



Restoring ecological function: Interactions between vertebrates and latrines in a reintroduced population of *Rhinoceros unicornis*

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ABSTRACT

Reintroduction is a highly effective strategy for rebuilding wildlife populations and restoring their ecosystem functions, but impacts on function are poorly documented. We addressed this gap by comparing the species richness and visit rate of mammals and birds that interact with rhino (*Rhinoceros unicornis*) latrines at two locations in Nepal: Chitwan National Park, with a stable rhino population, and Shuklaphanta National Park, where a rhino reintroduction program was conducted from 2003 to 2018. Camera-traps were used to monitor visitors to 30 latrines in both parks from 2020 to 2021 (669 camera-trap days). The reintroduction of rhinos to Shuklaphanta National Park has played a crucial role in restoring an important resource for other mammal and bird species. Despite a large difference in rhino abundance, and differences in the size, quality and some of the nutritional contents of latrines between sites, there were no significant differences in species richness of latrine visitors and in the frequency of most behaviours at the latrines. Visit rates of animals were higher at the reintroduction site, confirming latrines to be important, limited resources. Overall, 4 mammal and 4 bird species used the latrines to consume the dung, or insects and plants growing on and around the dung; a further two mammal species interacted only indirectly with the latrines. These findings provide evidence that even at low population densities, rhino reintroduction can successfully restore an important ecological function and provide vital resources for other species. Our study supports the rewilding of large-bodied animals to mitigate ecosystem deterioration.

1. Introduction

Megafauna (animals >1000 kg; Owen-Smith, 1988) play distinct roles in various ecological processes, such as nutrient recycling and redistribution (le Roux et al., 2018; Berzaghi et al., 2018), seed dispersal (Campos-Arceiz and Blake, 2011; McConkey et al., 2022), and herbivory (Terborgh et al., 2016; Ong et al., 2023). Consequently, they support other organisms sharing the same habitats (Ripple et al., 2016). This support is threatened, however, due to population declines and local extinctions of megafauna in response to human activities (Dirzo et al., 2014). Recent losses in megafauna have had cascading, negative impacts on ecosystems and pose a significant conservation challenge (Galetti

et al., 2018; Poulsen et al., 2018; Hyvarinen et al., 2021). Reintroducing megafauna could play a key role in restoring lost ecosystem functions, yet our understanding of how reintroduction can influence ecosystem processes is limited (Genes and Dirzo, 2022).

Herbivorous megafauna can produce several tons of dung annually (Pringle et al., 2023), providing a valuable resource within ecosystems. Megafaunal' dungs play crucial roles in nutrient recycling and geochemical cycles by transferring nutrients laterally across the landscape (Berzaghi et al., 2018; Doughty et al., 2013). The nutrient hotspots created by the dung also serve as an important food source for many animals due to the presence of seeds (Sekar et al., 2016), attraction of insects (Waltner-Toews, 2013), and facilitation of vegetation growth

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(Dinerstein, 1991; Waltmer-Toews, 2013). Some animals engage in coprophagy, consuming feces to obtain additional calories and essential nutrients that are otherwise scarce in the environment (Ranade and Prakash, 2015; Videvall et al., 2023). Additionally, dung provides microhabitats for amphibians, reptiles and invertebrates (Campos-Arceiz, 2009; Dinerstein, 1991). These interactions with dung underscore a significant ecological function of megafauna.

The greater one-horned rhinoceros (*Rhinoceros unicornis*) is currently classified as vulnerable on the IUCN Red List (Ellis and Talukdar, 2019). Once having a wide distribution across India, Nepal, Bangladesh, Bhutan and possibly Pakistan, the species is now extinct from most of this region due to the effects of human encroachment, habitat loss and poaching (Jhala et al., 2021). The current population of around 4000 individuals, is mainly found in the grasslands and riverine forests in India and Nepal (Dinerstein, 1991; Pant et al., 2022). Similar to other rhino species, the greater one-horned rhino deposits its dung in communal latrines, which serve as a vital means of olfactory communication among individuals (Dinerstein, 1991; Marneweck et al., 2018). These large communal latrines are probably important nutrient hotspots providing crucial resources for other animals, and are likely to differ from the single dung deposits produced by sympatric elephants – the other megafaunal species sharing the same landscape (Campos-Arceiz, 2009; Sekar et al., 2016). Therefore, the decline or loss of threatened rhino populations may result in missed opportunities for other animals to benefit from these resources.

In Nepal, over the past few decades, a successful reintroduction program has been implemented for the greater one-horned rhinos in areas where they were extinct (Subedi et al., 2017; Pant et al., 2022). The reintroduced individuals have not only survived but have reproduced, although the reintroduction sites still have lower rhino populations than within the original habitats (Subedi et al., 2013). A successful reintroduction program should not only focus on population dynamics of the animals, but also on the restoration of the ecosystem functions that these animals provide (rewilding; e.g., Nogués-Bravo et al., 2016). Yet, few studies have investigated recovery of function following reintroduction, and this gap is particularly acute in Asia (Genes and Dirzo, 2022). A knowledge gap on the recovery of the rhino's ecological roles hinders our understanding of the extent to which their reintroduction benefits ecosystems and supports the conservation of other species.

The aim of this study is to investigate whether rhino reintroduction has restored the ecological function of rhino latrines as a food source for other animals. Differences in latrine use between the original site and the reintroduction site will be influenced by different population densities of rhinos (original site has ~14 times more rhinos; see methods) and the relatively short period of time rhinos have been present at the reintroduction site (<20 years at the time of study). We expect that the site with more rhinos will have larger and more nutritious latrines due to a greater frequency of dung deposition and by more individual animals (although we could not measure the latter). Latrines are an emerging resource at the reintroduction site as the rhino population recovers, and it may take time for other animals to transition from their current nutrient or food sources to using the latrines. Alternatively, the latrines may provide a limited but essential resource that is targeted by the animals present at the site.

We focused on latrine use by mammals and birds as they could be monitored by camera traps. We addressed the following questions: (1) Are there differences in latrine size, frequency of rhino usage, and nutrient content between the original habitat and reintroduction site? (2) Does the species richness and abundance of vertebrates visiting rhino latrines differ between the two sites? (3) Do the behaviours exhibited by vertebrates at latrines differ between the original habitat and reintroduction sites? We hypothesized three possible outcomes regarding the comparative latrine use by mammals and birds between sites: (i) latrine use would be lower at the reintroduction site as the animals gradually adapt to the emerging and low-density resource; (ii) latrine use would be

similar among the two sites, because the latrines are being used to their maximum capacity and can only support a limited number of users; (iii) latrine use would be more prevalent at the reintroduction site because it is an essential very limited resource that is highly sought after.

2. Materials and methods

2.1. Study sites

The study was conducted in two geographically isolated regions: Chitwan National Park (CNP) (84.323170°E, 27.531686°N) and Shuklaphanta National Park (ShNP) (80.254478°E, 28.855631°N) in Nepal. CNP has a well-established population of rhinos, with a population size exceeding 694 individuals (~0.42 rhinos km⁻²): 128 males, 174 females, 392 unknown; 474 adults, 95 sub-adults, 125 calves (NTNC, 2021). ShNP hosts a translocated rhino population that was introduced between 2003 (starting with four animals from CNP) and 2018 (DNPWC, 2017). The population in ShNP is over 17 individuals (~0.03 rhinos km⁻²): 3 males, 4 females, 10 unknown; 13 adults, 4 calves (NTNC, 2021). Before the translocation program began there was a single resident rhino in ShNP (DNPWC, 2017).

Despite being 600 km apart, both protected areas have similar vegetation types, and mammal and bird species. However, the density of herbivores other than rhinos tends to be higher in ShNP, while primate densities are higher in CNP (Table S2). CNP covers a core area of 952.63 km², with an altitude range of 110 to 850 m asl; the surrounding buffer zone is 729.37 km². The region has a subtropical monsoonal climate, with three distinct seasons: monsoon, cool-dry, hot-dry, and average temperatures ranging from 8 °C in January to 36 °C in April. Annual rainfall is approximately 2036 mm, with over 80 % occurring during the monsoon season. CNP is a World Heritage Site and has over 600 bird species, and around 70 mammal species, including >30 Asian elephants (*Elephas maximus*) (CNP, 2021).

ShNP encompasses a core area of 305 km² with altitude ranging from 174 to 1386 m asl; there is a buffer zone of 243.5 km². The park has a more arid climate compared to the CNP, with annual rainfall ranging from 1300 to 2300 mm. ShNP harbors around 60 mammal species and 450 bird species (Poudyal et al., 2021). A population of 3–5 resident Asian elephants (*Elephas maximus*) and 25–30 migratory elephants are also present.

Both CNP and ShNP encompass a mosaic of habitats, including grasslands, wetlands, and mixed forests. The rhino populations use a combination of grasses, oxbow lakes, *Shorea robusta* forests, and alluvial floodplains, but their primary habitat are the riverine grasslands dominated by *Imperata cylindrical* and riverine forests dominated by *Trewia nudiflora* (Dinerstein, 1991; Subedi et al., 2017).

2.2. Camera trapping survey

Camera-trapping was conducted at rhino latrines in CNP and ShNP during the monsoon and post-monsoon seasons (August to November) of 2020 (19 latrines) and 2021 (11 latrines). The study period was constrained due to limited access during covid and availability of cameras, which were also used for a study on seed dispersal by rhinos. Riverine forest was chosen as the study habitat due to its importance as a defecation site for rhinos and the ease of camera placement. We surveyed an area of ~4 km² in the riverine forests of CNP and ShNP for latrines in August of each year (further details in Table S1, Figs. S1 and S2). From the 18 and eight latrines we located in CNP and ShNP, respectively, we selected latrines for camera-trapping. The selection criteria were that at least 200 m separated selected latrines, dung was fresh (estimated <1 week), latrine had a diameter of at least one meter, and the presence of a nearby tree suitable for camera placement. Fresh latrines were identified by their colour (ranging from greenish black to deep greenish brown), or by direct observations of rhinos defecating, or the presence of dung beetles (Awasthi et al., 2023). Older latrines were straw-coloured and

were not used. Latrine length was measured as the longest axis, and width was measured across the latrine middle; latrine area was calculated as length x width.

A single camera trap (Cuddeback, Bushnell, Campark) was strategically placed at each latrine site to monitor visits by mammals and birds. In 2020, a total of 19 cameras were used, with 14 cameras (416 camera-trap days, from September 6th to November 19th) placed in CNP and five cameras (77 camera-trap days, from September 14th to October 5th) in ShNP. In 2021, a total of 11 camera traps were deployed, with eight cameras (126 camera-trap days, from August 6th to September 17th) in CNP and three cameras (50 camera-trap days, from July 23rd to August 14th) in ShNP. Cameras were positioned at approximately 1 to 1.5 m height from the ground and recorded 30-s videos during the day and captured photos at night. Cameras were operational for 4 to 56 days, with occasional shortening of monitoring periods due to technical issues, wildlife interference, or other disturbances. Cameras were checked every 5–7 days, which involved replacing batteries and SD cards, as well as repositioning the cameras to different latrine locations.

Over 669 camera-trap nights, a total of 3492 videos captured animal activity (2629 in 2020, 1823 in 2021). All observed mammal and bird species were identified with reference to taxonomic sources (Griffiths et al., 2020; Jnawali et al., 2011; Grimmitt et al., 2000). Species richness of visitors and their visit rates were calculated based on all videos and photos collected and, therefore, covers both day and night visits. However, the direct and indirect behaviours exhibited by vertebrates visiting latrine sites were only identified during the day (6 am to 6 pm), when cameras recorded videos that enabled more accurate identification of the behaviours. We considered the exclusion acceptable because fewer visits were recorded during the night and no species visited only during the night-time; 14 % of visits to latrines were during the night at CNP, and 20 % at ShNP. However, the extent of this limitation varied among species (see Fig. S4 for more details).

The direct interactions recorded at latrines included the following behaviours: (i) consuming dung, plant fragments, or unidentified items within the latrine, (ii) consuming herbs, seedlings, or mushrooms growing on the latrines, or (iii) consuming insects found in, on, or near the latrine. Indirect interactions were identified when animals (i) grazed near the latrine, (ii) urinated or defecated on or in close proximity to the latrine, or (iii) exhibited noticeable sniffing behaviour towards the latrine. Interactions were considered independent when there was a minimum of 15 min between observations of the same species.

2.3. Latrine sampling and nutrient analysis

Five fresh latrine samples (1000–2000 g) were collected from both CNP and ShNP (at the end of the study period) for nutrient analysis, excluding the external dusty layer and the portion of latrine in contact with the ground to prevent soil contamination. The collected samples were dried at 70 °C for 24 h until a constant weight was achieved. The fresh mass of each fecal sample was determined by comparing its initial fresh mass before drying to its dry mass after being dried at 70 °C for 24 h. The dried samples were stored in an air-tight container for chemical analysis.

Chemical analysis was done at National Animal Nutrition Research Centre, Nepal Agricultural Research Council (NARC), Nepal and Agriculture Technology Centre, Pvt. Ltd., Nepal. Crude protein content (%) was analysed using the Micro-Kjeldahl method (AOAC, 2005). The Neutral Detergent Fiber (NDF%) and Acid Detergent Fiber (ADF%) were determined using the Van Soest method (Van Soest, 1982). Hemicellulose content was calculated as the difference between NDF% and ADF%, while cellulose content was determined as the difference between ADF% and Acid Detergent Lignin (ADL%) using the Van Soest method (Van Soest, 1982). Potassium levels were determined by the Wet Digestion (Flame Photometric) method, while total calcium and magnesium levels (g) were determined through Dry Ashing and EDTA methods. Total iron was determined using the Dry Ashing and AAS method (AOAC, 2005).

The Carbon-to-Nitrogen (C/N) ratio was calculated as the ratio of carbon to nitrogen content (Extended methods S2).

2.4. Data analysis

All statistical analyses were conducted in the R environment (R Core Team, 2023). We used generalized linear mixed effect models (GLMM) using lmer4 package (Bates et al., 2015) and general linear models (GLM). We used function *anova*, independent *t*-tests using Satterthwaite's method and GLHT Tukey contrast using *multcomp* (Hothorn et al., 2008) and *multcompView* (Graves et al., 2023) packages to test for differences and contrasts between sites. For visualization, the *ggplot2* package (Wickham, 2016) and functions available in base R were used. Data were tested for heteroscedasticity and normality and met the assumptions.

To determine whether latrine size and frequency of use by rhinos differed between sites general linear models were fitted, with the number of rhinos visiting each latrine considered as a random factor. To investigate differences in nutrient parameters in rhino latrines between sites, a linear mixed model was fitted. The nutrient amount in CNP and ShNP was compared, with nutrient type at each latrine as a random factor. These tests determined whether the quality and quantity of the resource differed between sites.

To determine if species richness of vertebrates visiting the latrines differed between sites we first plotted species accumulation curves for each site using Vegen package in R (Oksanen et al., 2017), to assess if our sampling effort was sufficient. A linear mixed model was fitted to determine differences between the species richness of all bird and mammal species visiting each latrine across the two sites. We included camera trap days and latrine size as a random factor to control for their influence on species richness. We could not include nutrient content as a random factor since we did not measure nutrients for all latrines.

We compared the compositional dissimilarity of species between the two sites, using the Bray-Curtis dissimilarity index (Bray and Curtis, 1957; Hao et al., 2019) and pairwise Jaccard's similarity indices (Voronov et al., 2013). To standardize the data, we divided the total number of individual species observed by the number of camera trap days at each site. (Extended methods S3).

The visitation rate of birds and mammals to latrines was calculated as the number of independent visits by an individual or group per 100 camera-trap days. To determine whether the visitation rate differed between CNP and ShNP, a linear mixed model was fitted. To examine whether visiting rate at latrines for mammals and birds was influenced by latrine freshness (using defecation rate of rhinos as a proxy) or latrine size, a linear mixed model was fitted using species name as a random factor. Details on group sizes are also presented but are not included in the tests because we could not make accurate counts for all visits.

To compare the behaviours of birds and mammal species at rhino latrines we separated observations into eight different behaviours: coprophagy, eat vegetation or fungi, insect eating, graze, defecation, urination, smell dung, rest on dung in CNP and ShNP. Each behaviour rate was quantified as the number of independent behaviour events detected by camera traps, per 100 camera trap days. Rates at each site were compared using a linear mixed model, with dung location included as a random factor. A linear mixed model was fitted to determine the effect of nutrient content on the behaviour of latrine visitors across sites. We included latrine location and site as random factors.

3. Results

3.1. Latrine quality and rhino visits to the latrines

More rhino visits and defecation events were recorded in CNP, than in ShNP. In CNP, we recorded 0.35 visits per camera-trap day ($n = 191$ visits to 22 latrines) of which 40 % were for defecation, and in the other visits they smelt the dung or walked past. In ShNP, we recorded 0.025

visits per camera-trap day ($n = 2$ visits to 8 latrines) of which 13 % were for defecation. Latrine size was significantly larger in CNP ($15.74 \pm 5.54 \text{ m}^2$) than in ShNP ($6.62 \pm 1.48 \text{ m}^2$) (Fig. 1A) (slope = -9.068 , SE = 1.969 , $t = -4.606$, $p < 0.0001$), but the overall defecation rate did not have an effect on the size of latrines in the two sites ($p = 0.729$).

Overall nutrient content did not differ significantly between CNP and ShNP (slope = 0.463 , SE = 3.615 , $t(198) = 0.128$, $p \leq 0.898$) (Table 1). However, two nutrients, namely crude fiber (%) (slope = 5.243 , SE = 1.856 , $t(190) = 2.82$, $p \leq 0.005$) and C/N ratio (slope = 5.977 , SE = 1.856 , $t(190) = 3.22$, $p \leq 0.001$) were significantly higher in ShNP, while energy (MJ/kg) (slope = -5.661 , SE = 1.856 , $t(190) = -3.052$, $p \leq 0.002$) was higher in CNP.

3.2. Composition and frequency of visitors to latrines

Fifteen species in CNP and 13 species in ShNP were recorded at the latrines (18 species in total across the sites; excluding rhinos), of which ten species in CNP and nine species in ShNP (10 species in total; 1–10 species per latrine) were observed to interact with the latrines. The species accumulation curves suggest CNP was adequately sampled, while ShNP was slightly under-sampled (Fig. 2). On average, 5.40 ± 2.44 species (mean ± 1 SD of species observed at each latrine) were recorded in CNP and 4.83 ± 2.63 species were recorded in ShNP and this difference was not significant ($p = 0.984$); number of camera-trap days and latrine size did not influence this result ($p = 0.956$).

The Bray-Curtis similarity index between the sites is 0.48, suggesting a moderate level of dissimilarity in the species visiting latrines between sites (48 % of the species present at one site are not shared with the other site). The Jaccard Similarity Index is 90, meaning that 90 % of the species in CNP are also present in site ShNP, or vice versa.

Spotted deer was the most frequently observed animal visiting latrines and interacting with the dung directly. They had a higher visit rate in ShNP and visited all monitored latrines (2.26 visits per camera-trap day; group size 1–17 individuals), than in Chitwan (0.89 visits per camera-trap day; visiting 18 of the 22 latrines, with group size 1–32) (Table S3). Other common visitors that directly interacted with the dung were wild boar (*Sus scrofa*: 0.099 visits in CNP and 0.130 in ShNP) and rhesus macaques (*Macaca mulatta*; 0.032 visits in CNP and 0.097 in ShNP). Peacocks (0.053 visits in CNP, and 0.067 visits in ShNP) and jungle fowl (0.037 and 0.075 visits in CNP and ShNP, respectively) were the most common birds interacting with latrines (Table S3). Six species had higher visit rates in ShNP, with two species (sambar deer, CNP = 0.082, ShNP = 0.033 visits; tiger, CNP = 0.067, ShNP = 0.006) having higher visit rates in CNP (Table S3). The remaining two species were rare visitors. Overall, the visitation rate of mammals and birds to latrines was

Table 1

The concentration of nutrients assessed in rhino latrine in Chitwan (CNP) and Shuklaphanta National Parks (ShNP). Values in bold were significantly different between sites.

Nutrient item	CNP (Mean \pm SD) (N = 5)	ShNP (Mean \pm SD) (N = 5)
Fresh dry matter (%)	17.93 \pm 1.19	17.64 \pm 1.25
Crude protein (%)	7.82 \pm 0.97	6.30 \pm 0.52
Neutral detergent fiber (%)	74.32 \pm 1.94	77.14 \pm 1.76
Acid detergent fiber (%)	52.02 \pm 2.18	51.33 \pm 2.36
Acid detergent lignin (%)	18.81 \pm 1.59	16.22 \pm 0.89
Crude fiber (%)	41.17 \pm 1.79	46.42 \pm 1.13***
Total ash (%)	15.32 \pm 2.53	15.88 \pm 3.37
Ether extract (%)	2.53 \pm 1.42	2.07 \pm 0.56
Energy (MJ/kg)	24.75 \pm 2.40	18.77 \pm 7.43**
Hemicellulose (%)	22.30 \pm 0.90	25.81 \pm 2.45
Cellulose (%)	33.21 \pm 2.18	35.11 \pm 2.50
Organic matter (%)	84.69 \pm 2.53	84.12 \pm 3.37
Organic carbon (%)	49.71 \pm 1.25	49.16 \pm 1.55
Nitrogen (%)	1.25 \pm 0.16	1.01 \pm 0.08
C/N ratio	40.28 \pm 5.54	49.06 \pm 4.40***
Phosphorus (%)	0.49 \pm 0.14	0.24 \pm 0.07
Potassium (%)	2.02 \pm 0.21	1.78 \pm 0.44
Calcium (%)	0.72 \pm 0.15	0.53 \pm 0.15
Iron (%)	0.16 \pm 0.06	0.17 \pm 0.07
Magnesium (%)	0.18 \pm 0.08	0.18 \pm 0.10

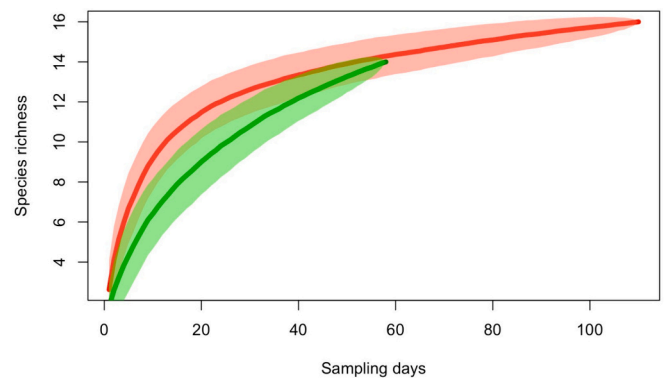


Fig. 2. Species accumulation curve for all mammal and bird species detected in Chitwan National Park (Pink colour, top line) and Shuklaphanta NP (green colour, bottom line). Sampling days refers to the number of days the camera-trap was active (See Fig. 3 for mammal only records). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

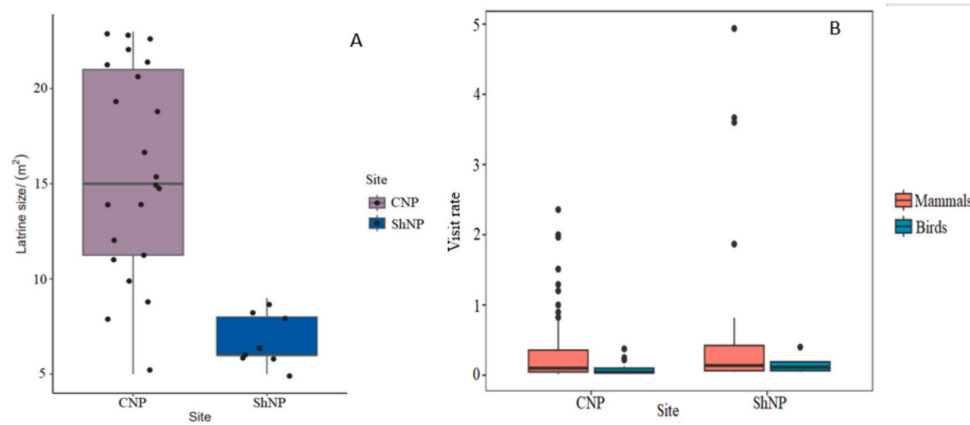


Fig. 1. (A) Latrine size (m^2) of rhinos in Chitwan (CNP; high rhino density) and Shuklaphanta (ShNP; reintroduction site, low rhino density) National Park. Latrine size was significantly larger in CNP. (B) Visit rate of mammals and birds to the latrines of rhinos in CNP and ShNP. Visit rate is the number of visits per camera trap days and it was significantly higher in ShNP.

higher in ShNP (0.51 ± 1.08) than in CNP (0.25 ± 0.41) (Fig. 1B) and this difference was significant (slope = 0.273, SE = 0.134, $t(171) = 2.035$, $p = 0.0434$). There was no significant effect of latrine size ($p = 0.705$) and rhino defecation rate ($p = 0.305$) on the visiting rate of the latrine visitors.

3.3. Behaviour of vertebrate visitors to rhino latrines

We documented eight distinct direct and indirect activities performed by animals on and around latrines (Figs. 3; S3). Of the three direct interaction-types observed, the most common were the consumption of herbs, seedlings, or mushrooms growing on the latrines by species such as spotted deer, barking deer, and wild boar (Table S4). This was closely followed by coprophagy, which involved the ingestion of dung, along with the consumption of plant fragments or unidentified items within the latrine. Consumption of insects on or around the dung was also frequently observed. The most prevalent indirect interactions recorded were grazing on vegetation immediately surrounding the latrines, smelling the latrine, urination, defecation, and utilizing the latrines to rest (Fig. 3; Table S4). The occurrence of different behaviours exhibited by latrine visitors did not show a significant difference between sites overall ($p < 0.944$). However, the consumption of vegetation or fungi was more commonly observed in CNP compared to ShNP (slope = 20.087, SE = 9.513, $t(85.02) = 2.111$, $p < 0.0377$). Similarly, grazing on or near the latrine was observed significantly more frequently in ShNP compared to CNP (slope = 21.39, SE = 10.27, $t(93.68) = 2.081$, $p < 0.041$) (Fig. 3).

Overall, we found that the nutrient amounts in dungs did not influence the various behaviours we observed by latrine visitors ($p = 0.995$). However, ‘grazing’ was influenced by the levels of crude fiber (slope = -0.047 , SE = 0.002, $t(0.06) = -2.133$, $p \leq 0.033$), carbon nitrogen ratio (C/N) (slope = -0.037 , SE = 1.869, $t(0.06) = -2.030$, $p = 0.042$), and hemicellulose (HC) (slope = -0.043 , SE = 1.973, $t(0.06) = -2.040$, $p \leq 0.027$). Likewise, the consumption of vegetation or fungi was influenced by the levels of fresh dry matter (slope = 0.062, SE = 2.769, $t(0.06) = 2.240$, $p = 0.025$).

4. Discussion

The reintroduction of greater one-horned rhinos to Shuklaphanta National Park (ShNP) in Nepal has successfully restored an important

ecological function in the area, by providing hotspots of nutrients, insects, fungi and other foods to 10 mammal and bird species. Even though rhinos are approximately ~ 14 times more abundant in the original site of Chitwan National Park (CNP) compared to the reintroduction site, and the communal latrines were larger and possibly more ‘nutritious’ in CNP, there was no significant difference in the species richness of visitors to latrines between the two sites. In fact, the visit rate of animals to latrines in ShNP was significantly higher than in CNP, indicating that latrines are a valuable and limited resource in this lower rhino-abundance site. This suggests that the reintroduction of rhinos can effectively restore important ecological functions, even at low population densities.

There were differences in both the quantity and quality of rhino latrines as a resource between the two sites. Rhinos visited latrines more frequently in CNP, resulting in larger and potentially ‘fresher’ dung resources. While the overall nutrient content of the dung did not differ between sites, the values for three important parameters (crude fiber percent, C/N ratio, energy) suggested that CNP had higher quality dungs for coprophagy and possibly plant growth. Crude fiber and C/N ratios were higher in ShNP indicating a higher component of indigestible material (Taylor et al., 1989), and potentially less accessible Nitrogen, which is an essential nutrient for mammalian herbivores (Grant and Scholes, 2006). These differences could result from more frequent use of latrines in CNP, differences in rhino diets, or more individual rhinos using each latrine in CNP (which we could not determine). Individual rhinos likely have varying ranging areas and diets, resulting in latrines used by more individuals being richer in certain nutrients. The nutrient content of latrines influenced the behaviour of visiting animals, with grazing observed more often at latrines with higher values for crude fiber, hemicellulose and C/N ratios, confirming the importance of these for plant growth (e.g., Williams and Haynes, 1995). Similarly, fresh dry matter was associated with more use of the latrines for vegetation and fungi.

We proposed three possible outcomes for comparing latrine-visitors between sites. If animals were adapting gradually to this ‘novel’ resource in ShNP, we expected reduced visitation in ShNP compared to CNP. Similar visitation rates between sites would suggest the nutrient hotspots are being used to their maximum capacity, while higher visit rates in ShNP (where the resource is less available), would indicate that it is an essential and highly sought-after resource. Our results show a combination of the last two predictions. Despite the larger and

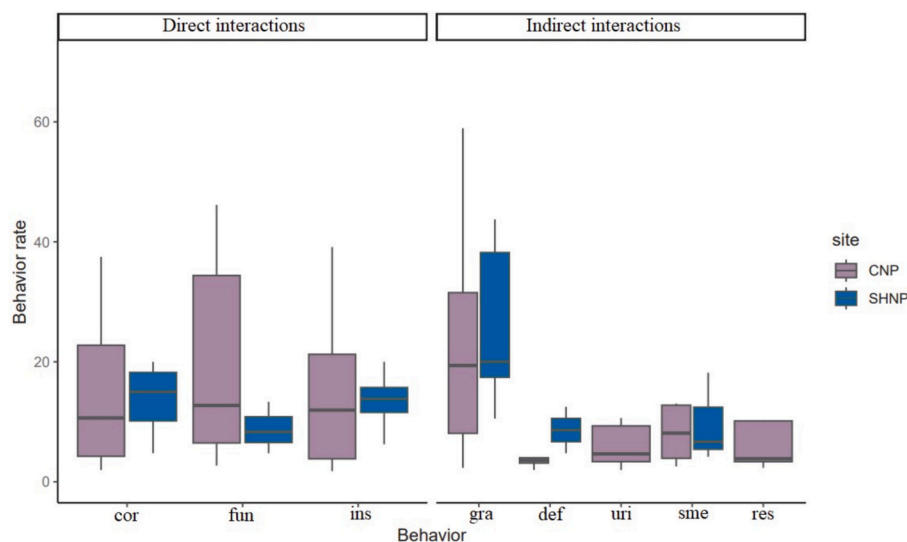


Fig. 3. Behaviour rate (per 100 camera trap days) of latrine visitors between Chitwan National Park (CNP; high rhino density) and Shuklaphanta National Park (ShNP; reintroduction site, low rhino density). Direct interactions are on the left and indirect interactions on the right; abbreviations: cor = coprophagy, fun = eat vegetation or fungi, ins = insect eating, gra = graze, def = defecation, uri = urination, sme = smell latrine, res = rest on latrine.

potentially more nutrient-rich latrines in CNP, the species richness and the identity of animals interacting with dungs were nearly identical between sites. Conversely, visit rates were higher in ShNP compared to CNP, except for sambar and tigers, which had higher populations in CNP (Table S2). Most herbivores had higher populations in ShNP (Table S2), contributing to the discrepancy and causing a moderate level of dissimilarity in visitor composition between sites. The higher spatial dispersion of latrines at the reintroduction site is probably also a strong influence on the relative latrine-use by different animals and possibly explains the slower rate of species accumulation shown in the species richness graphs. Overall, our results indicate that the reintroduction of rhinos has restored the function of creating nutrient hotspots, which are used by a select group of animal species and potentially to their maximum capacity.

Direct uses of the latrines were observed through coprophagy, and the consumption of plants and insects in and on the latrines, which probably occur at high densities as a consequence of the nutrients available (Gillet et al., 2010; Pinero and Avila, 2004). In sites where rhinos have been extirpated, such nutrient hotspots are unavailable, possibly affecting the health of other animals if essential nutrients and food sources are less available and predictable in space. For example, animals obtain essential nutrients, such as phosphorus and nitrogen through coprophagy (Aviles-Rosa et al., 2019; Körner et al., 2016; Soave and Brand, 1991), and it increases microbiome diversity, which has beneficial effects on digestion (Kobayashi et al., 2019; Kenagy et al., 1999) and body mass (Bo et al., 2020). Coprophagy has been observed in many species and with various types of dung (Nishikawa and Mochida, 2010; Ranade and Prakash, 2015; Van der Wal and Loonen, 1998; McConkey, 2005; Spitzer et al., 2023). Hence, in the absence of rhino latrines, animals could consume dung from other animals, such as from elephants and gaur (*Bos gaurus*), but neither species are common outside the national parks and the dung is smaller, more spatially-dispersed and dries out more quickly (B. Awasthi personal observation).

We observed indirect uses of latrines by five animal species, four of which also interacted directly with the dung. Spotted deer, the most common latrine visitor, would smell the dung, urinate and defecate on the latrines, graze around them, and occasionally rest on the dung. This and similar behaviour in barking deer possibly result from the overall attraction to, and time spent at, latrines by these deer. However, sambar deer also grazed around the latrines, indicating that the fertilizing effect of dung may have positive impacts on plant growth beyond the immediate vicinity of the latrines (Feeley, 2004; Valdés-Correcher et al., 2019). Tigers were observed urinating on a latrine, suggesting that they may serve as marking locations for species other than rhinos (Burger et al., 2008). We also observed frogs and invertebrates using the latrines as shelter, reflecting findings from other, brief, observational studies (Campos-Arceiz, 2009; Dinerstein and Wemmer, 1988). In Bardia National Park, another rhino reintroduction site in Nepal, a Burmese python was observed within a dung pile, with its head immersed and basking in the sun (B. Awasthi, personal observation).

Our study has several caveats that limits our understanding of the benefits animals receive from rhino reintroduction. Our observations on animal behaviour at latrines were limited to daylight hours and could underestimate rare nocturnal behaviours, although most animals were primarily diurnal visitors. Further, we could not determine whether animal health is affected by the absence of rhinos and the latrines they produce (e.g., Bo et al., 2020). To address this limitation, future studies could investigate animal health (in areas with and without rhinos), measure nutrient enrichment in the vicinity of latrines, and compare dung use with that of other large megafauna, such as elephants. The current study was conducted only during the monsoon and post-monsoon period and use of latrines might differ in other seasons. It would be also valuable to examine seasonal and habitat patterns in latrine use by wildlife, as nutrient requirements may vary during different times of the year, particularly during breeding seasons, or within different habitats (Fish et al., 2007; Pekins et al., 1998).

4.1. Management implications

The reintroduction of previously extinct animals has been proven to restore various ecological functions, such as seed dispersal (Genes et al., 2019; Landim et al., 2022), seed predation (Mills et al., 2017), and herbivory (Aguilera and Gibbs, 2023; Garrido et al., 2019) (see Genes and Dirzo, 2022 for a full review). Our study provides strong evidence that rewilding of rhinos can restore the function of latrines as nutrient hotspots for other organisms. Other ecological functions performed by the rhinos have probably also been restored, such as nutrient cycling, creation of lawns through grazing, seed dispersal (Dinerstein and Wemmer, 1988; Pringle et al., 2023), and the formation of waterholes through wallowing behaviour (Laurie, 1982). We suggest that restoration of functions should be explored further where rhino reintroduction has been conducted. These findings have implications for management strategies, as they demonstrate the positive cascading effects of rewilding, by which species not traditionally included in conservation efforts can benefit, and this evidence can be incorporated into the arguments for proceeding with rewilding.

5. Conclusions

Rhino latrines play a vital role in providing diverse resources for various bird and mammal species, including dung (coprophagy), insects, and increased plant growth. The reintroduction of rhinos has successfully restored this lost function, as evidenced by the similar species richness and visit rates observed at the reintroduction site compared to the original site. Interestingly, the reintroduction site with fewer rhinos exhibited higher visit rates, further highlighting the limited yet essential nature of latrines as a resource. These findings strongly support the positive cascading impacts of rewilding large herbivores within ecosystems and provide valuable evidence to strengthen rewilding proposals.

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CRediT authorship contribution statement

Balram Awasthi: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kim R. McConkey:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Conceptualization. **Sasith Tharanga Aluthwattha:** Writing – review & editing, Formal analysis. **Cheng Chen:** Writing – review & editing, Formal analysis. **Jin Chen:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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