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RESEARCH ARTICLE

African elephants influence browse availability for black rhinoceroses in Gonarezhou National Park, Zimbabwe

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Abstract

Translocations are essential for the establishment of new populations of the critically endangered black rhinoceros (*Diceros bicornis*), but success will largely depend on forage availability. We investigated the degree of competition for woody browse between African savanna elephants (*Loxodonta africana*) and a recently reintroduced population of rhinoceroses in Gonarezhou National Park in Zimbabwe in the dry season of 2022. We examined overlap in space use and selection for plant species, stem diameters, and feeding height by measuring use of shrubs by both species at 75 sites across a range of topo-edaphic conditions. Areas heavily used by rhinoceroses had high shrub densities, were close to water, and were on alkaline soils with elevated conductivity. Sites with medium to high levels of rhinoceros use were nested within areas of high elephant use. We also observed high elephant use in areas not favored by rhinoceroses, occurring farther from water and having lower shrub densities. Both species avoided thickets on acidic soils. There was substantial overlap in feeding areas, the plant species selected, and foraging height, although elephants used stems with larger diameters than rhinoceroses. Feeding by elephants on woody plants often resulted in a proliferation of small-diameter coppice stems, which rhinoceroses used more than non-coppice growth. Elephants did not appear to favor small coppice stems, indicating a degree of elephant-induced facilitation of browse for rhinoceroses. Evidence for competition with elephants indicates black rhinoceroses may be best introduced into areas with a low elephant density.

KEYWORDS

black rhinoceros, browse availability, coppice, elephant, facilitation, population reintroduction

The black rhinoceros (*Diceros bicornis*) is critically endangered (Emslie 2020) primarily because of poaching but also because of habitat loss (Duthé et al. 2020). Its distribution has shrunk to 5% of its historical range (Anderson et al. 2020), and the global population was reduced by 98% to 2,000 animals by the year 2000 (Duthé et al. 2020). Conservation efforts increased numbers to 5,250 by 2020 (le Roex and Ferreira 2020). These efforts included relocating rhinoceroses from poaching hotspots, re-introducing them into areas where they had become locally extirpated, and addressing the causes of local extirpations. However, the future of the species depends on continued population growth and range expansion. A goal is the re-establishment of subpopulations within the historical range where population growth of ≥5% per annum can be expected (Linklater et al. 2012), which is achieved by translocating founder groups to secure areas with suitable habitat. Establishment of new subpopulations is important because growth of existing populations will stagnate once numbers reach the carrying capacity of the land and density-dependent effects start to manifest. Successful reintroduction depends on the founder group's age-and-sex structure and social stability, and site-specific variables such as poaching pressure, habitat suitability, and the level of competition from other herbivores (Knight and Kerley 2010). Areas that are safe from poachers must contain suitable habitat characteristics (Emslie et al. 2009) and meet the feeding requirements of the species (Ganqa and Scogings 2007, Anderson et al. 2020). Specifically, diet selection, preferred plant species, and overlap with competing herbivores need to be understood in a new area so that forage limitations can be identified, and a sustainable density for black rhinoceros estimated (Muya and Oguge 2000, Buk and Knight 2010).

Species that include a substantial amount of browse in their diet such as African elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), eland (*Tragelaphus oryx*), greater kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), impala (*Aepyceros melampus*), and bushbuck (*Tragelaphus scriptus*) will all compete for food with black rhinoceros if they occur at sufficient density. However, elephants are likely to have the greatest influence on food availability for a founder population of black rhinoceroses because of their chronic use and greater level of damage to trees and shrubs (Laws et al. 1975), and their tendency to dominate the biomass of mammalian herbivores in African savanna systems (Fritz et al. 2002).

Space use by elephants and black rhinoceroses is subject to similar environmental constraints. Both are water-dependent (Stokke and Du Toit 2002, le Roex et al. 2019) and commit a substantial proportion of their daily time budget to foraging, such that factors that inhibit ease of movement are important. Steep slopes or rocky areas hinder the movement of either species (Wall et al. 2006, Odendaal-Holmes et al. 2014). Elephants, owing to a larger body size, can travel farther between feeding areas and water sources than rhinoceroses (le Roex et al. 2019, Sach et al. 2019), and thereby use a greater proportion of the landscape. Both elephants and black rhinoceroses are likely to frequent parts of the landscape where topo-edaphic features such as geological type, texture, depth, and nutrient status of soil, and topographic position result in the production of adequate quantities of nutritious plant material (Clegg and O'Connor 2017). Areas used by black rhinoceroses may therefore be nested within those used by elephants, resulting in competition.

Conspicuous competition for food between elephants and black rhinoceroses is expected owing to their physiological and ecological similarities. Both are hindgut fermenters that rely on a fast rate of food intake, show short ingesta retention times compared to ruminants, and rely heavily on easily digestible cell contents to meet their nutritional requirements (Clauss et al. 2005, O'Connor et al. 2007). Both species should therefore seek feeding locations that offer plants with abundant cell contents and a reduced proportion of structural tissue (O'Connor et al. 2007). Such locations usually have a greater availability of moisture and nutrients for plant growth (van Lieverloo et al. 2009, Okita-Ouma et al. 2021), which are in turn determined by topo-edaphic factors (Clegg and O'Connor 2017, Clegg et al. 2021).

The diet of both species is catholic (>100 plant species per locality) and varies considerably across localities (Oloo et al. 1994, Kerley et al. 2008, Buk and Knight 2010). However, a few plant species usually comprise the bulk of the diet (Clegg 2010, Anderson et al. 2020) and diet selection shows a pronounced seasonal pattern (Kerley et al. 2008, Duthé et al. 2020). Elephants make increasing use of browse during the dry season (Owen-Smith 1988, Clegg 2010), which has the potential to intensify competition with the black rhinoceros. Forbs comprise a substantial component of the wet-season diet of black rhinoceroses, who shift their diet to woody browse during the dry season when forb abundance declines (Goddard 1970*a*, Landman et al. 2013). Therefore, the black rhinoceros is expected to face heightened competition from elephants at the height of the dry season (Landman and Kerley 2014, Waweru and Githaiga 2014).

Despite the similarities in space use and diet mentioned above, the influence of a marked difference in body size on foraging behavior may promote ecological separation between the 2 species (Owen-Smith 1988). Elephants stand taller than black rhinoceroses, with shoulder heights of 3–3.5 m and 1.6 m, respectively (Skinner and Chimimba 2014). Elephants harvest forage from the ground up to 8 m but prefer to browse at 1–2 m (Smallie and O'Connor 2000, Stokke and Du Toit 2000), whereas rhinoceroses browse mainly between 0.5–1.5 m, with peak browse height <1 m (Ganqa et al. 2005, Adcock 2006). The range in height at which elephants can forage therefore encompasses that of rhinoceroses, but it has not been determined whether stratification of feeding height might develop between these 2 species. Both elephants and black rhinoceroses commonly feed by removing stems or twigs, but there may be a degree of separation in the stem diameter of the twig or branch removed. Elephants, owing to adept use of their trunk, can harvest branches with diameters of about 5 cm or less (Bowland and Yeaton 1997). By contrast, rhinoceroses harvest forage through biting and therefore are restricted to twigs up to 1.5 cm in diameter for hardwood species and 3 cm for succulents (Adcock 2006, Landman et al. 2013), although twigs <6 mm in diameter provide the best nutritional quality (Palo et al. 1992).

A heightened competitive influence of elephants on black rhinoceroses can be expected when elephants are at high density (Goddard 1970*b*, Kerley et al. 2008), movement of either species is constrained within a fixed area, elephants have already depleted the abundance of food sought by rhinoceroses, or during the dry season when dietary overlap between the 2 species is expected to increase because of resource limitation. Competition is expected to favor elephants owing to their larger size and greater foraging adaptations than rhinoceroses (Owen-Smith 1988, Landman et al. 2013). Indeed, elephants may force black rhinoceroses to shift their diet and eat less-preferred forage, including grass (Landman et al. 2013, Landman and Kerley 2014). Woody species differ markedly in their ability to respond to elephant impact, some resprouting strongly (Lewis 1991, Makhado et al. 2014), whereas others do not (Kerley et al. 2008). Sustained elephant use may therefore deplete availability of woody vegetation, but it may also increase the amount of food available to other browsers by eliciting dense coppice growth (Styles and Skinner 2000), often composed of many small-diameter stems bearing higher nutrient content than the original stems (Makhabu et al. 2006, Kohi et al. 2011). A primary question facing the reintroduction of the black rhinoceros is the extent to which the plant species impacted by elephants are those sought by rhinoceroses. A second question is whether resources are partitioned between black rhinoceroses and elephants, which may manifest in partial or complete spatio-temporal separation in use of habitat, plant species, plant parts, size of parts, or the height above ground of parts eaten (Voeten and Prins 1999, Wilson and Kerley 2003). Differences during the dry season, when resources are most limited in semi-arid savannas, are particularly critical.

The Gonarezhou National Park (GNP) in Zimbabwe provides a suitable test case for examining the potential impact of elephants on the success of a reintroduced population of black rhinoceroses. The park forms part of the historical distribution of black rhinoceroses, which were extirpated by 1938 (Du Toit et al. 2005), re-established in the 1970s but lost to poaching, and reintroduced again in 2021. However, elephant density in GNP has increased from 1 elephant/km^2 to 2 elephants/km^2 since the 1980s (Dunham 2022), which has considerably affected woodland vegetation (Cunliffe et al. 2012). Consequently, habitat for black rhinoceroses in GNP may be currently less suitable compared to historical conditions.

Given similarities in basic resource requirements, we hypothesized strong overlap in space use and use of plant species between black rhinoceroses and elephants. However, we hypothesized that a marked difference in body size should result in differences in feeding height and stem size selection when browsing on woody plants. To test these hypotheses, we investigated 1) if sites that are heavily used by rhinoceroses are also heavily used by elephants (and what site characteristics influence the extent of use by either species), 2) the extent of overlap in plant species selection by black rhinoceroses and elephants, 3) evidence of height stratification of feeding height between species, 4) differences in diameters of woody stems used by each species, and 5) if elephant-induced coppice growth of woody plants improves browse availability for black rhinoceroses. On the assumption that the dry season is the bottleneck period for acquiring food, we restricted our study to this period.

STUDY AREA

The GNP study area is located in the southeastern lowveld of Zimbabwe (21° 00′–22° 15′ S; 30° 15′–32° 30′ E; Figure 1). It covers 5,053 km^2, with elevation ranging from 165–578 m above sea level. The GNP has a tropical, semi-arid climate with a hot-wet season from November to March, a cool-dry season from April to July, and a hot-dry season from August to October. Mean annual rainfall is 466 mm at Chipinda Pools, 84% of which falls between November and March. Rainfall of the 2021–2022 season preceding this study was 392 mm. Mean maximum temperatures exceed 30°C in all months except June and July (Dunham 2012).

The study area was in northern GNP, which is bisected by the Runde River, with permanent water also available in pools along its tributaries, Massasanya Dam, and the Chiloveja Spring (Figure 1). Most of the study area is underlain by granophyre that forms the rocky Chuhonja-Sibonja Hills, rising 150 m above a basalt plain along the northwest boundary, and alluvial deposits along the Runde River (Cunliffe et al. 2012). Clay- and base-rich soils have formed from the basalt geology, whereas soils of intermediate fertility have formed from the granophyre that show considerable variation in depth and rockiness. The distribution of the 10 vegetation types recognized within the study area is strongly influenced by underlying geology (Cunliffe et al. 2012). Dominant woody species include mopane (*Colophospermum mopane*), red bushwillow (*Combretum apiculatum*), Lebombo ironwood (*Androstachys johnsonii*), mountain acacia (*Brachystegia torrei*), and tamboti (*Spirostachys africana*). Plant nomenclature follows the Flora of Zimbabwe (Hyde et al. 2024).

In May 2021, 29 black rhinoceroses were reintroduced into a 500-km^2 Intensive Protection Zone (IPZ; Figure 1) that was centered on historical rhinoceros habitat (Dunham and Robertson 2020). The founder animals were sourced from protected areas in Zimbabwe with semi-arid climates similar to that of Gonarezhou. The IPZ was bounded by a 1.1-m-high 2-strand electric fence that was impermeable to rhinoceros but semi-permeable to most other species because they can pass over or under it. Elephant breeding herds, buffaloes (*Syncerus caffer*), and hippopotamuses (*Hippopotamus amphibius*) are, however, mostly restricted by the fence. The elephant population of GNP was maintained at ≤1 elephant/km^2 prior to the 1991–1992 drought, but thereafter the population grew at a mean annual rate of 6.2% from 1995 to 2009 (Dunham 2012), with 10,812 individuals (2.14/km^2) recorded in 2022 (Dunham 2022). Elephants occurred at a density of 1.7 individuals/km^2 in the IPZ at the time of the introduction of rhinoceroses. Greater kudu was the next most abundant browser in the park.

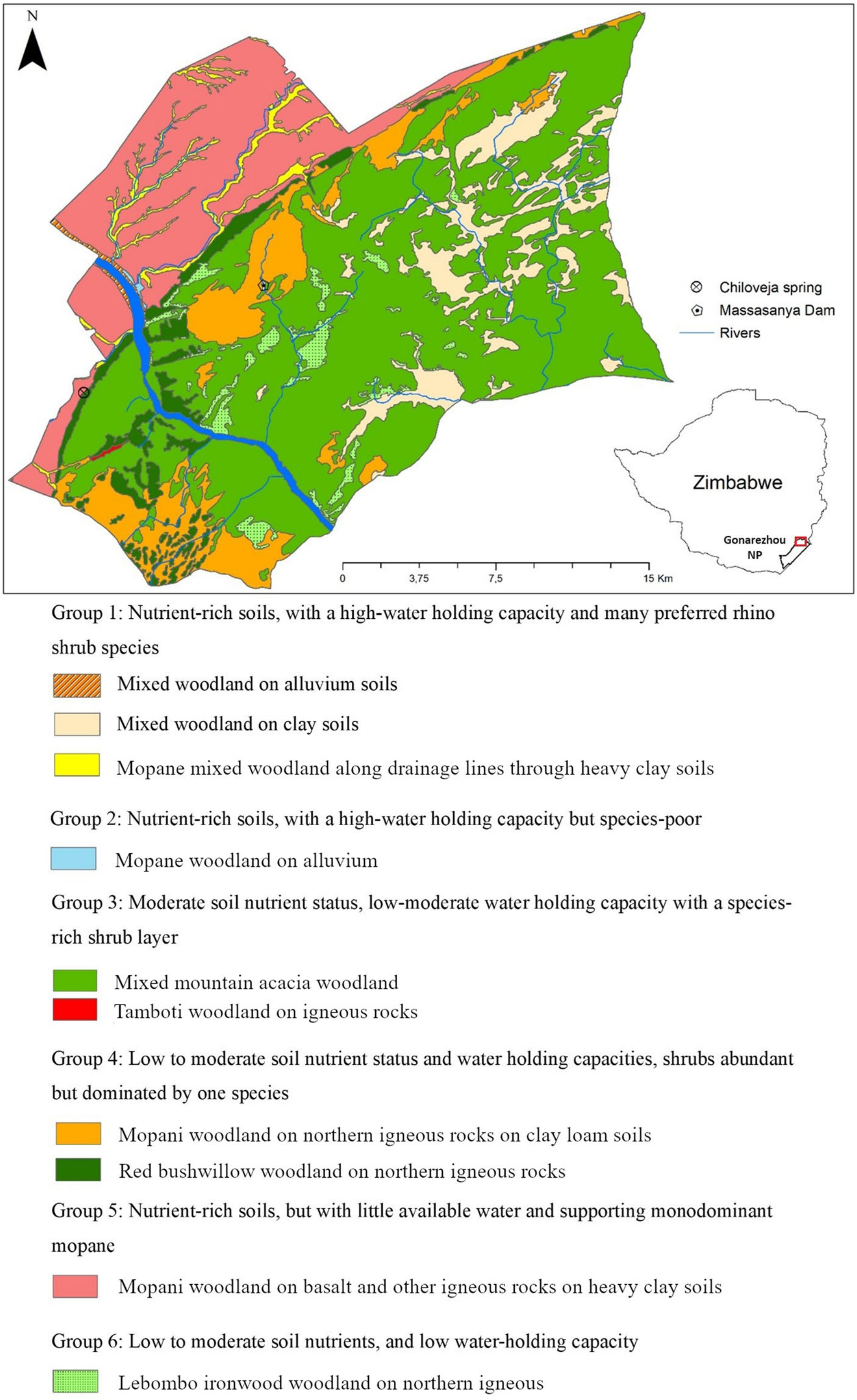

FIGURE 1 The vegetation types and water sources of the Intensively Protected Zone, northern Gonarezhou National Park (NP), Zimbabwe, 2022, with the inset showing the location of the park. Legend to the vegetation types, grouped according to perceived character.

METHODS

Sampling design and data collection

We identified suitable strata for sampling the level of browse use by rhinoceroses based on the movement patterns of 21 rhinoceroses old enough to have their horn fitted with a very high frequency (VHF) transmitter. We recorded 1,889 rhinoceros locations between their release in May 2021 and June 2022, which we used to create a heatmap of the local density of rhinoceroses across the IPZ using a kernel density analysis (Heatmap function of QGIS; QGIS Development Team 2021). The rhinoceroses were at low density in the IPZ (0.06/km^2) and had only been using the area for a year, so we used a small radius (200 m) for the kernel analysis to maintain a close spatial association between the utilization distribution depicted by the heatmap and the actual sighting data. We subjectively reclassed the continuous data of the heatmap into discrete low-, medium-, and high-use zones (cutoffs: low = <3; medium = ≥3 and <6; high = ≥6) to create a putative stratification for sampling. We then selected 25 random points in each stratum for sampling (Figure 2). The purpose of the stratification was to increase the probability that the sample sites adequately represented the range of levels of browse use by rhinoceroses in the study area and we did not use the stratification in subsequent statistical analyses. We maximized the distance between sample points to ensure spatial independence, but because we purposely kept the high-use zone small to increase the probability of encountering rhino use during field sampling, we were restricted to a minimum distance of 180 m between points. The mean distance between the 75 sample points and their nearest neighbor sample point was 979 m, with 28 of the points having their nearest neighbors 180 m away. There was no correlation between the level of browse use by rhinoceroses at a sample point and the level of use at its nearest neighbor sample point for the full data set

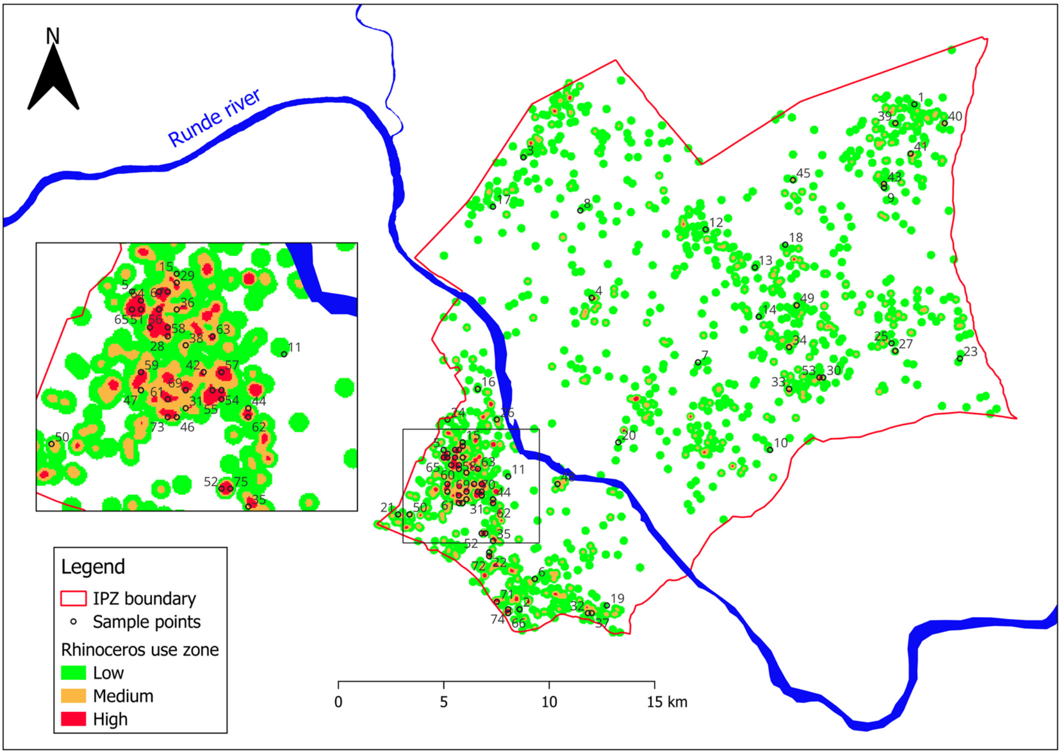

FIGURE 2 Position of sampling points within the low, medium and high black rhinoceros use zones within the Intensively Protected Zone (IPZ), Gonarezhou National Park, Zimbabwe, 2022.

($r_s = -0.041$, df = 75, $P = 0.73$) or the subset of the points that had nearest neighbors 180 m away ($r_s = -0.134$, df = 28, $P = 0.498$). This suggests a level of independence between sample points that is possibly explained by the high level of topographic variation over short distances within the study area.

We used a global positioning system (GPS) unit to navigate to each of the 75 field sampling locations. Upon arrival at a sample point, we conducted a search of woody plants within a 50-m radius and designated the first shrub encountered that had been browsed by a rhinoceros as the northeastern corner of a rectangular sampling plot. A stem bitten by a rhinoceros is usually easily distinguished from elephant browsing because a rhinoceros makes a sharp, clean bite at 45° to the stem, whereas elephants make a rough break (Joubert 1971). If we were unsure whether a small twig had been bitten off by an animal other than a rhinoceros (e.g., greater kudu), we did not attribute the bite to rhinoceros browsing. We laid out a 50-m measuring tape in a southerly direction from the browsed shrub to form the length of the plot. The width of the plot was increased to the west until a minimum of 30 individual woody plants were included (usually a width of 5–10 m was required depending on plant density). Plots were never long or wide enough to extend into nearby plots so spatial independence was not compromised. We recorded plot corners using a GPS. For each woody plant within a plot, we recorded its species identity, measured its height (cm) up to a maximum of 5 m, its maximum canopy diameter (cm) using a builder's measuring tape, and the canopy diameter at right angles to that of the maximum canopy diameter (cm), scored canopy shape as 1 of 7 possible shapes (Melville et al. 1999), and visually ranked the percentage of canopy volume removed by elephants (% damage score) using an 8-point scale (0, 1–10, 11–25, 26–50, 51–75, 76–90, 91–99, 100%; see Walker 1976 for more detail).

For each woody plant in a plot that had been used by a rhinoceros, we measured the stem diameter (mm) and height above the ground (cm) of each bite using a digital vernier caliper and a staff, respectively. We also measured the stem diameter and height above the ground of the branches broken by elephants. However, to limit sampling to manageable proportions (because often a large number of canopy branches had been broken off by elephants per plant), we sampled 1 randomly selected plant for measurement of elephant break points from each of the 5 dominant species in a plot. We measured branches broken by elephants only if they were <5 m above the ground. We also recorded whether a stem browsed by a rhinoceros or elephant was the result of coppice growth or not, and whether the coppice was due to elephants.

We characterized the environment of each plot in terms of soil properties, distance to permanent water, and landscape influence on soil water regime. We collected 4 samples of the top 15 cm of soil at each corner of a plot using an auger. We submitted a well-mixed composite of the 4 samples to the Agrianalysis Centre in Harare, Zimbabwe for analysis of pH, nitrogen before and after incubation, conductivity, phosphorus, calcium, magnesium, sodium, potassium, and the percentage of sand, silt, and clay. We recorded the topographical position of a plot as either crest, upper slope, mid-slope, lower slope, or valley bottom. We estimated boulder cover using the same 8-point scale that we used to measure elephant browsing.

We determined the distance from a plot to surface water during the season of study in QGIS using a modified normalized difference water index layer (Huang et al. 2018), which was calculated using Sentinel 2 satellite imagery captured on 21 September 2021 (a cloud-free day), at the height of the late-dry season when availability of surface water was at its lowest in the IPZ. We calculated the topographic wetness index (TWI) of a plot using an ALOS Palsar RTC high-resolution (12.5 m) digital elevation model (Alaska Satellite Facility 2015), and the System for Automated Geoscientific Analyses TWI algorithm of QGIS (QGIS Development Team 2021). The TWI quantifies the effect of surface topography on the soil moisture regime of a site.

Data analysis

We performed all data analyses using R (R Core Team 2023). We investigated overlap in use between rhinoceroses and elephants across space and plant species in the following manner. For each plot, we calculated the level of browse use by rhinoceroses as the sum of the cross-sectional area of all stems bitten off per unit ground area

(cm^2/m^2), with the cross-section of each stem assumed to be circular. We also calculated rhinoceros use scores for individual plant species in the same way except that the values for each shrub species were converted to proportions of the total stem cross-sectional removed with calculations being restricted to individual plant species with a sample size of ≥15 individuals. We calculated browse use by elephants per plot as the average percent volume of woody canopy removed (Walker 1976), by first calculating a weighted damage (WD) score (%) for each shrub:

$$\text{WD} = \text{V}_\text{R}(\text{damage \% [midpoint of range]}),$$

where V_R is reconstructed shrub volume calculated as

$$\text{V}_\text{R} = \text{V}_\text{M}(100/(100 - \text{\% damage})),$$

where V_M is the measured volume.

We calculated percent damage for a plot as the sum of the weighted damage scores of the shrubs in a plot divided by the total reconstructed shrub volume of the plot:

$$\text{Plot percent elephant damage} = \sum_i^n WD_i / \sum_i^n V_{ri},$$

where WD_i is the weighted damage score for the ith shrub in a plot and V_{ri} is the reconstructed canopy volume of the ith shrub in the plot. We calculated elephant damage scores for individual plant species in a similar manner except that the values for each shrub species were converted to percentages of the total biomass removed by elephants (%) and by limiting the calculation to individual plant species with a sample size ≥15 individuals.

Analysis of overlap in space use demands the simultaneous comparison of rhinoceros and elephant use at a site. Multiple regression analyses such as generalized linear modeling or generalised additive modeling cannot accommodate the simultaneous analysis of multiple dependent variables that are measured using different scales, and given that elephant and rhinoceros browse-use-scores were not directly comparable because they were measured using different scales, we examined the relation between levels of rhinoceros and elephant use across plots (spatial overlap) using Pearson's correlation and model-based clustering. Plots were clustered into 4 groups based on pairings of the level of rhinoceros and elephant browse use (high elephant–high rhinoceros, high elephant–medium rhinoceros, high elephant–low rhinoceros, low elephant–low rhinoceros) using model-based clustering based on a Gaussian finite mixture model (package mclust; Scrucca et al. 2016), and using the Bayesian Information Criterion (BIC) to determine the model with the best fit (Burnham and Anderson 2004). The number of use categories was based on the optimal numbers of clusters selected by running models with 1 to 9 latent classes, each with 14 different covariance matrix parameterization possibilities (Scrucca et al. 2016). We calculated the thresholds of each use category using the predict.Mclust function.

We then investigated the relationship between rhinoceros and elephant browse use across space and the topo-edaphic environment using linear discriminant analysis (LDA). After checking for collinearity using Pearson's correlation coefficient as a diagnostic and a threshold value of $r < 0.8$, we dropped nitrogen before incubation, calcium, and clay from the analysis. Use category, determined using model-based clustering of plots, was the (categorical) dependent variable, and the topo-edaphic variables were predictors. We conducted the analysis using the lda and LDA functions of the R packages MASS and flipMultivariates, respectively (Venables and Ripley 2002, Displayr 2023). The LDA function identifies the predictor variables that best discriminate between 2 or more dependent categories. We transformed topo-edaphic variables, after centering and standardization, to the best approximation of a normal distribution using the bestNormalize function (Peterson and Cavanaugh 2020) to meet model assumptions. We randomly split the data into 2 subsets of 80% for training and 20% for assessing accuracy of the LDA.

To investigate overlap in the use of plant species between rhinoceroses and elephants, we compared the average total cross-sectional area of stems removed by rhinoceroses and the average percent biomass removed by elephants for the plant species with a sample size ≥15. We were not able to conduct simultaneous comparisons of use of a plant species by elephants and rhinoceroses using standard multiple regression because of the different units of measurement but instead conducted comparisons by grouping plant species into 9 categories depending on pairings of the level of use by each animal species (high elephant–high rhinoceros, high elephant–medium rhinoceros, high elephant–low rhinoceros, moderately high elephant–low rhinoceros, high elephant–no rhinoceros, medium elephant–high rhinoceros, medium elephant–low rhinoceros, low elephant–low rhinoceros, low elephant–no rhinoceros) using model-based clustering (Scrucca et al. 2016). We chose the optimum number of use categories by running models with different numbers of latent classes and covariance matrix possibilities and used BIC to determine the model with the best fit (Burnham and Anderson 2004).

To determine overlap in feeding height and use of stem sizes we constructed kernel density plots depicting the distribution of the heights above the ground and the diameters of stems used by rhinoceroses or elephants using ggplot2 (Wickham 2016). We used generalized linear mixed effects models (GLMMs) to test for differences between rhinoceroses and elephants in either variable. Our dependent variable was the height above the ground of a bite, or the diameter of the stem used. Animal species was a fixed predictor variable, and plot identity and woody plant species were crossed random effects.

To determine overlap in use of coppice versus non-coppice growth, we calculated the percentage of coppiced versus non-coppiced stems browsed by rhinoceroses or elephants for each woody plant in a plot. We examined this response variable using a GLMM, assuming binomial errors and a logit-link function, with animal species as a fixed predictor variable, and plant species and plot identity as crossed random effects. We fitted models using lme4 (Douglas et al. 2015), standardized predictor variables to zero mean and unit variance, computed confidence intervals (95%) and *P*-values using a Wald *t*-distribution approximation, and checked each model for linearity, normality, and homoscedasticity, although GLMM results are fairly robust to heteroscedasticity (Schielzeth et al. 2020).

RESULTS

Spatial and environmental patterns of use

There was no correlation between the levels of rhinoceros and elephant use across plots ($r_s = 0.04$; df = 73; $P = 0.75$). The best model for clusters of elephant and rhinoceros use was one with the use categories of high elephant–high rhinoceros, high elephant–medium rhinoceros, high elephant–low rhinoceros, and low elephant–low rhinoceros (Figure 3). Seventy-four percent of the plots had high levels of elephant use (>50% of woody biomass removed) and at least some rhinoceros use and 12% had medium to high levels of rhinoceros use, all of which also had high levels of elephant use, indicating substantial spatial overlap between the foraging locations of the 2 species.

In terms of the relationship between browse use and the topo-edaphic environment, the first 3 linear discriminant functions of the LDA accounted for 66.7%, 21.6%, and 11.7% (total of 100%) of the variation in site characteristics among the 4 use categories. Model accuracy was 67%. Of 14 predictor variables, only shrub density ($R^2 = 0.19$, $P = 0.002$), pH ($R^2 = 0.18$, $P = 0.01$), and magnesium ($R^2 = 0.19$, $P = 0.01$) had a significant role in discriminating between use categories (Table 1), possibly owing to limited variation in edaphic conditions across plots (e.g., sandy loam, 76%; loamy sand, 13%; sandy clay loam, 9%; sandy clay, 1%), although a number of the other topo-edaphic variables were strong predictors for one or more of the use categories.

The first discriminant function (LD1) represented a gradient from dense shrub thickets, dominated by millettia (*Millettia usaramensis*), that were close to permanent water on acidic soils rich in potassium and phosphorus, to more open shrublands that were farther from water on alkaline soils rich in nitrogen, sodium, and magnesium (Figure 4A). This axis corresponds with a gradient in elephant use, with higher levels of elephant use occurring on alkaline than

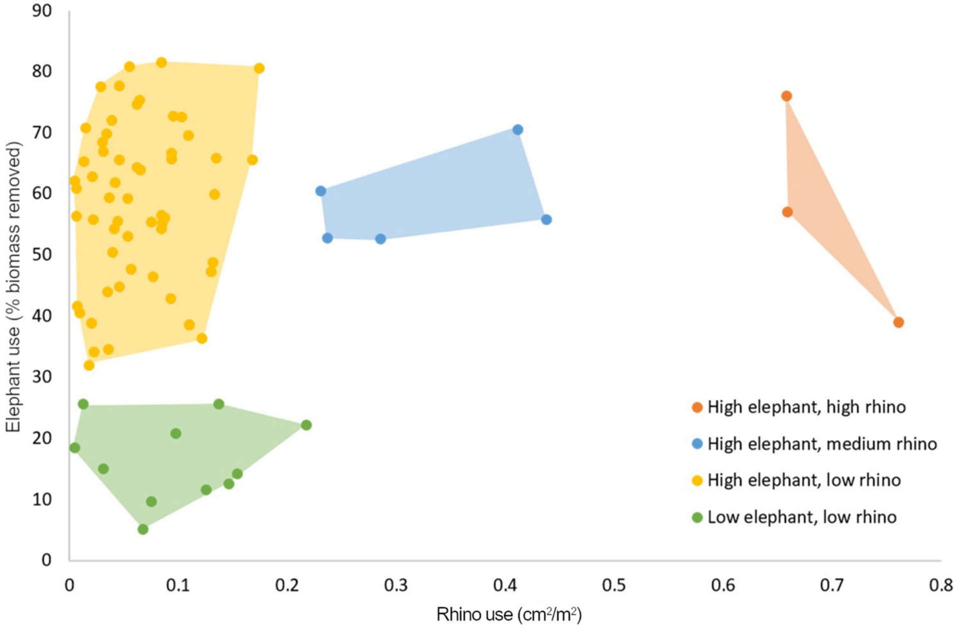

FIGURE 3 Cluster analysis of sample plots in terms of use by black rhinoceroses and African elephants, sampled in the Intensively Protected Zone, Gonarezhou National Park, Zimbabwe, during the hot dry season of 2022. Four clusters were identified and are represented in different colors. Elephant use (% biomass removed) is represented by an index based on average damage to shrubs within a plot. Rhino use (cm^2/m^2) represents the proportional stem cross-sectional area removed by rhinoceroses.

on acidic substrates, despite the higher shrub density and closer proximity to surface water of the thickets on acidic soils. Magnesium and pH were both significant in discriminating between the use categories of high elephant–high rhinoceros and low elephant–low rhinoceros.

The second discriminant axis (LD2) corresponded with the overall variation in rhinoceros use, showing a gradient from sites close to surface water with a high shrub density on silty soils with high conductivity that were rich in sodium, to more open shrublands farther from water with sandy soils rich in magnesium and phosphorus (Figure 4A). Rhinoceroses fed more at sites close to water with silty soils rich in sodium rather than at sites farther from water with sandy soils and elevated levels of magnesium. Shrub density was significant in discriminating between the categories high elephant–high rhinoceros and high elephant–low rhinoceros, illustrating that areas of high shrub density were selected by black rhinoceroses in GNP. Magnesium and pH both discriminated between the categories high elephant–high rhinoceros and low elephant–low rhinoceros, indicating that both species fed more in areas with elevated pH and lower levels of magnesium.

The third discriminant axis (LD3) separated the plots with medium levels of rhinoceros use from the other categories (Figure 4B), and was represented by a gradient from gently sloping, boulder-strewn sites that were close to water and with a high TWI and soil conductivity and a dense shrub layer, to steeply sloping sites farther from water with lighter textured acidic soils. Rhinoceroses fed more at sites with a dense shrub layer, high TWI, and elevated conductivity even if they were characterized by high boulder cover.

Plots with both high elephant and high rhinoceros use occurred close to surface water and had elevated soil nutrient levels, and plots in the high elephant–medium rhinoceros use category were characterized by high values of TWI and shrub density. The LDA predicted the correct use category for 85.3% of the sample plots, indicating that, for the most part, the measured variables were able to correctly discriminate between use categories (high

TABLE 1 The mean, standard error, R^2, and *P*-values of the predictor variables for 4 classified categories of use by African elephants and black rhinoceroses in Gonarezhou National Park, Zimbabwe, sampled during the hot dry season of 2022.

Site characteristic variable	High elephant, high rhino	SE	High elephant, medium rhino	SE	High elephant, low rhino	SE	Low elephant, low rhino	SE	R^2	*P*
Boulder coverage (%)	29.50	26.79	30.30	17.75	32.20	4.56	28.30	9.68	0.00	1.00
Distance to permanent surface water (m)	1,377.0	736.30	3,288.0	753.40	3,161.0	247.60	3,144.0	510.0	0.06	0.60
Topographic wetness index	8.10	1.99	13.30	0.32	9.50	0.53	9.40	1.22	0.05	1.00
Shrub density (number/m^2)	0.38	0.04	0.55	0.23	0.23	0.03	0.33	0.04	0.19	0.002
Slope (°)	10.01	4.05	3.19	0.57	4.16	0.48	3.64	1.28	0.07	1.00
pH	6.20	0.35	5.70	0.23	5.70	0.07	5.00	0.19	0.18	0.01
Conductivity (µs/cm)	159.0	42.10	117.20	25.03	95.80	6.23	59.90	3.89	0.14	0.19
Phosphorus (mg/L)	27.0	5.51	17.20	2.46	21.80	1.42	18.60	1.91	0.04	1.00
Magnesium (mEq)	4.19	0.83	2.27	0.23	3.02	0.23	1.53	0.22	0.19	0.01
Potassium (mEq)	0.51	0.14	0.41	0.11	0.38	0.03	0.32	0.03	0.03	1.00
Sodium (mEq)	0.14	0.04	0.08	0.02	0.09	0.01	0.05	0.01	0.13	0.17
Nitrogen post incubation (mg/L)	38.30	17.37	40.60	5.24	41.80	1.69	30.30	1.92	0.12	0.12
Sand (%)	68.60	9.02	76.60	2.45	74.30	1.04	74.10	1.46	0.02	1.00
Silt (%)	13.30	4.67	9.20	1.62	10.40	0.54	10.0	1.0	0.02	1.00

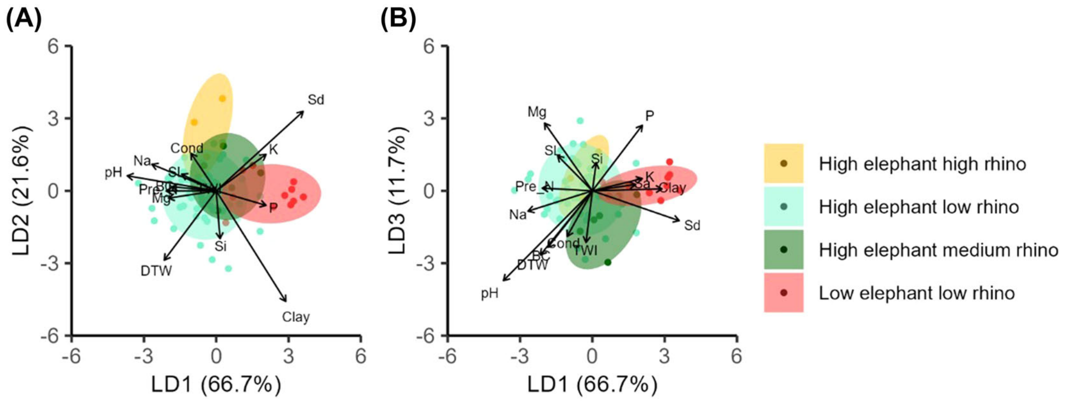

FIGURE 4 Linear discriminant analysis biplot of the relationship between African elephant and black rhinoceros browse use categories and topo-edaphic environment based on plots (represented by colored dots) sampled in the Intensively Protected Zone, Gonarezhou National Park, Zimbabwe, during the hot dry season of 2022. Shown are A) axes 1 and 2 (LD1 and LD2), and B) axes 1 and 3 (LD1 and LD3). Ellipses were calculated at $P = 0.8$. The length and direction of the arrows indicate the strength and direction of influence of each environmental variable in relation to the discriminant axes. Variables include sand (Sa), silt (Si), potassium (K), sodium (Na), magnesium (Mg), pH (pH), topographic wetness index (TWI), nitrogen after incubation (N), phosphorus (P), slope (SL), boulder cover (BC), distance to permanent water (DTW), conductivity (Cond), and shrub density (Sd).

elephant–high rhinoceros: 67%; high elephant–low rhinoceros: 95%; high elephant–medium rhinoceros: 20%; low elephant–low rhinoceros: 73%).

Overlap in use of plants

The best model identified 9 categories based on use by rhinoceroses and elephants, for which rhinoceros use ranged from none to high, and elephant use ranged from low to high (Figure 5). Twenty-one percent of the identified plant species had high levels of elephant use (>50% of woody biomass removed), while 13% had high levels of rhinoceros use. Rhinoceroses were recorded to browse on 46 plant species, of which bean tree (*Markhamia zanzibarica*), mopane, and red bushwillow were used the most (Figure 6A). Elephant use was recorded across 87 plant species, with mopane, red bushwillow, and russet bushwillow (*Combretum hereroense*) having the greatest volume of canopy removed (Figure 6B). All plant species with high or medium levels of rhinoceros use also had high levels of elephant use, indicating substantial dietary overlap during the dry season.

Elephants broke branches at an average height of 93.2 ± 1.01 (SE) cm above the ground, which did not differ from the average height at which rhinoceroses fed of 81.6 ± 0.61 cm (Figure 7; Table S1, available in Supporting Information), indicating strong potential feeding overlap between the 2 species in the vertical plane (GLMM: R^2-marginal = $3.35e^{-04}$, R^2-conditional = 0.62, $P = 0.118$). Elephants broke branches with an average stem diameter of 1.27 ± 0.019 cm, while rhinoceroses were found to feed on smaller twigs averaging 0.49 ± 0.003 cm in diameter (GLMM: R^2-marginal = 0.23, R^2-conditional = 0.41, $P < 0.001$), indicating a degree of separation between the 2 species at the level of the plant stem (Figure 8; Table S2, available in Supporting Information). Rhinoceroses fed more on coppiced stems than elephants, whereas elephants fed more on non-coppiced stems (GLMM: R^2-marginal = 0.01, R^2-conditional = 0.03, $P < 0.001$; Figure 9; Table S3, available in Supporting Information), indicating that elephants potentially facilitate the future availability of browse for black rhinoceroses.

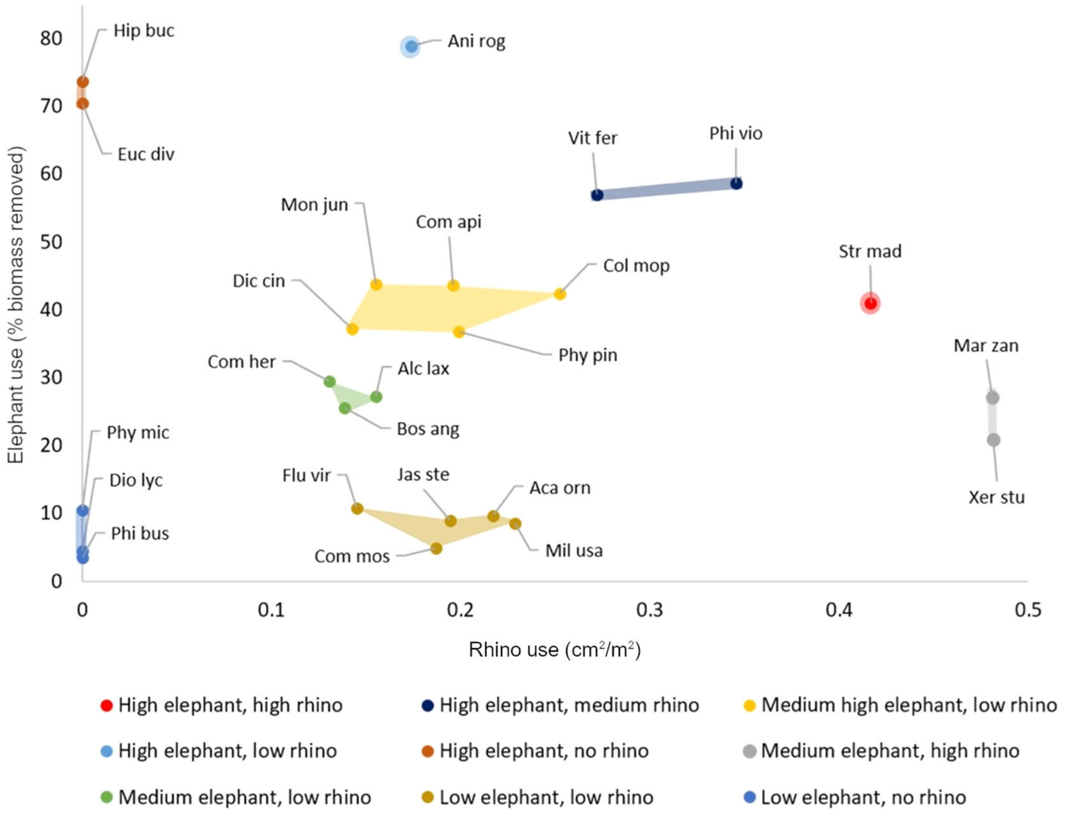

FIGURE 5 African elephant and black rhinoceros use across different plant species within the Intensive Protection Zone, Gonarezhou National Park, Zimbabwe, during the hot dry season in 2022. Species include *Acalypha ornata* (Aca orn), *Alchornea laxiflora* (Alc lax), *Anisotes rogersii* (Ani rog), *Boscia angustifolia* (Bos ang), *Colophospermum mopane* (Col mop; mopane), *Combretum apiculatum* (Com api; red bushwillow), *Combretum hereroense* (Com her; russet bushwillow), *Combretum mossambicense* (Com mos), *Dichrostachys cinerea* (Dic cin), *Diospyros lycioides* (Dio lyc), *Euclea divinorum* (Euc div), *Flueggea virosa* (Flu vir), *Hippocratea buchananii* (Hip buc), *Jasminum stenolobum* (Jas ste), *Markhamia zanzibarica* (Mar zan; bean tree), *Millettia usaramensis* (Mil usa; millettia), *Monodora junodii* (Mon jun), *Philenoptera bussei* (Phi bus), *Philenoptera violacea* (Phi vio), *Phyllanthus micranthus* (Phy mic), *Phyllanthus pinnatus* (Phy pin; Lebombo potato bush), *Strychnos madagascariensis* (Str mad; black monkey orange), *Vitex ferruginea* (Vit fer), *Xeroderris stuhlmannii* (Xer stu; wing pod). English common names are provided parenthetically for species mentioned in the text. Elephant use (% biomass removed) is represented by an index based on average damage to shrubs within a plot. Rhino use (cm^2/m^2) represents the proportional stem cross-sectional area removed by rhinoceroses.

DISCUSSION

We did not detect a pattern of spatial segregation between elephants and rhinoceroses based on our measures of browse use. This is attributed to a high density of elephants within the IPZ that apparently precluded rhinoceroses from finding suitable foraging areas where elephant density was low. Plots with medium or high rhinoceros use also had high levels of elephant use; areas showing low elephant use were invariably also unfavorable to black rhinoceroses, indicating both species use similar criteria when choosing foraging patches (Goddard 1970*a*, Sach et al. 2019). The habitat used by rhinoceroses was, therefore, primarily nested within the habitat used by elephants within the IPZ (Figure 3).

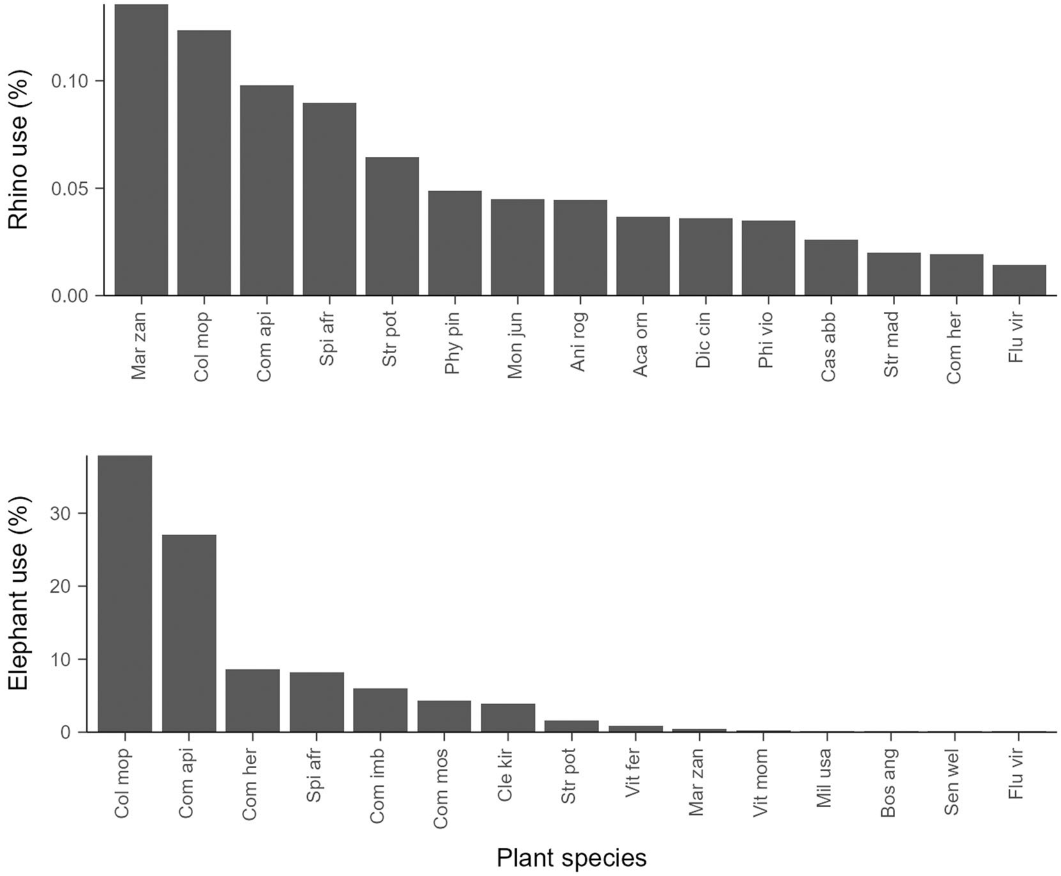

FIGURE 6 The 15 plant species that contributed the largest proportion to A) black rhinoceros and B) African elephant diet in the Intensive Protection Zone, Gonarezhou National Park, Zimbabwe, during the hot dry season of 2022. Species include *Acalypha ornata* (Aca orn), *Anisotes rogersii* (Ani rog), *Boscia angustifolia* (Bos ang), *Cassia abbreviata* (Cas ab), *Cleistochlamys kirkii* (Cle kir), *Colophospermum mopane* (Col mop; mopane), *Combretum apiculatum* (Com api; red bushwillow), *Combretum hereroense* (Com her; russet bushwillow), *Combretum imberbe* (Com imb), *Combretum mossambicense* (Com mos), *Dichrostachys cinerea* (Dic cin), *Flueggea virosa* (Flu vir), *Markhamia zanzibarica* (Mar zan; bean tree), *Millettia usaramensis* (Mil usa), *Monodora junodii* (Mon jun), *Philenoptera violacea* (Phi vio), *Phyllanthus pinnatus* (Phy pin; Lebombo potato bush), *Senegalia welwitschia* (Sen wel), *Spirostachys africana* (Spi afr; tamboti), *Strychnos madagascariensis* (Str mad; black monkey orange), *Strychnos potatorum* (Str pot), *Vitex ferruginea* (Vit fer), *Vitex mombassae* (Vit mom). English common names are provided parenthetically for species mentioned in the text. Rhino use (%) represents the percentage of the total bite cross-sectional area contributed by each plant species across all plots. Elephant use (%) represents the percentage of the total canopy volume removed across all plots for each plant species.

Some differences in habitat use by elephants and rhinoceroses were evident when environmental factors were considered (Figure 4). Previous studies have shown that black rhinoceroses are highly selective when choosing habitats (Tatman et al. 2000); their selection is influenced by distance to permanent water, browse availability, elephant density, topography, and human disturbance (Goddard 1970*a*, Mukinya 1973, Odendaal-Holmes et al. 2014), especially during the dry season (Duthé et al. 2020). This study provided further evidence for GNP that rhinoceroses' space use was influenced by shrub density, distance from water, and topography (Figure 4). An expected influence of soil texture on rhinoceroses' space use was not evident possibly because sandy-loam soils dominate the IPZ. Nevertheless, some topo-edaphic variables were important.

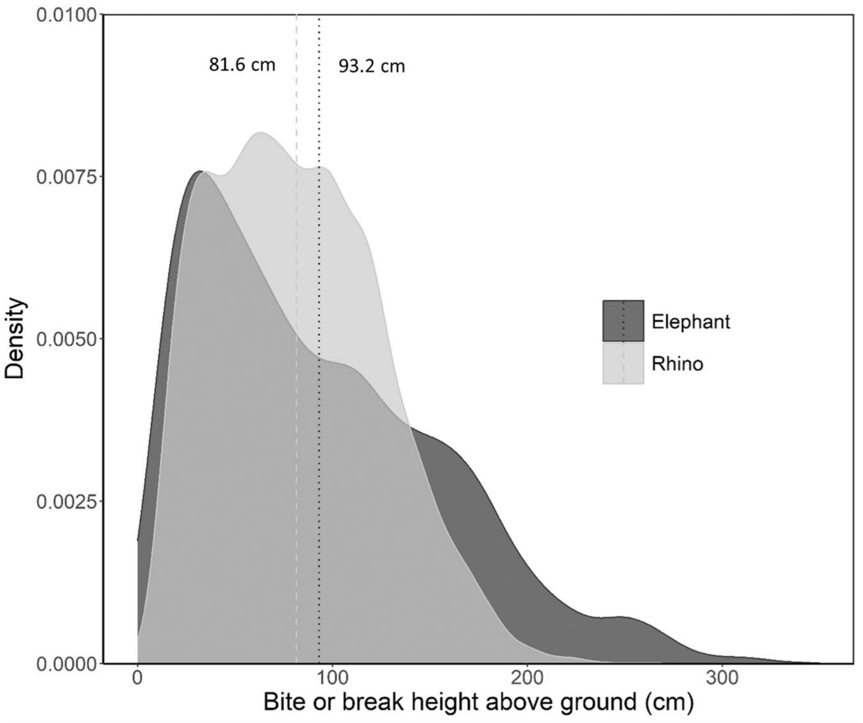

FIGURE 7 Kernel density plot of the height distribution of black rhinoceros bites and African elephant breaks recorded from sample plots in the Intensively Protected Zone, Gonarezhou National Park, Zimbabwe, during the hot dry season of 2022. Vertical short dash line is the mean elephant bite height and the long dash line is the mean rhinoceros break height.

Rhinoceroses fed more on vegetation growing on silty, high-conductivity soils. Both elephants and rhinoceroses used more alkaline substrates with low levels of magnesium, avoided relatively acidic soils where millettia thickets were found, and used areas with high sodium levels, an association recorded elsewhere in Zimbabwe for elephants that resulted in greater use of vegetation (Anderson and Walker 1971; Weir 1969, 1972). The influence of topo-edaphic variables on vegetation use by the black rhinoceros or elephants warrants further investigation.

Elephants and rhinoceroses responded differently to distance from water. Rhinoceroses fed more in areas close to water, an expected behavior for this water-dependent species in a semi-arid environment (le Roex et al. 2019). The black rhinoceros can behave as a water-independent species when succulent vegetation is available (le Roex et al. 2019), but this does not apply to GNP. By contrast, elephants fed both close to and farther away from water. Adult male elephants can forage up to 15 km from water (Conybeare 2004), while female-calf herds are limited to areas <10 km from water (Stokke and Du Toit 2002). Elephants' greater mobility therefore allows them access to a substantially larger area than rhinoceroses. However, vegetation close to water points is heavily affected by elephants (Bax and Sheldrick 1963, Chamaille'-Jammes et al. 2009, Wilson et al. 2021) and this likely negatively affects rhinoceroses. There were therefore limited refuges for rhinoceroses from elephant browsing pressure in the IPZ.

The importance of shrub density for rhinoceroses (Figure 4A) may owe to foraging needs and behavioral demands. The black rhinoceros does not like to feed in the open and needs to escape heat (Lamprey 1963). Also mothers require a hiding place for calves when they travel to drink at night (Thomson 1971).

An anomalous finding was that of higher levels of rhinoceros use in areas of high boulder cover, as black rhinoceroses have been reported to avoid steep slopes and rocky ground (Thomson 1971). Their use of these areas in the IPZ may be a consequence of limited boulder-free range with suitable forage.

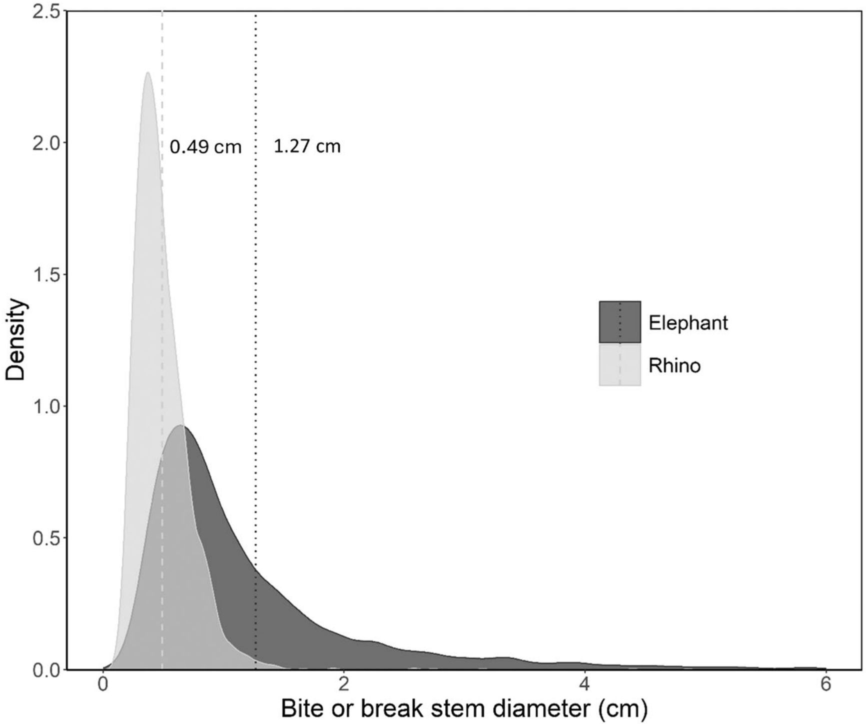

FIGURE 8 Kernel density plot of the stem diameters of black rhinoceros bites and African elephant breaks recorded from sample plots in the Intensively Protected Zone, Gonarezhou National Park, Zimbabwe, during the hot dry season of 2022. Vertical lines show mean diameters for rhino and elephant.

The findings of this study describe the relationship between elephants at high density that have always used the area, and a recently introduced (<2 years ago) rhinoceros population at very low density (<0.06 individuals/km^2). Regardless of potential changes in rhinoceros home ranges as the population settles (Linklater and Swaisgood 2008), it is unlikely that competition can be avoided, as elephant use was high across most of the IPZ. This prediction is supported by the fact that elephants usually dominate the biomass of herbivore communities in semi-arid savannas (Cumming 1982), use a large proportion of available resources (Owen-Smith 1988), and disproportionately influence other herbivores and ecosystem functioning (Fritz et al. 2002, Valeix et al. 2011).

Mega-herbivores are confronted with cost-and-benefit decisions (Muya and Oguge 2000) such that the large amount of forage required per day usually results in reduced selectivity in favor of widely available browse that may be less preferred (Morris 2003). Black rhinoceroses consequently become less selective during the dry season when resources become limited (Duthé et al. 2020). In GNP, mopane and red bushwillow, both considered of low palatability for black rhinoceroses by Adcock (2006), contributed the second and third highest proportion of browse for rhinoceroses (Figure 6). The high contribution of these 2 plant species to the diet of black rhinoceroses during the dry season may be attributed to their high abundance relative to that of other plant species (Styles and Skinner 1997, Makhado et al. 2016). The extent of use of mopane and red bushwillow in GNP may indicate that rhinoceroses are choosing browse based on availability rather than on preference.

While this study focused on competition between elephants and rhinoceroses during the dry season when both species depend on woody browse (Kerley et al. 2008, Landman et al. 2013), foraging patterns during the wet season should also be examined because wet-season nutritional gains can influence the reproductive success of long-lived mammalian herbivores (Owen-Smith 2002). Conspicuous differences in the wet-season diet between these 2 species are well recorded, with elephants favoring green grass, and both species making considerable use of forbs at

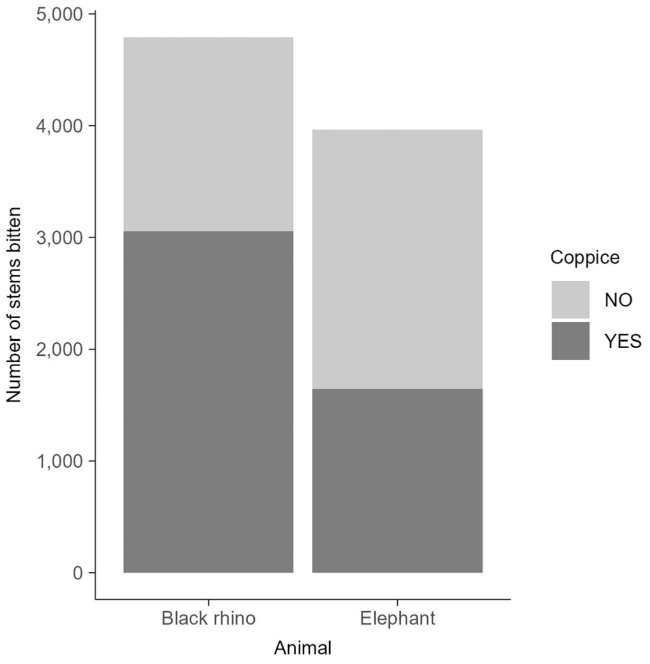

FIGURE 9 Number of bites taken by African elephants and black rhinoceroses on coppiced versus non-coppiced stems recorded from sample plots in the Intensively Protected Zone, Gonarezhou National Park, Zimbabwe, during the hot dry season of 2022.

this time (Landman et al. 2013, Landman and Kerley 2014). The degree of separation in use of forbs remains to be determined but would be difficult to assess because browsing of forbs by rhinoceroses is difficult to identify (Kotze and Zacharias 1993) and elephants may remove forb plants entirely (Clegg 2010).

There was substantial overlap in feeding height, and hence strong evidence for competition, between elephants and rhinoceroses (Figure 7). Elephants fed at an average height of 93 cm in GNP, which is consistent with their recorded preference of foraging at a height of 1-2 m (Guy 1976, Smallie and O'Connor 2000). Rhinoceroses are restricted to a browsing height of 2 m (Adcock 2006) and were found to feed at an average height of 82 cm in GNP, which is closely comparable with the average height of elephant feeding. The low feeding height of elephants recorded in GNP may largely be a consequence of elephant-induced changes in vegetation structure that have transformed trees to browsing hedges of <3 m in height (Cunliffe et al. 2012, O'Connor et al. 2024). These hedges offer an increased availability and quality of browse owing to a higher shoot density (Makhabu et al. 2006), which is favored by elephants (Smallie and O'Connor 2000, Styles and Skinner 2000) and other browsers. Along with elephants, these other herbivores are likely to compete with rhinoceroses. For example, kudu, a relatively abundant species in GNP (Dunham 2022), feeds on twigs of similar height and diameter as black rhinoceroses (de Boer and IJdema 2007).

Elephants and rhinoceroses were segregated in the diameter of twigs taken. The diameter of stems taken by rhinoceroses in GNP ($\bar{x}$ = 0.49 cm) is comparable with the <0.6 cm in diameter twigs selected by rhinoceroses in the Eastern Cape, South Africa (Ganqa et al. 2005), whereas the diameter of branches taken by elephants was 2.5 times larger ($\bar{x}$ = 1.27 cm). Considering that nitrogen concentration and digestibility of twigs decrease, and fiber increases, with increasing stem diameter (Palo et al. 1992), rhinoceroses appear to be optimizing nutrient intake over energy intake (Wilson and Kerley 2003, Owen-Smith and Novellie 2016). Elephants often remove whole branches, initially leaving behind low-quality browse on stems whose diameters are too large for black rhinoceroses to feed upon (Fritz et al. 2002). The subsequent resprouting ability of species fed upon by elephants is therefore key to the availability of twigs whose size and nutritional value are appropriate for rhinoceroses.

In this study, elephants apparently increased available browse for rhinoceroses by causing shrubs to coppice, resulting in twigs too small for elephants but of a suitable diameter, and at an appropriate height, for rhinoceroses (Figure 8). Compared with un-browsed trees, coppiced individuals usually offer a greater biomass concentration of foliage, higher nutrient concentration within foliage, lower concentrations of secondary compounds in leaves, and maintain green leaves longer into the dry season (Rutina et al. 2005, Makhabu et al. 2006, Kohi et al. 2011). Pertinent examples of species whose elephant-induced coppice contributed substantially to the dry-season diet of rhinos in GNP were bean tree (Makhabu et al. 2006) and mopane (Styles and Skinner 2000). Elephants can select for plants that they have caused to coppice (Smallie and O'Connor 2000), but a useful insight gained from this study was their facilitation for rhinoceroses of small-twigged browse through coppicing. Similar facilitation of browse availability by elephants for other browsers has been recorded for Chobe National Park, Botswana (Rutina et al. 2005), where seasonal movements of elephants (Gibson et al. 1998) ensure a period of regrowth of plants, and therefore the prolific production of coppice shoots, during the growing season (Makhabu et al. 2006). However, this temporal pattern of alleviation of elephant impact is not likely to occur with high elephant densities in medium-sized areas, such as the IPZ, where movement is constrained (O'Connor and Page 2014, O'Connor 2017) and the vegetation receives no reprieve through seasonal dispersal of elephants (Landman and Kerley 2014, Landman et al. 2014). By contrast, facilitation by elephants of browse availability for other herbivores may be compromised when elephants are at very low density or absent (Kerley et al. 2008).

CONSERVATION IMPLICATIONS

The findings of this study have implications for future reintroduction of the black rhinoceros. A suitable area for reintroduction has been profiled to some degree in terms of its environmental features. Suitable habitats would have a high shrub density, be close to permanent surface water, and include soils with high conductivity and pH. For areas with comparable vegetation composition, a high abundance of highly used species, such as bean tree, black monkey orange (*Strychnos madagascariensis*), and wing pod (*Xeroderris stuhlmannii*), and a low abundance of little-used species (e.g., millettia) should be sought. Coppicing need not only be maintained by elephants but can also be maintained by fire (Palo et al. 1992, Anderson et al. 2020). However, the use of fire should be carefully considered because fire has had significant long-term impacts on vegetation within Gonarezhou (Gandiwa and Kativu 2009).

A high degree of spatial and dietary overlap between black rhinoceroses and elephants was shown for GNP. This level of competition is unlikely to be sustainable for black rhinoceros in the long term (Landman et al. 2013) because a chronic high elephant density will inevitably result in a reduction of woody plants in semi-arid savanna (Cumming et al. 1997, Baxter and Getz 2005). A threshold density of 1.6 elephants/km^2 is purported to be the level beyond which the availability of browse for black rhinoceroses declined in a system with succulent thicket vegetation (Landman et al. 2013), but an equivalent threshold for semi-arid savanna vegetation is expected to be between 0.5–1 elephants/km^2 (Cumming et al. 1997, Baxter and Getz 2005). The current high elephant density in the IPZ mitigates against rapid growth of this founder rhinoceros population. This study indicates that the black rhinoceros should ideally be reintroduced to areas with low elephant density, but these results are specific to the IPZ and should be extrapolated with caution.

ACKNOWLEDGMENTS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

We had the consent of Zimbabwe National Parks (permit 23(1)(C)(11)56/2022) to conduct this research. No animals were captured, handled, or harmed in this observational study.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the authors.

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