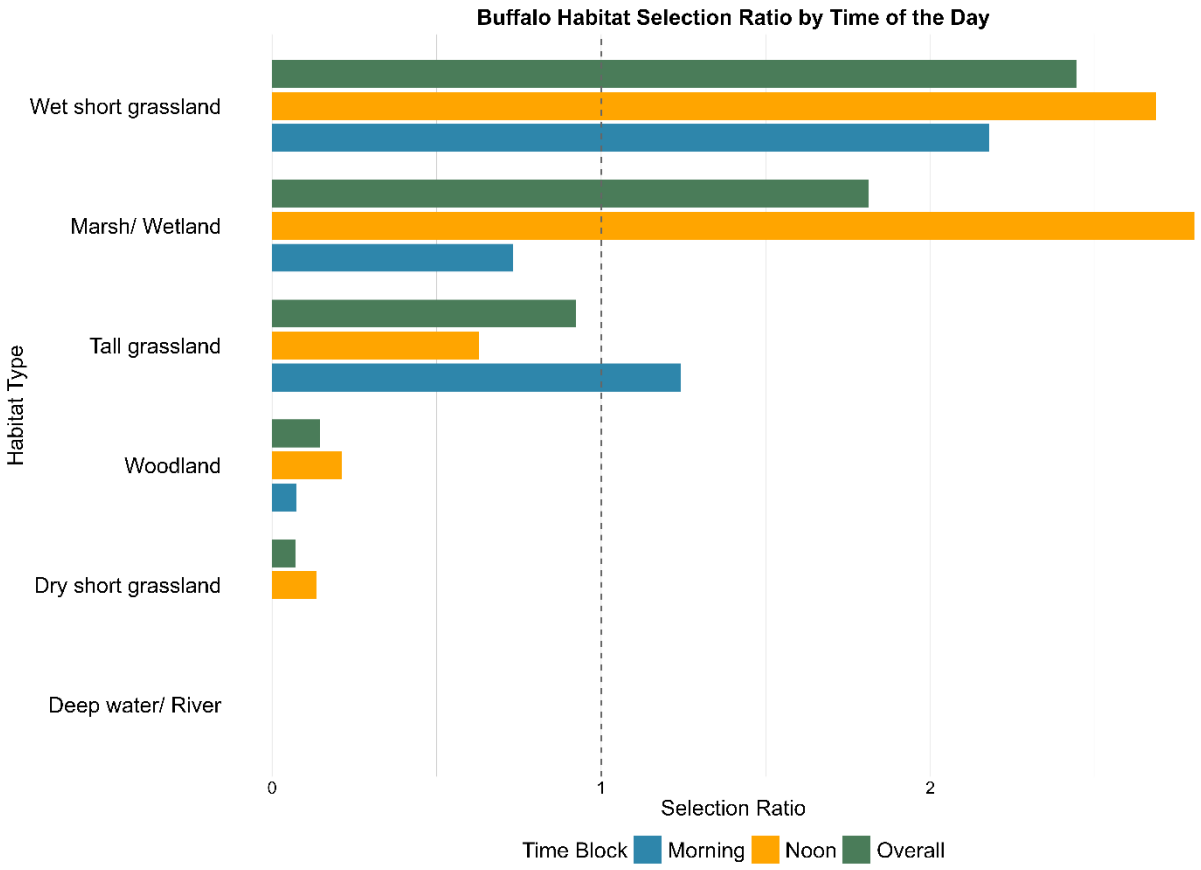

Figure 9 Selection ratio of buffalo for different habitat types by time blocks (selection ratio 1 represented by dashed line)

Models	df	LogLik	AIC	AICc
used ~ habitat	1249	-596.60	1205.21	1205.27
used ~ habitat + c3_cattle	1248	-596.41	1206.81	1206.90
used ~ habitat * c3_cattle	1243	-594.75	1213.51	1213.76
used ~ habitat * c3_cattle + time_block	1242	-594.75	1215.51	1215.80
used ~ habitat + time_block	1248	-596.60	1207.20	1207.29
used ~ habitat + time_block + c3_cattle	1247	-596.41	1208.81	1208.93
used ~ habitat + time_block * c3_cattle	1246	-596.28	1210.56	1210.70
used ~ habitat * time_block	1243	-593.78	1211.55	1211.80
used ~ habitat * time_block + c3_cattle	1242	-593.52	1213.05	1213.34

Table 7 Comparison of candidate models with the best-fitted model for point-based rhino habitat selection, arranged in increasing order of AICc

Predictors	Estimate	Std. Error	Z value	Pr(>|z|)
Dry short grassland (Intercept)	-2.773e+00	5.154e-01	-5.380	7.46e-08 ***
Tall grassland	1.627e+00	5.230e-01	3.111	0.00186 **
Marsh/wetland	2.242e+00	5.644e-01	3.972	7.12e-05 ***
River/deeper water	7.006e-14	1.152e+00	0.000	1.00000
Wet short grassland	1.465e+00	5.515e-01	2.657	0.00789 **
Woodland	1.897e-01	5.735e-01	0.331	0.74081

Table 8 Coefficients of the best-fitting point-based resource selection function for rhino habitat selection

4.4 Activity pattern

Rhino Activity by time block - Grazing dominated in both periods *(Table 9),* increasing from 63% in the morning to 92% at noon, while resting declined from 36% in the morning to 2.7% at noon. Temporal distribution *(Table 10)* showed that 90% of resting records occurred in the morning, whereas 68% of grazing records occurred at noon, indicating a preferential time period for specific activity.

Rhino Activity by habitat - Across habitats, grazing was the primary activity and resting was the main secondary activity, with small habitat-specific differences. Tall grassland accounted for the largest share of all observed activities.

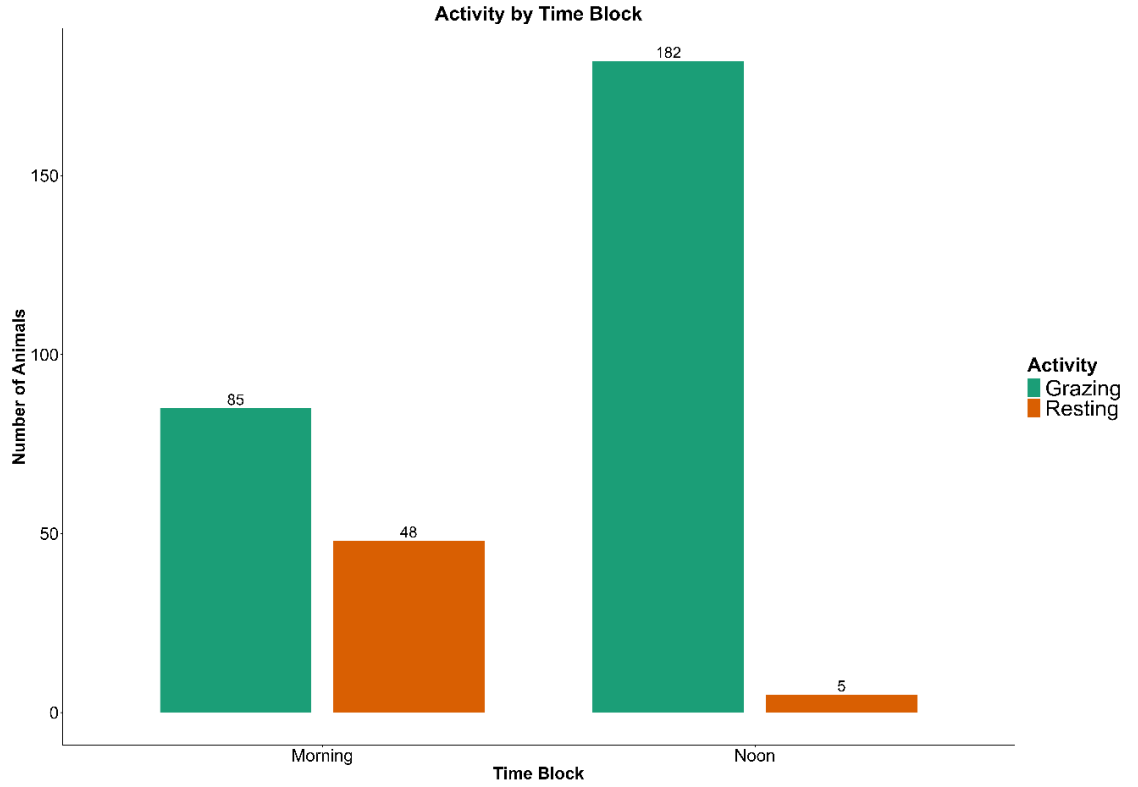

Figure 10 Rhino's major activity composition by time block

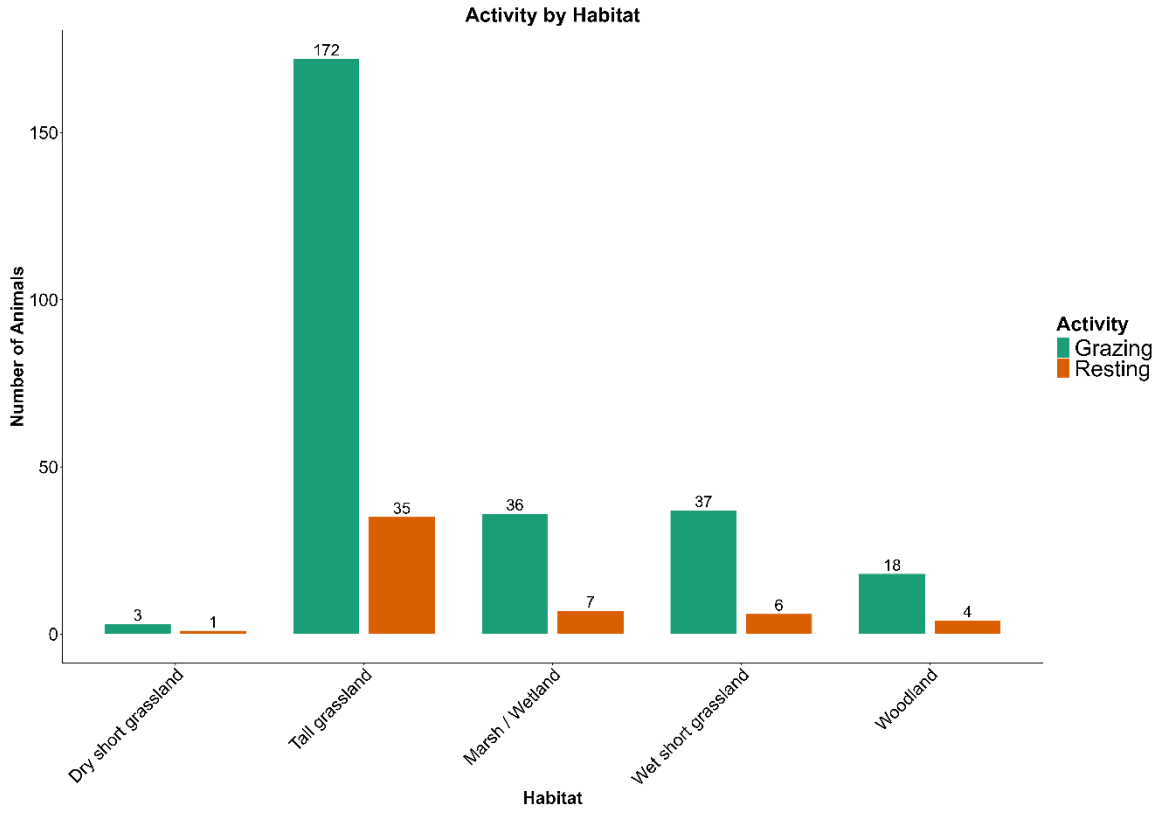

Figure 11 Rhino's major activity composition by habitat type

Activity	No. of animals	Morning (%)	Noon (%)
Fighting	3	0.00	1.51
Grazing	267	63.91	91.46
Moving	3	0.00	1.51
Resting	53	36.09	2.51
Wallowing	6	0.00	3.02

Table 9 Activity-time composition: percentage of each activity within each time block

Activity	No. of animals	Morning (%)	Noon (%)
Fighting	3	0.00	100.00
Grazing	267	31.84	68.16
Moving	3	0.00	100.00
Resting	53	90.57	9.43
Wallowing	6	0.00	100.00

Table 10 Temporal distribution of activities: percentage per activity across time

Activity	No. of animals	Tall grassland	Dry short grassland	Marsh/ Wetland	Deep water/ River	Wet short grassland	Woodland
Fighting	3	1.38	0.00	0.00	0.00	0.00	0.00
Grazing	267	79.26	75.00	80.00	100.00	86.05	81.82
Moving	3	1.38	0.00	0.00	0.00	0.00	0.00
Resting	53	16.13	25.00	15.56	0.00	13.95	18.18
Wallowing	6	1.84	0.00	4.44	0.00	0.00	0.00

Table 11 Activity-habitat composition: percentage of each activity within each habitat type

Activity	No. of animals	Tall grassland	Dry short grassland	Marsh/ Wetland	Deep water/ River	Wet short grassland	Woodland
Fighting	3	100.00	0.00	0.00	0.00	0.00	0.00
Grazing	267	64.42	1.12	13.48	0.37	13.86	6.74
Moving	3	100.00	0.00	0.00	0.00	0.00	0.00
Resting	53	66.04	1.89	13.21	0.00	11.32	7.55
Wallowing	6	66.67	0.00	33.33	0.00	0.00	0.00

Table 12 Habitat-wise distribution of activities: percentage per activity across habitat type

4.5 Nutritional differences

Descriptive statistics showed modest differences between rhino (n = 67) and cattle (n = 56) dung for all parameters and their ratio indices. Rhino and cattle dung differed significantly across almost all parameters *(Table 14)*. Six of the seven parameters remained significant after Bonferroni correction (all p_bonf < 0.05), and all seven were significant under the Benjamini-Hochberg

FDR control. Rhino dung had higher Ash%, CP%, ADF%, and ADL% and higher CP-based ratios (CP: ADF, CP: ADL), with large effect sizes for most of these. The weakest contrast was CP: ADL, which was not significant after Bonferroni correction (p_bonf = 0.176) but remained significant under the FDR adjustment. The mixed-effect models confirmed these findings, even after accounting for grid-level variation.

PERMANOVA on the standardised dung-chemistry variables detected a highly significant multivariate difference between species ($F = 47.894$, $R^2 = 0.284$, $p = 0.001$), with species identity explaining approximately 28.4% of the total multivariate variation and the remaining ~71.6% attributable to within-species variation. Betadisper analysis found no significant difference in within-group dispersion between species, by both ANOVA ($F = 0.731$, $p = 0.394$) and the permutation test ($F = 0.731$, $p = 0.383$). Therefore, the significant PERMANOVA result can be attributed to differences in group centroids (location) rather than to unequal dispersion. Overall, these results indicate that rhino and cattle dung differ markedly in their Ash%, CP% and ADF% composition.

Species	variable	Median	Q1	Q3	Mean	SD
Cattle	Ash %	20.60	17.92	24.00	21.27	5.14
Rhino	Ash %	26.20	23.90	29.50	26.80	3.73
Cattle	CP %	7.46	6.60	8.77	7.95	1.87
Rhino	CP %	10.36	9.45	11.17	10.29	1.30
Cattle	ADF %	50.78	50.00	52.90	51.39	2.69
Rhino	ADF %	54.80	52.40	56.80	54.45	3.14
Cattle	ADL %	14.20	12.20	18.40	15.38	4.83
Rhino	ADL %	18.20	16.00	20.90	18.35	3.31
Cattle	CP:ADL	0.51	0.47	0.59	0.54	0.15
Rhino	CP:ADL	0.55	0.51	0.61	0.57	0.10
Cattle	CP:ADF	0.15	0.13	0.17	0.16	0.03
Rhino	CP:ADF	0.19	0.17	0.20	0.19	0.02
Cattle	ADF:ADL	3.59	2.87	4.15	3.65	1.15
Rhino	ADF:ADL	3.02	2.67	3.38	3.05	0.46

Table 13 Summary of faecal nutritional parameters and derived ratios for rhino and cattle: median, first quartile (Q1), third quartile (Q3), mean and standard deviation(SD)

Parameter	W	p value	Cliffs_d	magnitude	p_bonf	p_BH	significane
Ash %	622	0	-0.668	large	0	0	*
CP %	563.5	0	-0.7	large	0	0	*
ADF %	849	0	-0.547	large	0	0	*
ADL %	1039	0	-0.446	medium	0	0	*
CP:ADF	678	0	-0.639	large	0	0	*
CP:ADL	1395	0.0147	-0.256	small	0.1764	0.0147	*
ADF:ADL	2578	4.00E-04	0.374	medium	0.0048	5.00E-04	*

Table 14 Mann–Whitney U (Wilcoxon rank-sum) test with effect sizes as Cliff's delta (Cliffs_d). p-values adjusted using Bonferroni (p_bonf) and Benjamini-Hochberg corrections (p_BH).

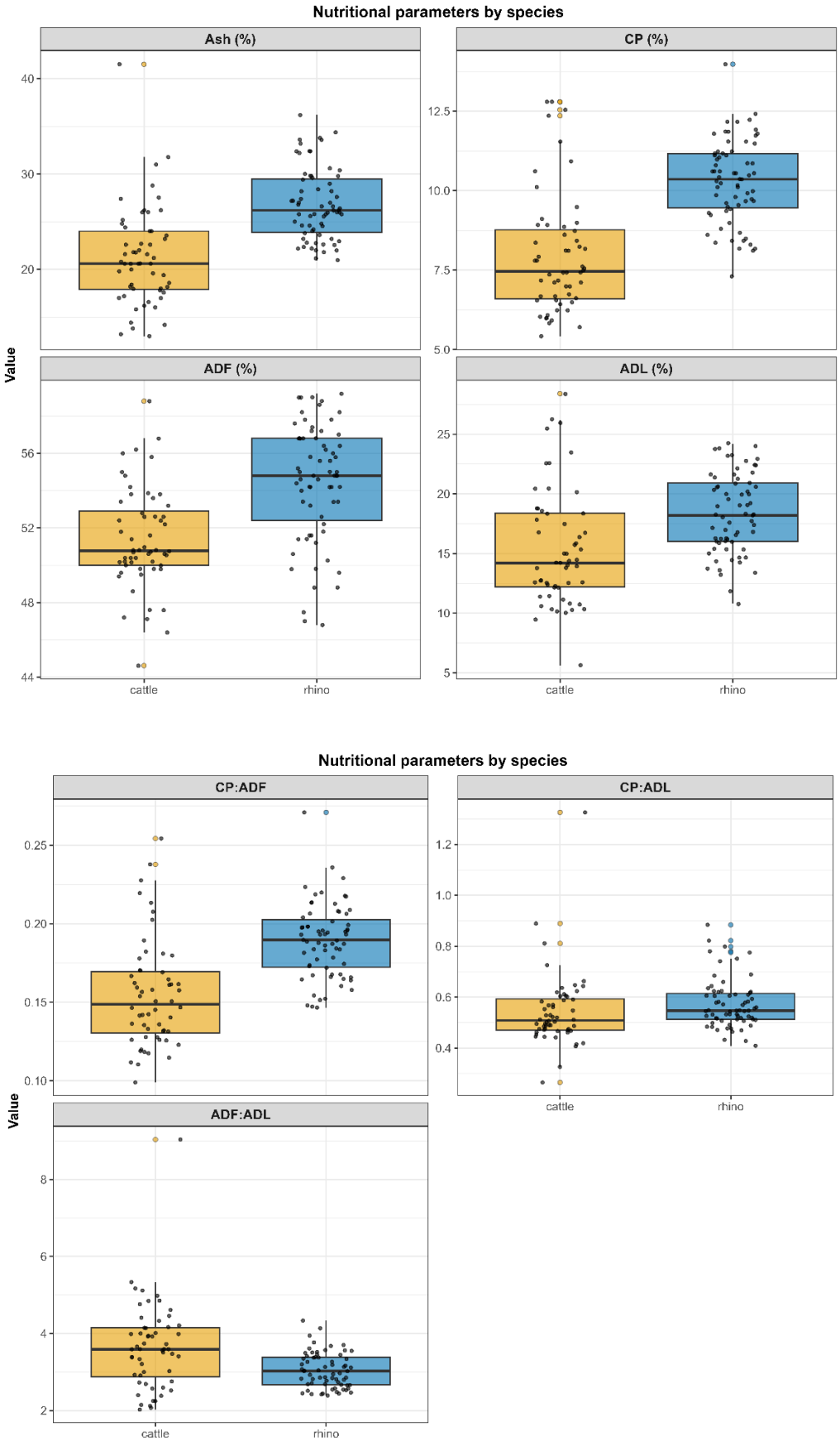

Figure 12 Boxplots of faecal nutritional parameters by species (yellow = cattle, blue = rhino)

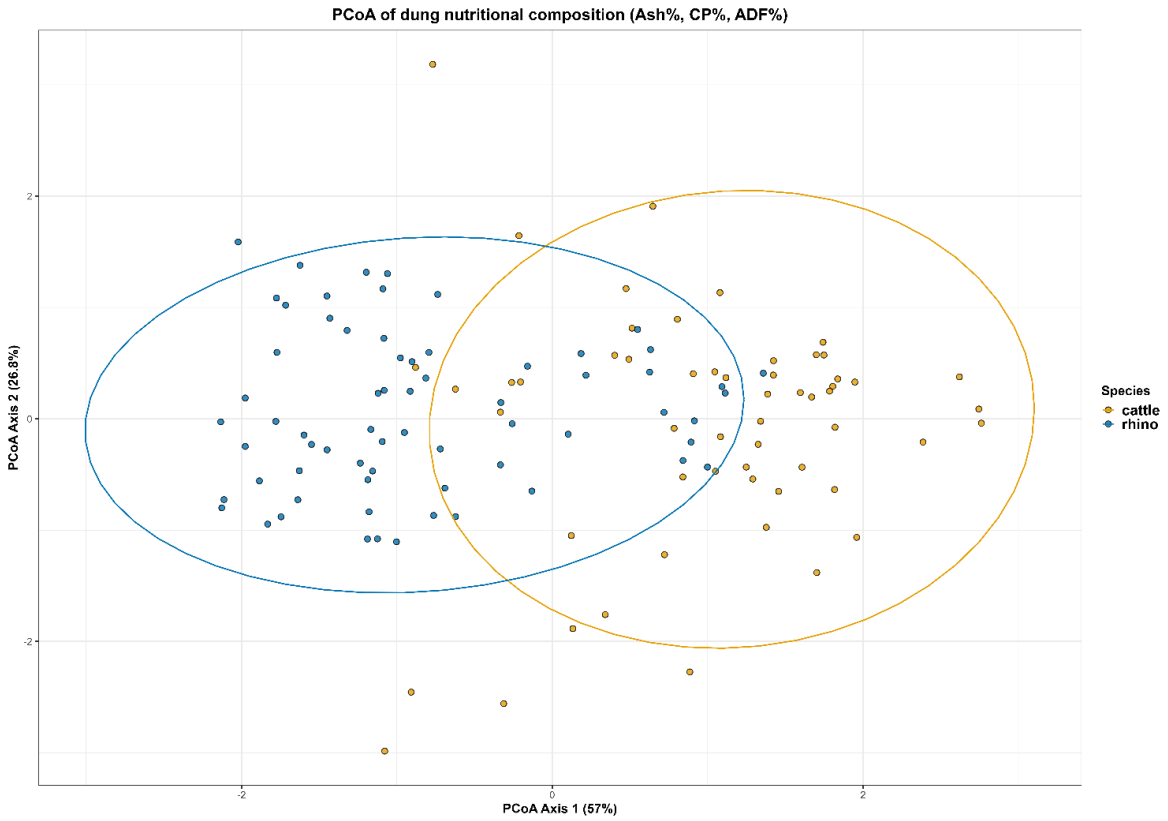

Figure 13 Principal Coordinates Analysis (PCoA) of non-collinear faecal nutritional parameters for rhino and cattle, illustrating differences in dung chemistry

4.6 Influence of habitat selection on rhino nutrition

Parameter	AIC	Estimate	Std.Error	p_value	R^2_m	R^2_c	Significance
Ash %	356.93	0.55	0.21	0.02	0.18	0.381	*
CP %	229.54	0.04	0.09	0.70	0.01	0.372	ns
ADF %	337.21	0.23	0.21	0.28	0.05	0.395	ns
ADL %	348.89	0.15	0.21	0.48	0.02	0.329	ns
CP:ADF	-290.35	0.00	0.00	0.92	0.00	0.348	ns
CP:ADL	-101.27	0.00	0.01	0.44	0.02	0.103	ns
ADF:ADL	91.70	-0.01	0.03	0.64	0.01	0.322	ns

Table 15 Coefficients from models of each nutritional parameter using grid quality score as predictor and Grid ID as random effect; R^2 marginal (R^2_m) – proportion of variance explained by fixed effects, R^2 conditional (R^2_c) – proportion of variance explained along with random effect

Among all faecal nutrient parameters analysed, only ash content varied significantly with the quality score ($p < 0.05$) of the grid *(Table 15)*; all other parameters showed no significant relationship. This indicates that habitat selection primarily influenced faecal ash content, which is irrelevant to diet quality, and had negligible effects on other metrics, especially the diet quality indicator CP: ADL.

4.7 Vegetation structure

Observation and preliminary analysis showed that dominant vegetation varied with habitat type: tall grasslands were mainly composed of *Chrysopogon zizanioides* (locally Birina), *Imperata cylindrica* (Kher) and *Flemingia lineata*; wet short grasslands were dominated by *Cynodon dactylon* (Dubori) with *Hygrophila polysperma*; and dry short grasslands were characterised by *Cynodon dactylon* and *Axonopus compressus*. In woodland habitats, the undergrowth was dominated by *Oplismenus compositus* (Bah phutia) and ferns, notably *Diplazium esculentum* and *Thelypteris* spp. (commonly called dekhiya).

All the species in 2x2 m quadrats were used to calculate forage volume since the actual diet of rhinos is not known in this case. Because forage volume is correlated with plant height, it likewise varied with habitat type and was highest in the tall grasslands *(Figure 15)* compared to all other habitats. In contrast, nutritional analysis of dominant grass species showed that tall grassland had the lowest quality compared to other habitat types *(Table 16)*.

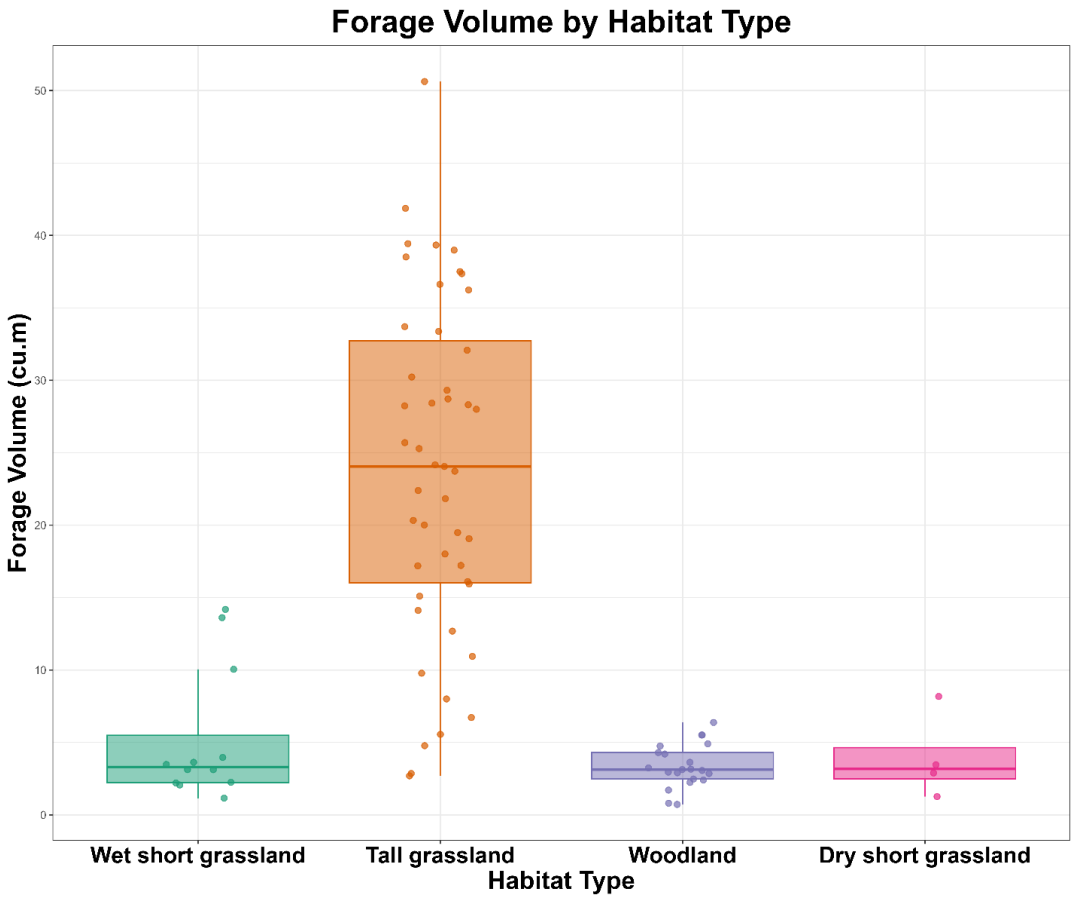

Figure 14 Boxplot of forage volume across habitat types

Plant species	Ash %	OM %	CP %	ADF %	ADL %	CP: ADL
Axonopus compressus	13.8	86.2	12.79	31.6	3.2	3.99
Chrysopogon zizanioides (Birina)	10	90	5.39	48	7.6	0.71
Cynodon dactylon (Dubori)	20	80	10.48	31.6	4.8	2.18
Diplazium esculentum (Dekhiya)	14	86	19.72	41	8.8	2.24
Imperata cylindrica (Kher)	10	90	10.55	48.4	7.6	1.39
Oplismenus compositus (Bah phutia)	19.8	80.2	12.98	36.8	6	2.16

Table 16 Nutritional parameters of dominant plant species

5 Discussion

5.1 Habitat Use and Activity

The spatial distribution maps of rhino, cattle and buffalo in PWLS showed distinct patterns of habitat use. Rhino and buffalo exhibited high spatial overlap with similar hotspots concentrated around marshy habitats, whereas cattle were spatially segregated with hotspots predominantly along the study area boundary near village access points. The western boundary is an elevated road, and the southern boundary is partially bordered by a river/stream, limiting access to livestock from these sides. Hence, the spatial segregation in this context raises the question of whether this pattern resulted from differential habitat preference and use or from interspecific competition. Literature on competition emphasises that niche overlap/segregation is necessary but insufficient to determine competition. For an interaction to be considered competitive, three conditions have to be met: the resource must be shared by species, the resource must be limited, and depletion of the resource should affect one or both species negatively (or affect them in different magnitudes) (Prins, 2000; Young et al., 2005). At the same time, the impact of interaction can be competitive or facilitative; a study in African savannas showed wild ungulates influenced cattle performance differently depending on the season (Odadi et al., 2011). These findings suggest the need for an alternative study framework that can distinguish between spatial segregation and actual competitive exclusion, which requires evidence of shared limited resources, not mere spatial coincidence or segregation.

Both the selection ratio analyses of rhinos and buffalo and the fine-scale habitat use analyses for rhinos showed preference for tall grassland, marsh/wetland and wet short grassland habitats. This shared preference explains the high overlap indices between the two species (UDOI = 1.1503, BA = 0.9296). The preference of rhinos for tall grassland and wetland habitat mosaic is consistent with their evolutionary history and has been documented by multiple studies

(Dinerstein & Price, 1991; Dutta et al., 2012; Laurie, 1978; Ranabhat et al., 2026). Similarly, buffalo are known to depend heavily on wetland and short grassland habitats for grazing and wallowing. Buffaloes rely more on these habitats than cattle do because they lack the dewlap (present in cattle), which aids in thermoregulation (Krishnan, G et al., 2023). The co-occurrence of rhino and buffalo hotspots in marshy areas likely reflects their shared reliance on these moisture-dependent habitats, rather than competitive exclusion. Cattle, on the other hand, showed selection for dry short grassland, which coincided with their boundary access-associated hotspots.

The grid-based analysis at 1 x 1 km scale revealed that rhino distribution was negatively associated with the proportion of dry short grassland within each grid cell and positively associated with grid area and medium continuity with the landscape. A model with a habitat type of negative influence (dry short grassland) outperformed habitat types with potential positive influence, implying that poor-quality habitat exerts a stronger influence than positive drivers. Since dry short grasslands are predominantly found along the boundaries *(Figure 2)* and overlap with cattle hotspots, this suggests a possibility of an indirect effect of cattle on the rhino distribution. The causal direction of association between cattle and dry short grassland remains unanswered. Two possible scenarios are that cattle preferentially select dry short grassland along the boundary because it is more accessible from nearby villages or that sustained grazing pressure from cattle has prevented their succession to taller grasslands in those areas. Several studies have shown that livestock grazing can alter vegetation structure and composition, resulting in conditions less suitable for other species (Proesmans et al., 2022; Tian et al., 2025). Distinguishing between these scenarios is important because habitat modification by cattle (the second scenario) could result in a delayed indirect competitive effect on rhinos, even without direct spatial overlap at any given moment. However, the fine-scale habitat use model did not detect a direct effect of cattle presence on rhino site use, suggesting

that if the habitat is suitable, rhinos will use a site even in the presence of cattle. Grid area was a significant positive predictor, as larger areas are expected to provide more resources and can therefore support more individuals. Based on field observations, the positive effect of medium landscape continuity, together with the negative effect of high connectivity, suggests that rhinos may be selecting a sweet spot of intermediate connectivity. Such areas may allow them to stray at night while still limiting access by people and livestock.

The grid-based model showed a significantly higher encounter rate of the rhino at noon; however, time of day did not significantly influence rhinos' site usage/selection (point-based habitat use model). This pattern was similar to that of the abundance-weighted KDE, which showed that the utilisation distributions did not vary substantially across time periods, with consistently high overlap indices. This contradiction could be explained by activity-related differences in detectability. Resting was more frequently observed in the morning. Since rhinos preferentially rest in tall grasslands (as shown by activity distribution across habitat-time), a behaviour of seeking cover for rest, especially when with calves, would affect their detectability during the morning hours. These findings reinforce that habitat availability and quality are the primary determinants of rhino distribution of rhinos in PWLS, aligning with the statement “Indian Rhino is more habitat specialised than any other large herbivore mammals” (Hazarika & Saikia, 2012).

Analysis of rhino activity patterns also showed that grazing was the primary activity during both the morning and noon observation periods. This finding is consistent with the digestive physiology of rhinos; as hindgut fermenters, they rely on bulk intake to satisfy energy and nutrient requirements (Clauss et al., 2005). Hindgut fermentation (occurring in the caecum and colon) allows the consumption of abundant fibrous material such as grasses, but it provides lower digestive efficiency than foregut fermentation (seen in ruminants). Hence, prolonged grazing and high biomass consumption are needed to maximise nutrient acquisition. Rhinos

are known to wallow in wetlands and marshes to regulate body temperature during the hot hours of the day (Dinerstein & Price, 1991; Laurie, 1978), which aligns with the noon-time peak in wallowing in PWLS.

An investigation of what aspect of habitat drives the preferences revealed an interesting pattern. Nutritional analysis of the selected dominant plant samples revealed that woodland-dominant species - *Diplazium esculentum* and *Oplismenus compositus*, and the species dominating short grasslands - *Axonopus compressus* and *Cynodon dactylon* had comparatively high nutritional quality values, indicated by high CP to ADL ratios. If a strict nutritional preference were the determining factor, high use of woodland and short grasslands would be expected, but this was not the case. Spatial use and habitat selection appear to be influenced by the large daily biomass requirements of megaherbivores, as discussed earlier (Clauss et al., 2005; Owen-Smith, 1988). Both woodland and short grasslands had low forage volume (calculated from height and grass cover percentage), an indirect, non-invasive indicator of biomass. Grazing in these habitats would substantially increase their time spent foraging, thereby increasing energetic costs. Hence, the rhino's foraging strategy would be using tall grasslands with comparatively lesser quality but high biomass (forage volume), which can form the bulk of the diet, while meeting the nutritional needs with wet short grasslands. Additionally, the vertical structure of tall grasslands 1-2 m tall provided cover, reducing their risk of conflict with conspecifics and humans, particularly for mothers with calves, although no clear aversion to human presence was observed during the study. Additionally, their thermoregulatory requirements during high temperatures limit their movement farther from wetland and marshy habitats. Rhinos might also be utilising aquatic plants from these habitats. Therefore, habitat selection by rhinos is driven by a balance of nutritional quality, physiological requirements, foraging energetics and risk mitigation. This explains why population hotspots are concentrated around a mosaic of tall grassland, wet short grassland, and marshy wetland habitats.

5.2 Nutritional quality

Non-parametric tests and mixed effect models both showed significant differences in faecal nutritional parameters between cattle and rhinos. Rhino dung showed significantly higher values than cattle for Ash content, crude protein (CP), acid detergent fibre (ADF), acid detergent lignin (ADL), CP: ADF and CP: ADL ratios. The most important parameter is the CP-ADL ratio, a strong indicator of diet quality, significantly higher than that of cattle with a small effect size. This suggests that rhinos are still doing better than expected, selecting for a high-protein and low-lignin diet. PERMANOVA and PCoA ordination of the three non-interrelated parameters (Ash, CP, ADF) further confirmed that both species occupy distinct positions in multivariate nutritional space. This difference is attributable to distinct species physiologies rather than diet quality. The ruminant digestive system is characterised by more efficient microbial fermentation in a four-chambered foregut; in contrast, hindgut fermenters like rhinos.

To understand the influence of habitat selection on nutrition, habitat quality (grid quality score) was used as the predictor to test the parameters. Of all faecal nutritional parameters, only ash content showed a significant association with the predictor. Higher ash content values could be due to several factors, such as coarse feeding, grazing close to the ground, and feeding on soil-deposited forage. The primary indicator of diet quality CP: ADL, did not vary with quality score. However, this inference is tentative without the information on the complete diet of the animal. Considering high gut retention time in rhinos, which means the faecal parameters reflect an average of the diet from the past 24-48 hours (Clauss et al., 2005), assigning a quality score based on grids reduces the inferential power of the analysis. Rhinos in PWLS have been reported to leave the sanctuary in search of forage, a behaviour also observed during my fieldwork. If rhinos consume forage outside the sampled grids or the sanctuary during unobserved hours, as is likely here, the faecal samples collected will not represent their full

nutritional intake. For a better understanding of their actual movement and diet, telemetry-based and diet-focused studies would be essential.

Moreover, a more robust design to test the impact of competition would be to compare nutritional parameters between areas with and without cattle. In the relatively small PWLS, all grids were exposed to some degree of livestock grazing. Alternatively, an experimental before-and-after livestock-exclusion study, followed by monitoring of nutritional responses, would be more informative. However, the feasibility of such studies would depend on the size of the study area and overall scale of the research.

5.3 Limitations and way forward

- Certain limitations of this study provide direction for future research. All surveys were conducted during the morning and noon hours, leaving nocturnal life unrecorded. The well-documented behaviour of rhinos moving out at night means that the habitat use of this study captures only a partial picture of the species. An alternative to this would be telemetry-based collaring of individuals to obtain spatiotemporal data throughout the day.
- The nature of this study doesn't explain the causal relationship between cattle and habitat. Since the findings suggest a potential indirect effect through habitat modification, an experimental study design that excludes livestock from certain areas, with before-and-after vegetation monitoring and assessment of rhino use, would be required to distinguish causation from association.
- Habitat selection addresses only one dimension of resource selection. The other dimension, the actual diet, was not quantified. Microhistological analysis or DNA metabarcoding of faecal samples would enable calculation of niche overlap indices between species. The vegetation sampling conducted in this study was also limited by over-grazing, since the identification of grass species is practically impossible without inflorescences (dry winter

season). Detailed, seasonally replicated vegetation surveys across habitat types, combined with faecal diet analysis, would provide a complete picture of resource use and overlap between species.

- Given the small area of the study area, cattle-free control areas could not be established for comparative analysis. In a larger landscape with gradients in livestock density, or in comparative studies involving multiple parks/sanctuaries, it would be possible to directly test the effect of cattle presence on rhino habitat use and nutritional quality.

5.4 Conclusion

This study shows that rhino and buffalo share similar habitat preferences, with both preferentially selecting tall grasslands, marshes/wetlands, and wet short grasslands. Cattle use most of the study area, but hotspots are concentrated along the accessible parts of the boundary. At the scale of 1km, habitat area, medium landscape continuity (positive effect), and proportion of dry short grassland (negative effect) shape the rhino distribution, with no detectable direct effect of cattle density. Similar results from the point-based approach further confirm the finding. Further detailed studies would be needed to rule out indirect competitive effects mediated by habitat modification. Although species differences may explain variation in raw faecal parameters, the higher CP: ADL ratio observed in rhinos suggests that their diet quality remains adequate. However, the absence of samples from cattle-free areas and a lack of forage data limit the ability to draw strong conclusions about competitive effects on rhino nutrition. Based on the study's findings, the expansion of suitable rhino habitat through acquisition and restoration is essential. Creating connecting corridors with other suitable habitats would also be impactful. Given that the effective rhino habitat is only about 15.8 km² of the sanctuary's 38.8 km², active management measures are needed to reduce the proportion of dry short grassland through regulation of livestock and wetland hydrology. It is also recommended to evaluate these actions with further detailed research.

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7 Appendices

Photographs of the study area

Photographs of wildlife in PWLS

Bengal monitor (*Varanus bengalensis*)

Golden jackal (*Canis aureus*)

Fishing cat (*Prionailurus viverrinus*)

Grey-headed Fish Eagle

Blossom-headed parakeet

Red-breasted parakeet

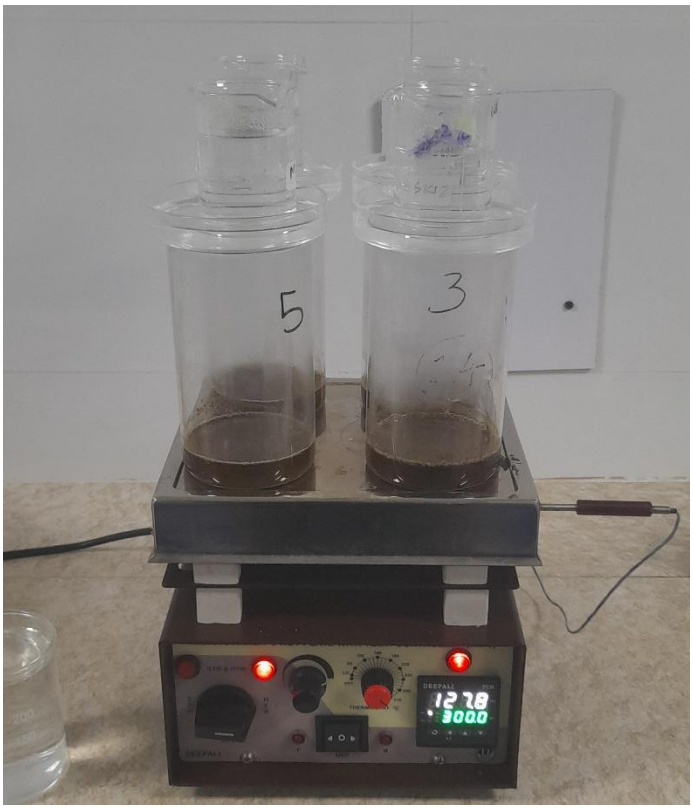
Photographs of the rhino and livestock interaction in PWLS

Photographs of field surveys

Photographs of vegetation sampling and dung sample collection

Photographs of Laboratory methods

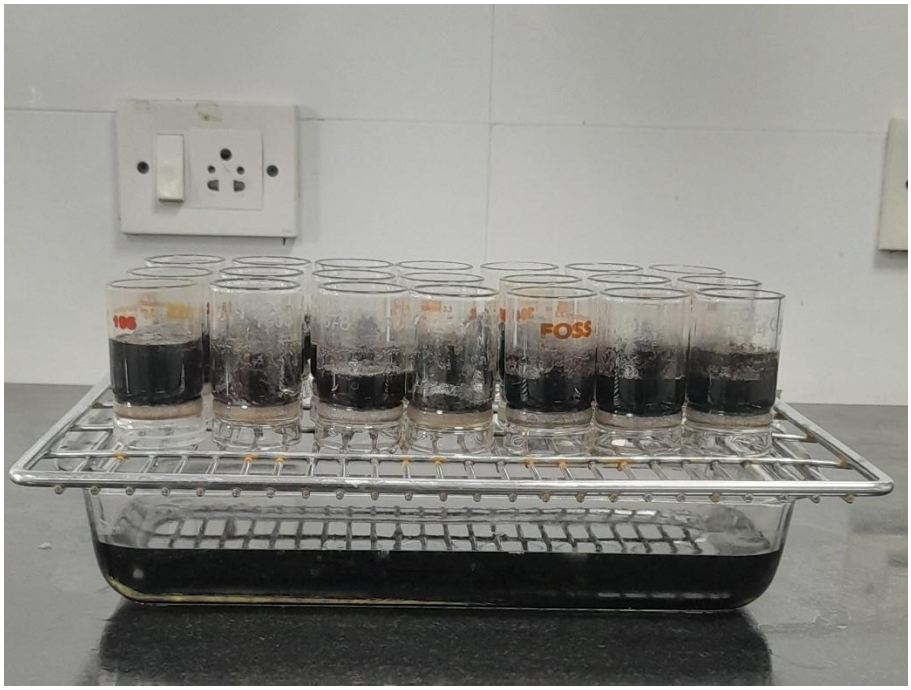
Residue after combustion in muffle furnace for Ash content



Refluxing of samples in acid detergent solution for ADF estimation

Filtering of refluxed sample using low vacuum for ADF estimation

Oven drying samples overnight for ADF estimation



Treating ADF residue with 72% sulphuric acid for ADL estimation

Combustion of final residue in muffle furnace for ADL estimation