Biological Conservation 323 (2026) 112114

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

The effects of intra- and inter-specific competition on the population dynamics of black rhinos (*Diceros bicornis*)

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ARTICLE INFO

Keywords:
Allee effects
Browser
Density-dependence
Herbivore
Mixed feeder

ABSTRACT

Both intra- and inter-specific competition can influence population dynamics of endangered species. At the population level, intra-specific competition generally manifests as density-dependence wherein population size or density influences population growth parameters. Managers of density-dependent endangered species can leverage this trait to facilitate population growth, but if populations are too small, they could go extinct. Simultaneously, endangered species can face pressure from inter-specific competition where an increase in one species can lead to decrease in another. Managers may intervene with other species to support an endangered population. We evaluated the relative influences of intra- and inter-specific competition on population growth and related parameters (i.e., birth, conception, mortality, sex allocation, age at first conception, inter-calving interval) in black rhino (*Diceros bicornis*). Thirteen reserves that had black rhinos for 6–23 years provided population data as well as game counts of mixed feeders and browsers (i.e., potential competitors). We found that population growth was zero or positive in 159 of 170 site-years. Black rhino density influenced all parameters except conception, but potential competitors only influenced birth occurrence and mortality rate. However, no variables affected population growth, which may reflect these reserves' strategy of establishing small populations to avoid negative density-dependence. The robustness of population growth indicates that, thus far, managers have avoided some pitfalls of small populations, but we caution that meta-population management approaches may be necessary in the future, especially to preserve genetic diversity. Overall, our findings support density-focused management of black rhino and similarly density-dependent endangered species.

1. Introduction

Conserving populations of endangered species in situ requires a good understanding of the ecological factors influencing population growth and persistence, including competition (Cao et al., 2025; Roth et al., 2016). Two important types of competition are intra-specific competition (i.e., competition with conspecifics), and inter-specific competition (i.e., competition with heterospecifics; Chesson, 2000). Both types of competition can affect endangered populations (Cao et al., 2025; Roth et al., 2016). Therefore, managers may make decisions about populations of multiple species in an ecosystem with the goal of supporting the population of an endangered species (Roemer et al., 2002; Zavaleta et al., 2001). However, if the nature or strength of competition is unknown, such interventions could lead to unexpected or even unwanted outcomes (Zavaleta et al., 2001).

Intra-specific competition generally influences population dynamics via density dependence (Chesson, 2000). In density-dependent species, population density or size influences per capita population growth (Hassell, 1975; Ohlberger et al., 2014). In relatively large or dense populations, negative density-dependence causes population growth or fitness components to decrease, but it can stabilize stochastic population dynamics (Fig. 1; Müller et al., 2013; Ohlberger et al., 2014; Sinclair and Pech, 1996; Walker et al., 2010). If a population reaches carrying capacity, growth becomes negative causing the population to decline below carrying capacity again. The population can then enter a cycle in which density repeatedly increases and decreases around carrying capacity, and long-term population growth is approximately zero (Müller et al., 2013; Sinclair and Pech, 1996).

Because they are often small and dispersed, populations of endangered species can be subject to Allee effects (i.e., positive density-dependence) wherein as population size increases, per capita population growth or fitness components increase (Fig. 1; Allee, 1927; Kramer et al., 2009). Mild Allee effects, in which population size or density is large enough that population growth is positive, may be leveraged for

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https://doi.org/10.1016/j.biocon.2026.112114
Received 5 June 2026; Received in revised form 23 August 2026; Accepted 12 September 2026
Available online 16 September 2026

conservation management (Kramer et al., 2009; Tobin et al., 2011). However, strong Allee effects, which occur when size or density is so low that growth is negative, can result in the population declining to extinction, a real risk for populations of endangered species (Angulo et al., 2007; Berec et al., 2007; Reed, 1999). Thus, evaluating the effects of density-dependence in managed populations of endangered species is vital for effective management, especially in populations intentionally held at lower densities to facilitate population growth.

When multiple species target the same resources during interspecific competition, an increase in one species may result in a decrease in another (Connell, 1961). Competition in herbivores often manifests through scramble competition, where multiple species compete indirectly for the same food (de Boer and Prins, 1990; Minor and Koprowski, 2015). Scramble competition can occur between species within the same or different feeding guilds (de Oliveira et al., 2016; Schoener, 1983). However, herbivores using the same forage may not be competing. Rather, they might facilitate each other by inducing coppicing, in which feeding stimulates plants to produce new growth that is higher in nutrients and lower in chemical defenses (Arsenault and Owen, 2002; Cromsigt and Kuijper, 2011; Fornara and Du Toit, 2007). To support populations of endangered species, managers may manage their competitors (Roemer et al., 2002). But management interventions targeting potential competitors could result in unexpected outcomes if ecological relationships, such as facilitation, are not understood.

The black rhinoceros (*Diceros bicornis*; hereafter black rhino), is a solitary, aggressive, and critically endangered megaherbivore (Shrader et al., 2025). In southern Africa, managers have raised concerns about sympatric herbivores, particularly other browsers such as greater kudu (*Tragelaphus strepsiceros*; U. Rusch, pers. comm., 2025). One study documented evidence of shifting resource use by black rhino in the presence of a mixed feeder, African elephants (*Loxodonta africana*; Landman et al., 2013), but we are unaware of studies evaluating whether sympatric herbivore populations influence black rhino population dynamics. Black rhino populations have been reported to be subject to negative density-dependent effects (Hall-Martin and Penzhorn, 1977; Law et al., 2013). Aggression is thought to be a primary mechanism of density-dependence in black rhino, which may be tied to competition for home ranges with access to mates and the protection of young (Greaver et al., 2014; Stein and Shrader, 2026). However, low density black rhino populations might be subject to Allee effects (Hrabar and du Toit, 2005).

One of the most important management interventions of in situ black rhinos is translocation, which is used to establish new populations and supplement existing populations (Knight and Kerley, 2009). When establishing new populations, managers may try to avoid negative density-dependent effects and encourage population growth by limiting the number of individuals released relative to the size of the region and habitat quality (Hearne and Swart, 1991; Linklater and Swaisgood, 2008). Most black rhino populations are small (i.e., <100 individuals) and as larger reserves fill, managers are establishing progressively smaller populations (Ferreira et al., 2022; Muya, 2019). Yet, establishing such small populations might subject them to strong Allee effects. Despite increasingly restricted population sizes, few studies have evaluated potential Allee effects or non-linear density-dependence in black rhino populations. Further, to our knowledge, no study has evaluated the relative magnitude of density-dependence and inter-specific competition on black rhino population dynamics even though managers have historically managed both.

Our objective was to evaluate the relationship of intra- and inter-specific competition to population growth parameters in small populations of black rhino in southern Africa. We expected that population density would exert more influence on black rhino populations than inter-specific competition because black rhinos are density-dependent partly as a result of intra-specific aggression, and because they forage

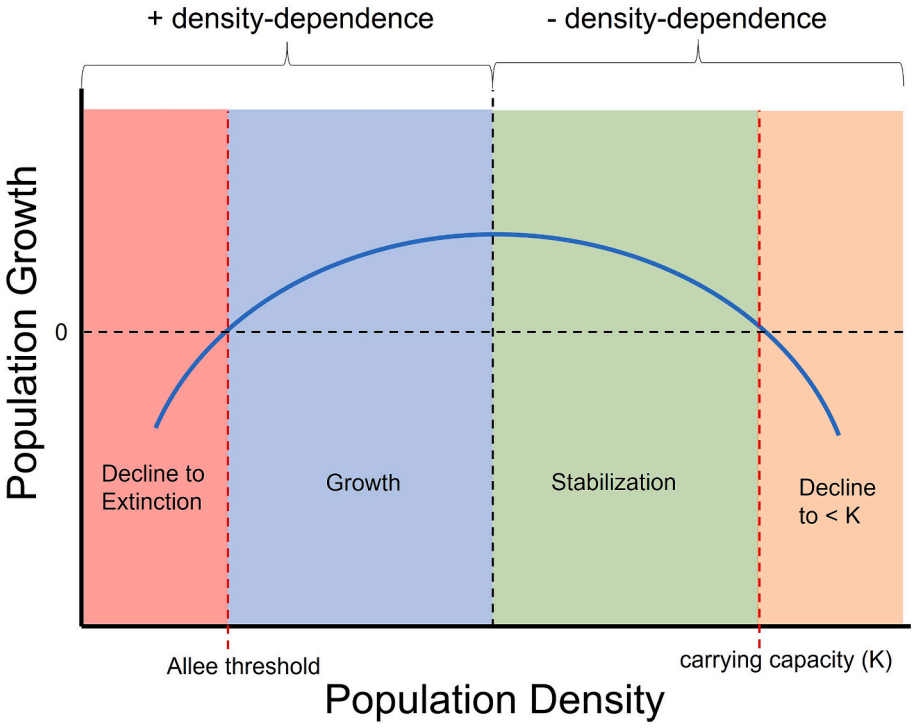

Fig. 1. A generalized density-dependent growth curve displaying the effects of density on population growth. The left-hand side of the graph displays the effects of positive density-dependence (i.e., Allee effects). If density is low and growth is negative (i.e., the Allee threshold), the population will decline to extinction. The right-hand side of the graph displays the effects of negative density-dependence. If density is such that population growth remains positive, negative density-dependence can stabilize population dynamics. However, if density increases until growth becomes negative (i.e., exceeds carrying capacity), the population will decline to below carrying capacity and will typically enter a cycle during which density oscillates around carrying capacity such that in the long term, population growth will be approximately zero (Müller et al., 2013; Ohlberger et al., 2014; Sinclair and Pech, 1996; Walker et al., 2010).

on a variety of vegetation so that they rarely lose condition, even during the dry season (Hall-Martin and Penzhorn, 1977; Hrabar and du Toit, 2005; Shrader et al., 2025). Additionally, because the studied populations were small, and reintroduced at low densities to promote population growth, we expected to find evidence of Allee effects and non-linear density-dependence, particularly on overall population growth. However, we also expected to find some evidence of negative density-dependence because the older populations in the study have been allowed to grow with minimal translocation of individuals. We also expected that, although less influential than black rhino density, herbivore (i.e., browser and mixed feeder) abundance would either be associated with decreasing growth parameters due to competition (Connell, 1961), or with increasing growth parameters due to facilitation (Arsenault and Owen, 2002). Finally, we expected that increasing vegetation productivity would lessen or even negate the effects of either type of competition.

2. Methods and materials

2.1. Study sites

We received data from 13 fenced reserves in southern Africa that had black rhinos for 6–23 years (2002–2024). One site was located in the Machinga District of Malawi. The other twelve sites were in four provinces in South Africa: Limpopo, Gauteng, KwaZulu-Natal, and the Eastern Cape (Fig. 2, Table 1). Climactic conditions, and subsequently vegetation communities, varied between the sites. However, black rhino were historically distributed across much of sub-Saharan Africa and are adapted to these varied conditions (Rookmaaker and Antoine, 2012).

2.2. Data collection and processing

The sites provided demographic data on 620 individuals, 24–98 individuals (mean = 48) at each site. To protect the security of these sensitive populations, we cannot report site-specific black rhino population numbers. The data included introductions, removals, births, deaths, sex, and mother-calf relationships. A few young calves ($n = 44$) had not been sexed. The sites provided birth dates of individuals born on site which they estimated based on the last sighting of a female without a calf, the first sighting of the female with a new calf, and the size of the calf (Hitchins, 1978). The data also included estimated birth dates for individuals that had been introduced from other sites, but we assumed some error in those estimates because of the difficulties of estimating the age of adults (Hitchins, 1978). Every individual was identifiable by unique ear notches applied by staff as part of routine monitoring (Goodman, 2013). The study was approved by the University of Pretoria Animal Ethics Committee (approval number NAS301/2024).

We calculated multiple site-level population vital rates. First, we counted the number of births, known conceptions, and deaths that occurred in a year. We counted known conceptions after estimating the conception date of each calf as the date 15 months prior to estimated birth date (Shrader et al., 2025). We adjusted the mortality counts because 31% ($n = 41$) of mortalities were directly attributed to human causes (i.e., poaching, vehicle collisions, etc.; Supporting Information Table 1) and 1.8% ($n = 11$) of individuals were translocated to other sites not included in the study. We did not treat human-caused mortalities or translocations as mortalities but did remove those animals from the population count in the subsequent site-year and altered all vital rates accordingly. To calculate the rates, we divided each count (birth,

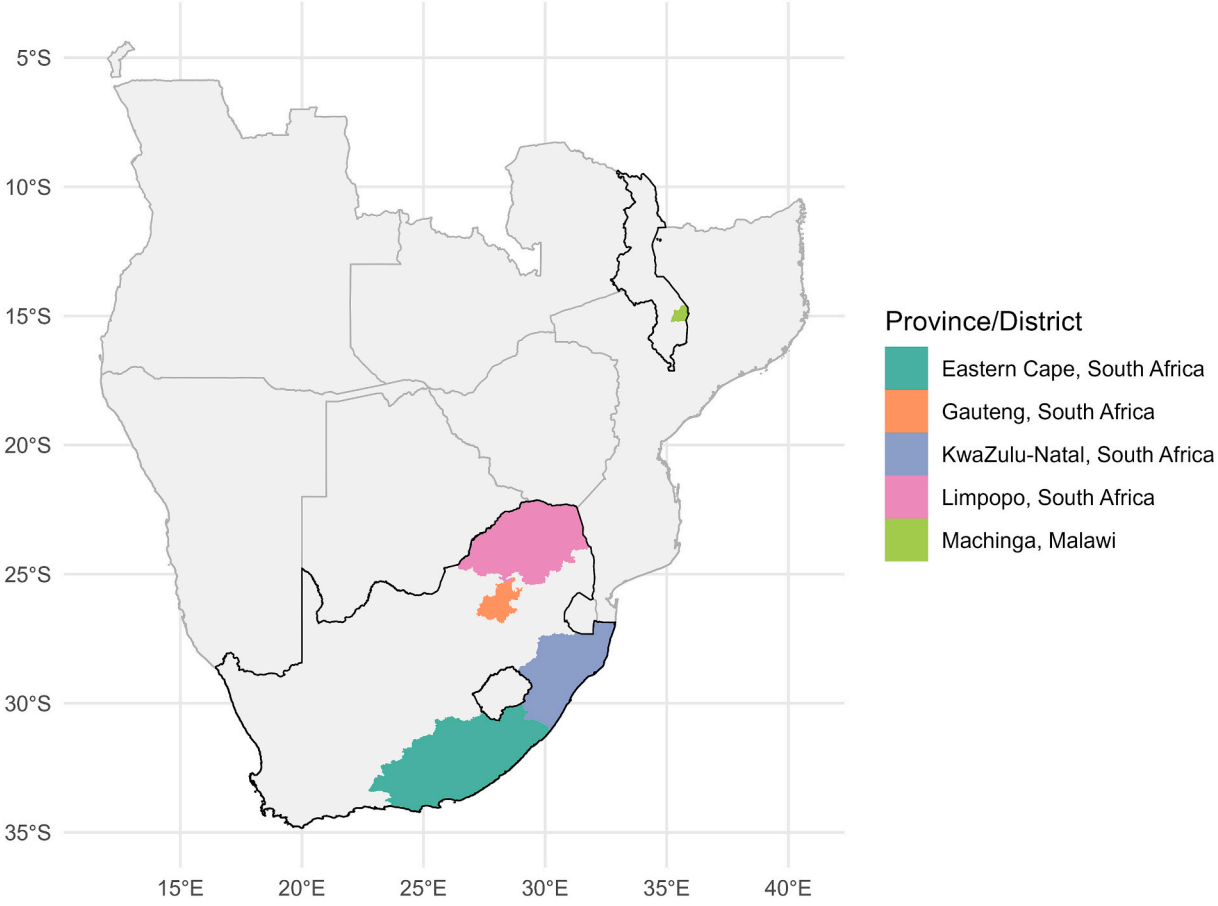

Fig. 2. Regions containing study sites in southern Africa. The two countries, Malawi and South Africa are outlined in black and the provinces and district of the study sites are colored according to the legend. We generated this map using data from GADM (GADM, 2022).

Table 1
General study site characteristics. Study sites were located in South Africa and Malawai (Fig. 2). For every Province/District, we display mean annual precipitation (A. Prec.) calculated using data from the nearest South Africa Weather Service Station to each South African study site (Department of Forestry Fisheries and the Environment, 2025). Mean precipitation for Liwonde National Park was calculated using unpublished data collected by staff. Bioregion, vegetation unit and description for the South African sites were identified and described using Mucina and Rutheford (2006). The description for Liwonde National Park was summarised based on Dudley (2001).

Country	Province/ District	A. Prec. (mm)	Bioregion	Vegetation Unit	Description	Study Site
South Africa	Eastern Cape	412	Albany Thicket	Sundays Noorsveld	low karoo shrubs and *Eupohrbia* spp.	Buffalo Kloof Private Game Reserve Kwandwe Private Game Reserve
	KwaZulu-Natal	535	Lowveld	Zululand Lowveld	savannas, dense thickets and woodlands	Manyoni Private Game Reserve Mpilo Nature Reserve Munywana Conservancy Pongola Game Reserve Somkhanda Game Reserve Thanda Safari Private Game Reserve
			Sub-Escarpment Grassland	Northern KwaZulu-Natal Moist Grassland	tussock grassland	Nambiti Private Game Reserve
	Gauteng	610	Central Bushveld	Springbokvlakte Thornveld	shrubby grasslands and low thorn savannas	Dinokeng Game Reserve
	Limpopo	430	Lowveld	Granite Lowveld	Dense thicket, tall shrubland, low woodland and open savannas	Greater Makalali Private Game Reserve Selati Game Reserve
Malawi	Machinga	688	–	–	riverine thicket, floodplain grasslands, palm savannas and forests	Liwonde National Park

conception, mortality) by the number of animals alive in the site-year. We also calculated annual population growth rate as (number of births – number of mortalities)/ starting population size. We calculated annual black rhino density (rhino/km^2) by dividing the number of rhinos alive during a site-year by site area.

Additionally, we calculated metrics associated with reproductive females which could influence population growth. For every reproductive female, we estimated age at first conception. We focused on age at first conception rather than age at first birth because black rhinos rarely drop condition except during extreme environmental conditions, and gestation is 15 months (Shrader et al., 2025), so the occurrence of reproduction should primarily be driven by condition at conception. Two females were introduced as adults older than 20, well after first reproduction usually occurs so we assumed that their first birth was not recorded and did not estimate their age at first conception. The other introduced females ($n = 57$) were younger when introduced (max age = 16) and specifically selected for translocation partly because prior observations indicated that they had not given birth. We calculated inter-calving interval lengths for every interval for every female, as length in days from birth to birth. We also calculated annual sex ratio of the calves produced as males/(males+females) because biased sex ratios can influence population growth (Grayson et al., 2014; Le Galliard et al., 2005) and multiple studies have reported male-biased black rhino populations (Berger, 1995; Weladji and Laflamme-Mayer, 2011).

Twelve of the reserves, all except Liwonde, provided game counts of their browsers and mixed feeders (i.e., guilds that might compete with black rhinos). Some reserves conducted game counts every year they had black rhinos, but most conducted counts once every 2–3 years, with some longer intervals between counts. The reserves largely conducted aerial counts in which staff counted animals along set flight paths in fixed-wing planes or helicopters. Some reserves used those counts to provide us with population estimates, but to maintain consistency, we focused on the count data as an index of relative abundance of the two guilds within each reserve. Community composition varied by reserve and year, but the most common browsers were greater kudu and southern giraffe (*Giraffa giraffa*) and the most common mixed feeders were impala (*Aepyceros melampus*) and nyala (*T. angasii*). We used Coe et al. (1976)'s estimates to calculate approximate biomass of each species counted within each site-year and summed these values by guild. We then divided this value by reserve size to obtain an index of the relative density of browsers and mixed feeders (kg/km^2) for each site-year (Supplementary Information Table 2). Because herbivore populations can fluctuate year to year (Valeix et al., 2008), we did not extrapolate estimates for site-years without game counts.

Finally, we estimated annual vegetation productivity as a coarse index of forage availability using the Normalized Difference Vegetation Index (NDVI) which is an index of relative photosynthetic activity indicative of vegetation quantity and quality that has been connected to herbivore distribution and biomass (Borowik et al., 2013; Ryan et al., 2012). We extracted NDVI from the MODIS MOD13Q1 16-day, 250 m composite NDVI product which we selected because it lessens the influence of atmospheric anomalies such as clouds (Didan, 2015). For every site-year, we used Google Earth Engine (Gorelick et al., 2017) to gather all available images. We then averaged NDVI across all pixels overlapping the site to estimate average NDVI for that site-year.

2.3. Data analyses

We evaluated the factors influencing black rhino population growth parameters using the *glmmTMB* and *lme4* R packages (Bates et al., 2015; Brooks et al., 2017). Response variables in the model sets included birth occurrence and rate, conception occurrence and rate, mortality occurrence and rate, growth rate, sex of individual calves, annual calf sex ratio, female age at first conception, and inter-calving interval (Table 2). We selected model structures according to the distribution of the response variable. We evaluated birth, conception, and mortality using a two-step hurdle approach because black rhinos are slow growing and long-lived; so, there were multiple site-years in which there were no births, conceptions, or mortalities; of the 170 site-years in the data set, in 28 there were no births, in 26 no conceptions, and in 104 no non-human mortalities. Thus, for each of these variables, we first modeled occurrence (e.g., any birth vs no birth), then, in the site-years with rates greater than 0, we modeled rate.

For each model set, we fit the population-level models with all combinations of the following predictors, including interactions between pairs of predictors: black rhino density, non-linear black rhino density (i.e., density^2), NDVI, browser density, and mixed feeder density. For the individual female analyses we included intrinsic variables:

Table 2
Model Set Descriptions. We ran multiple model sets evaluating multiple growth-related dynamics. We ran all combinations of the variables tested (including pairwise interactions) and ranked the models by AICc and against a null model, which was a random intercept only model. The table displays the model sets by response, variables tested, notes about calculation of those variables, the random intercepts, and the distributions. Model sets were run twice, once with all variables only in the site-years with game counts, and once without the competitor variables in all available site-years.

Response	Variables Tested	Notes	Random Intercept(s)	Distribution
Birth Occurrence	rhino density, rhino density^2, NDVI, browser density, mixed feeder density	–	site	Binomial
Birth Rate	rhino density, rhino density^2, NDVI, browser density, mixed feeder density	–	site	Beta
*Conception Occurrence	rhino density, rhino density^2, NDVI, browser density, mixed feeder density	calculated in conception year	site	Binomial
Conception Rate	rhino density, rhino density^2, NDVI, browser density, mixed feeder density	calculated in conception year	site	Beta
Mortality Occurrence	rhino density, rhino density^2, NDVI, browser density, mixed feeder density	–	site	Binomial
Mortality Rate	rhino density, rhino density^2, NDVI, browser density, mixed feeder density	–	site	Beta
Growth Rate	rhino density, rhino density^2, NDVI, browser density, mixed feeder density	–	site	Gaussian
Sex Individual Calves	rhino density, rhino density^2, NDVI, browser density, mixed feeder density	calculated in conception year, only known sex	female ID	Binomial
^Annual Sex Ratio Produced	rhino density, rhino density^2, NDVI, browser density, mixed feeder density	calculated in conception year, only known sex	site	Negative Binomial
Age at First Conception (years)	rhino density, rhino density^2, origin (introduced vs. born on site), NDVI, browser density, mixed feeder density,	averaged across the female's life at the site prior to conception	site	Gamma
Inter-Calving Interval (days)	rhino density, rhino density^2, origin, age at conception, sex of previous calf, NDVI, browser density, mixed feeder density	averaged across each interval	site, female ID	Gaussian

* The conception occurrence model set was only run once because conceptions occurred in every site-year with game counts. ^We reran these model sets using only site-years in which more than 3 calves were produced as a robustness test.

the origin of the female (introduced vs. born on site) and the age of the female and sex of the previous calf (but only in the inter-calving interval analysis; Table 2). In all model sets we included a random intercept for site except in the individual calf sex models because modeled variation of the random effect was nearly 0 causing the models to be flagged as singular. However, in the individual calf sex models we added a random intercept for female ID to account for females that had produced more than one calf. Similarly, in addition to the random intercept for site, we included a random intercept for female ID in the inter-calving interval models because many females had multiple intervals. Predictor variables in the age at first conception model sets were averaged across the years that the female had been present at the site. In the inter-calving interval model sets, predictors were averaged across each interval. All numeric predictors were centered and scaled prior to fitting the models. We ranked the models in each set against a random intercept-only null using Akaike's Information Criterion adjusted for small sample size (AICc; Hurvich and Tsai, 1989).

Of the 170 site-years for which we had data, we had game counts for only 85 and so we ran each model set twice. First, with all the variables but only in the site-years with game counts. Then, we reran the model sets without browser and mixed feeder density but using the data from all site-years to increase power. However, there was a conception in every site-year with a game count, so we did not run the conception occurrence model set with the smaller game-count years only dataset. Thus, every model set in Table 2 was run twice except for conception occurrence. Finally, because less than 3 calves were conceived in an average site-year, which could lead to spurious results, we conducted a robustness check by rerunning the annual sex ratio model sets only in the site-years with more than 3 calves.

3. Results

Across the 13 sites, 140 adult females produced 365 calves. In any given site-year, 0–9 (mean = 2.1 ± 1.8) conceptions, 0–8 (mean = 1.9 ± 1.6) births, and 0–4 (mean = 0.5 ± 0.8) deaths from non-human causes occurred. Vital rates, population metrics, and environmental metrics were not significantly different between the smaller (i.e., site-years with game counts) and larger (i.e., all site years) datasets (Supporting Information Table 3) and so here we summarize rates from the larger dataset. Unsurprisingly, average birth rate (0.083 ± 0.056 births/rhino/site-year) and conception rate (0.095 ± 0.070 conceptions/rhino/site-year) were not significantly different. Average mortality rate from non-human causes was low (0.025 ± 0.041 mortalities/rhino/site-year), also unsurprising given that no non-human mortalities were recorded in 61% ($n = 104$) of site-years. On average, annual population growth was 0.067 ± 0.074. Population growth was only negative in 6% ($n = 11$) of site-years but positive in 71% ($n = 121$), and zero in 22% ($n = 38$) of site-years indicating that the populations in the study were generally stable or growing. Annual sex ratio in each site-year varied widely and included site-years in which only males or only females were produced (mean = 0.46 ± 0.39). Sex ratio of calves produced during the study period at individual study sites varied from 0.20 to 0.64 (mean = 0.48 ± 0.12). Across the full study, we did not find evidence of sex bias in the calves of known sex (sex ratio = 0.49; 158 males, 163 females); but 44 calves had not been sexed. On average, females conceived for the first time at 7.74 ± 2.74 years old and their inter-calving intervals were 960.91 ± 325.90 days (i.e., 2.63 ± 0.89 years). In each site-year, black rhino density varied from 0.038 to 0.237 rhino/km^2 (mean = 0.117 ± 0.051).

Birth and mortality occurrence were both influenced by black rhino density (Table 3; Supporting Information Table 4). In the small dataset, the top birth occurrence model included rhino density ($\beta = 1.042$, p-value = 0.033), relative mixed feeder density ($\beta = -0.333$, p-value = 0.359), and an interaction between them ($\beta = -0.928$, p-value = 0.028). The model indicated that increasing rhino density was associated with increasing likelihood of at least one birth occurring, but the effect may be lessened or even reversed with increasing mixed feeder density. However, the only variable in the large dataset birth occurrence model was a marginally insignificant effect of rhino density ($\beta = 0.515$, p-value = 0.096). No models were ranked higher than their respective nulls in the conception occurrence or rate, or birth rate model sets (Supporting Information Table 4).

We found that rhino density also influenced mortality occurrence in the large dataset where increasing rhino density was associated with

Table 3
Top ranked models in each model set. The smaller dataset only includes data from site-years in which there were game counts. The larger dataset includes all site-years but the mixed feeder and browser variables were not included as predictors. We display only the top model if it was ranked significantly higher than the null (i.e., ΔAICc ≥2.00; Supplementary Tables 4–6). Sex is coded as male relative to female and origin is coded as whether the female was introduced or born in the reserve. The density variables are displayed according to group (e.g., rhino refers to black rhino density). Variables significant at α = 0.05 are bolded. Variables marginally insignificant (0.05 > α < 0.10) are marked with an asterisk.

Response	Data Set	n	Variable	coef	SE	*p*-value
Birth Occurrence	Small	85	**rhino density**	**1.042**	**0.488**	**0.033**
			mixed feeder density	−0.333	0.363	0.359
			rhino density*mixed feeder density	**−0.928**	**0.423**	**0.028**
	Large	170	rhino density	0.515	0.309	0.096*
Mortality Occurrence	Large	170	**rhino density**	**0.384**	**0.182**	**0.035**
			NDVI	−0.097	0.189	0.607
			rhino density*NDVI	**−0.427**	**0.176**	**0.015**
Mortality Rate	Small	37	**mixed feeder density**	**0.294**	**0.083**	**<0.001**
			browser density	**−0.227**	**0.077**	**0.003**
			rhino density	**−0.278**	**0.059**	**<0.001**
			NDVI	**−0.133**	**0.066**	**0.042**
	Large	66	**rhino density**	**−0.353**	**0.099**	**<0.001**
Sex Individual Calves	Small	193	**NDVI**	**0.482**	**0.186**	**0.009**
	Large	321	rhino density^2	0.117	0.112	0.297
			NDVI	**0.590**	**0.196**	**0.003**
			NDVI* rhino density^2	**−0.391**	**0.142**	**0.006**
Annual Sex Ratio	Small	85	NDVI	0.370	0.229	0.106
			mixed feeder density	0.375	0.208	0.072*
	Large	144	rhino density^2	0.233	0.134	0.082*
			NDVI	**0.586**	**0.226**	**0.009**
			NDVI* rhino density^2	**−0.444**	**0.155**	**0.004**
Age at First Conception	Small	82	**origin**	**0.302**	**0.068**	**<0.001**
			rhino density	−0.057	0.035	0.097*
			rhino density^2	**−0.084**	**0.026**	**0.001**
	Large	104	**origin**	**0.298**	**0.061**	**<0.001**
			rhino density	−0.063	0.034	0.061*
			rhino density^2	**−0.057**	**0.029**	**0.045**
Inter-calving Interval	Small	126	**female age**	**0.104**	**0.033**	**0.002**
			mixed feeder density	−0.032	0.033	0.337
	Large	224	**female age**	**0.064**	**0.019**	**<0.001**
			rhino density	**0.042**	**0.019**	**0.030**

increasing likelihood of a mortality (β = 0.384, *p*-value = 0.035). The top model included NDVI, which was not significant alone (β = −0.097, *p*-value = 0.607), but did significantly interact with rhino density (β = −0.427, *p*-value = 0.015) such that the increased likelihood of mortality occurrence with increasing density was lessened or reversed with increasing NDVI. However, in the small dataset, no model explained mortality occurrence better than the null (Supporting Information Table 4). Density was correlated with population size ($r = 0.73$) so the occurrence results may partly reflect that larger populations have more animals from which at least one birth or mortality might occur. The significant interactions with mixed feeder density and NDVI show that such a numerical response may not be the entire explanation for the results, nonetheless we recommend cautious interpretation.

Mortality rate was also related to rhino density where increasing density was associated with decreasing mortality rate in both model sets ($\beta_{small} = -0.278$, $p\text{-value}_{small} < 0.001$; $\beta_{large} = -0.353$, $p\text{-value}_{large} < 0.001$). The top model in the mortality rate model set using the small dataset also included NDVI (β = −0.133, *p*-value = 0.042), relative browser density (β = −0.227, *p*-value = 0.003), and relative mixed feeder density (β = 0.294, *p*-value <0.001) such that increasing NDVI and increasing browser density were both associated with decreasing mortality rate, but increasing mixed feeder density was associated with increasing mortality rate. However, there were only 37 site-years in the small mortality rate dataset and 66 in the large dataset, so the models should be interpreted cautiously.

Sex allocation may be connected to black rhino density and NDVI, but sex ratio across the dataset was largely unbiased (0.49) and the annual sex ratio results were not supported by the robustness check (Table 3; Supporting Information Table 5). In the model sets using all site-years, the top sex of individual calves and annual sex ratio models included a significant effect of NDVI ($\beta_{individual} = 0.590$, $p\text{-value}_{individual} = 0.003$; $\beta_{annual} = 0.586$, $p\text{-value}_{annual} = 0.009$), an insignificant effect of nonlinear black rhino density ($\beta_{individual} = 0.117$, $p\text{-value}_{individual} = 0.297$; $\beta_{annual} = 0.233$, $p\text{-value}_{annual} = 0.085$), and a significant interaction between the two ($\beta_{individual} = -0.391$, $p\text{-value}_{individual} = 0.006$; $\beta_{annual} = -0.444$, $p\text{-value}_{annual} = 0.004$). These models indicate that when NDVI was high in the year of conception, more males than females were produced. But that effect was moderated by black rhino density wherein this pattern persisted at moderate densities but reversed at both low and high densities. The top models using the smaller dataset, however, differed to the large dataset. The top model in the small individual calf model included only NDVI (β = 0.482, p-value = 0.009) and the top model of the small annual sex ratio model set included NDVI (β = 0.307, p-value = 0.106) and mixed feeder density (β = 0.375, p-value = 0.072). Thus, NDVI appears to be the most influential variable affecting sex allocation. However, in the robustness check, no models ranked higher than the null (Supporting Information Table 5). In the context of the robustness check and the lack of bias across the study, we caution conservative interpretation of the sex allocation models, which may reflect the small number of calves produced in most site-years.

Age at first conception and inter-calving interval were influenced by variables intrinsic to the females and black rhino density (Table 3, Supporting Information Table 6). In both age at first conception model sets, the top model included female origin (i.e., introduced vs. born on site) and rhino density, both linear and non-linear. The models indicated that introduced females initially conceived later than females born on site ($\beta_{small} = 0.302$, $p\text{-value}_{small} < 0.001$; $\beta_{large} = 0.298$, $p\text{-value}_{large} < 0.001$). Although the linear density variable was marginally insignificant in both models ($\beta_{small} = -0.057$, $p\text{-value}_{small} = 0.097$; $\beta_{large} = -0.063$, $p\text{-value}_{large} = 0.061$), the non-linear density variable was significant ($\beta_{small} = -0.084$, $p\text{-value}_{small} = 0.001$; $\beta_{large} = -0.057$, $p\text{-value}_{large} = 0.045$) indicating that at low and high densities, females

initially conceived later in life, and at moderate densities they initially conceived earlier. Specifically, the models predicted that age at first conception was lowest at a density of about 0.136 rhinos/km^2 in the small data set and at about 0.112 rhinos/km^2 in the large.

The most important variable in the top inter-calving interval models was age of the female ($\beta_{small} = 0.104$, p-value$_{small} = 0.002$; $\beta_{large} = 0.064$, p-value$_{large} < 0.001$) indicating that older females had longer inter-calving intervals. The top model in the small dataset included an insignificant effect of mixed feeder density ($\beta = -0.032$, p-value $= 0.337$). In contrast, the top model in the large dataset included a significant effect of rhino density ($\beta = 0.042$, p-value $= 0.030$) indicating that increasing density was associated with longer inter-calving intervals.

Although the tested variables were tied to birth occurrence, mortality occurrence and rate, sex allocation, age at first conception, and inter-calving interval, we did not find evidence that any variables influenced annual population growth rate (Supporting Information Table 4).

4. Discussion

Our results illustrate that, as expected, black rhino population density was more strongly tied to black rhino population growth parameters than inter-specific competition. However, annual population growth was robust to all measured variables (Table 3; Supporting Information Tables 4–6).

As predicted, we found some evidence of potential Allee effects (i.e., positive density-dependence) and non-linear density-dependence. But we also found evidence of negative density-dependence (Table 3). Given these results, our finding that density was not associated with population growth does not seem surprising. Population growth is responsive to most of the modeled growth parameters, and these did not have a uniform relationship with density. Our birth and mortality results, the variables directly tied to population growth, provide further context. Density was positively associated with birth and mortality occurrence, but because of density's correlation to population size, this finding may be partly a result of more animals resulting in more opportunity for a birth or death to occur. In contrast, density was not tied to birth rate but was negatively associated with mortality rate. Yet, the mortality rate models included only 44% and 39% of the site-years included in the population growth models, and there were no more than four mortalities in a year, so the effect of density on mortality rate may not be strong enough to influence population growth.

Our study is only the second we know of to find evidence that small black rhino populations may be subject to Allee effects or non-linear density dependence (Hrabar and du Toit, 2005). Our documentation of multiple density effects is likely a result of two management strategies enacted in the studied populations. These include establishing small populations to encourage growth, and minimal removal of individuals in subsequent years. Annual black rhino density in our study varied from 0.038 to 0.237 (mean = 0.117 ± 0.051) rhino/km^2. Hrabar and du Toit (2005) found that increasing density was associated with higher calving success until the population reached a density of 0.085 rhino/km^2, similar to our mean. In contrast, even the densest site-years in our study were low density relative to literature documenting negative density-dependence (e.g., 0.1–5.2 rhino/km2; Hall-Martin and Penzhorn, 1977; Law et al., 2013). Thus, all except the least dense black rhino populations ($< \sim 0.1$ rhino/km^2) are probably subject primarily to negative density-dependence.

Allee effects are a major concern for management of endangered populations because strong Allee effects can cause populations to spiral toward extinction (Fig. 1; Angulo et al., 2007; Berec et al., 2007; Reed, 1999). If a true Allee effect, the birth occurrence result may point to a mate-finding mechanism where increasing density improves access to appropriate mates (Régnière et al., 2013). The mortality rate findings might reflect recent findings that black rhinos are more social than previously expected and associate with the same individuals over time, which may reduce risk of aggression (Stein and Shrader, 2026). Thus, increasing density might provide more appropriate associates with which to safely socialize. Density did not influence population growth, showing that these effects were probably not strong enough to pose an existential threat to these populations, a conclusion supported by our finding that population growth was stable or positive in 93.5% ($n = 159$) of site-years. However, the oldest population in the study had only been reintroduced 23 years prior, and our study did not account for the effects of small population size on genetic diversity, so further studies are required. Across their range, black rhinos persist within and are being reintroduced as small populations, some even smaller than those in our study (Ferreira et al., 2022; Muya, 2019).

We had expected that browser and mixed feeder density would either be associated with negative effects on growth parameters, reflecting competition (Connell, 1961), or positive effects, reflecting facilitation (Arsenault and Owen, 2002). In the two models which included a significant effect of mixed feeder density, we found evidence for competition (Table 3). A previous study found evidence of competition from elephants, a mixed feeder, wherein elephant activity may have caused black rhinos to shift their forage selection (Landman et al., 2013). In our study, we included elephants in the mixed feeder estimates, but elephant herds were small and the most abundant mixed feeder was impala. We cannot confidently determine whether a particular species is competing with black rhino or for what resource, only that there is some evidence that mixed feeder abundance may be negatively related to black rhino population parameters potentially reflecting competition. In contrast, we found that increasing browser density was associated with decreasing mortality rate. This result could point to facilitation wherein foraging by the other browsers causes plants to coppice, producing new, easily digestible growth (Arsenault and Owen, 2002; Fornara and Du Toit, 2007; Makhabu et al., 2006), or this may simply reflect that general browser density is an indicator of good habitat for black rhino. However, the mortality rate model with competitors only included 37 site-years and so should be interpreted with caution (Table 3). An assumption of competition and facilitation in the context of our study is that forage is limiting. Yet, black rhinos forage on a variety of species and rarely lose condition, even during periods of scarcity (Hall-Martin and Penzhorn, 1977; Hrabar and du Toit, 2005; Shrader et al., 2025), which might be why we found so little evidence that interspecific competitors affected black rhino population dynamics. Future research is needed that better quantifies competitor population size, forage abundance and quality, foraging activity, and habitat use.

As expected, when NDVI was significant, it was associated with increased population growth rates and lessened the potential negative effects of density-dependence (Table 3). We also found that NDVI might be tied to sex allocation, where increasing NDVI was associated with production of more male calves relative to female. This result may be indicative of mechanisms associated with the Trivers-Willard Hypothesis (Trivers and Willard, 1973). When the cost of producing one sex is higher, females in poor condition should produce the cheaper sex (Hamilton, 1967), an effect which should be particularly evident if the more expensive sex also has more variable reproductive potential (Trivers and Willard, 1973). Adult black rhino males are substantially larger than females (males ~1350 kg; females ~900 kg), although at birth they are not significantly different in size (Shrader et al., 2025), and so may be more costly to raise. Because black rhinos are polygynous, the reproductive potential of males is more variable than females (Shrader et al., 2025). Thus, the life history traits of black rhinos meet key assumptions of the Trivers-Willard Hypothesis (Trivers and Willard, 1973). Our NDVI results indicate that when environmental conditions that could affect maternal condition were more favorable, more males were produced. However, we did not measure female condition, only NDVI, and the results were not supported by the robustness check, so additional research is required.

Intrinsic factors affected age at first conception and inter-calving

interval more than density (female age and origin; Table 3). The effect of female age on inter-calving interval is likely indicative of a physiological constraint consistent with previous studies on both black rhino (Law et al., 2013) and Indian rhino (*Rhinoceros unicornis*; Pluháček et al., 2017) that found that increasing age was tied to increasing inter-calving intervals. Our finding that translocated females conceived later than those born on site (Table 3) may be consistent with other studies indicating that translocation stress might depress reproductive potential (Tarszisz et al., 2014). However, our findings may also reflect a management bias in females selected for translocation. In most cases, managers selected nearly full-grown subadult females that had not given birth and were probably not pregnant to minimize risk of stress-induced abortion. Thus, females that conceived early were less likely to be selected for translocation. Further studies are required to disentangle the relative influences of selection bias and translocation stress.

Overall, the most important variable affecting the modeled growth parameters was black rhino density, which supports the focus managers of the studied populations place on population density. However, our results should be interpreted cautiously because the small population sizes likely increased stochasticity in our dataset. Across their range, most black rhino populations are isolated and small (Ferreira et al., 2022; Muya, 2019). As such, long-term persistence of individual populations, and the species, is dependent on continued translocation efforts which should be informed by meta-population management approaches. Most reserves contributing to this study are part of the Black Rhino Range Expansion Project (BRREP), a partnership between WWF South Africa, Ezemvelo KZN Wildlife, Eastern Cape Parks and Tourism, and numerous reserves, which works to expand the species range via reintroduction to new reserves. BRREP is also managing populations of the participating reserves as a larger meta-population (World Wildlife Fund South Africa, 2025). Although we did not find evidence of strong Allee effects in these populations, some BRREP populations are smaller than those studied, which might place them in danger of Allee effects. However, those small populations are more likely to persist long-term because they are managed as part of the BRREP meta-population. Nevertheless, most black rhino populations are not managed by such partnerships, which could reduce their long-term persistence, and we encourage managers to enter similar meta-population management partnerships.

CRediT authorship contribution statement

Rachel M. Stein: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Adrian M. Shrader:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During this study, the authors used OpenAI's ChatGPT to assist with identification and correction of coding errors in analysis scripts. All outputs were reviewed, verified, and edited by the authors prior to use in the analyses. No AI tools were used in study design, data analysis, interpretation, or manuscript writing.

Funding

Our study was supported by a grant from the International Rhino Foundation (R-2023-5) awarded to AMS.

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.

Acknowledgements

We thank our partners at WWF South Africa, the Black Rhino Range Expansion Project, Ezemvelo KZN Wildlife, and Eastern Cape Parks and Tourism Agency. The data used in this study was gathered and generously shared by Liwonde National Park and African Parks, Buffalo Kloof Private Game Reserve, Dinokeng Game Reserve, Greater Makalali Private Game Reserve, Kwandwe Private Game Reserve, Manyoni Private Game Reserve, Mpilo Nature Reserve, Munywana Conservancy, Nambiti Private Game Reserve, Pongola Game Reserve, Selati Game Reserve, Somkhanda Game Reserve, and Thanda Safari Private Game Reserve.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.112114.

Data availability

The authors do not have permission to share data.

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