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RESEARCH ARTICLE

Does the resource dispersion hypothesis predict grouping behaviour in a solitary megaherbivore?

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Abstract

1. The resource dispersion hypothesis (RDH) predicts that when resources are abundant and heterogeneously distributed, multiple individuals may satisfy their resource needs in a shared area without imposing large costs on one another. Under such conditions, groups can form even in the absence of other benefits, and other life history traits may not entirely explain group composition. For example, groups forming under conditions associated with the RDH may not display a biased sex ratio even if otherwise expected.
2. Solitary herbivores, which are unlikely to gain benefits from grouping, may be strongly subject to the RDH, especially during growing seasons when there is an abundance of resources. However, to the best of our knowledge, no study has evaluated whether grouping behaviours in any solitary herbivore follows RDH predictions.
3. To explore this, we used 48,678 sightings of black rhinos (*Diceros bicornis*) from 13 reserves in southern Africa to assess whether grouping behaviour in this solitary megaherbivore aligned with predictions of the RDH, or reflected predictions informed by the species ecology.
4. We found that group formation and size largely followed RDH predictions where groups were more likely to form when resources were heterogenous and of high quality. Additionally, groups were larger during the growing season and when resources were heterogeneous. In contrast, as resource quality increased, group size decreased. Similarly, two of the four group composition results followed RDH predictions, where increasing group size was associated with decreasing within-group familiarity and an unbiased sex ratio in opposition to usual expectations. The other two followed species ecology predictions wherein increasing group size was associated with an increasing proportion of subadults and all large groups included at least one cow–calf pair.
5. Ultimately, our results show that, in solitary herbivores, the RDH may be useful in predicting group formation and size and may explain instances when group composition diverges from species-specific expectations. Understanding grouping behaviour in endangered solitary species such as black rhino may improve

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management by allowing managers to identify conditions under which individuals are more tolerant of conspecifics.

KEYWORDS
aggregation, black rhino, *Diceros bicornis*, forage, group, herbivore, social

1 | INTRODUCTION

In solitary species, adults usually forage and sleep alone (Makuya & Schradin, 2024a). However, in many solitary species, individuals have been observed aggregating into groups, prompting questions about what drives grouping behaviour (Elbroch & Quigley, 2017; Goddard, 1967; Twining et al., 2024). One factor that may instigate grouping behaviour is reproduction (Elbroch & Quigley, 2017; Joy & Crews, 1986). But resource access could also play a key role. For example, Twining et al. (2024) found that group formation in solitary species in the family *Musetelidae* was driven by resource-related factors, especially heterogeneity, where more heterogeneously distributed resources facilitated group formation. Similarly, groups of up to 9 unrelated mountain lions (*Puma concolor*) have been observed around large kills (Elbroch & Quigley, 2017).

Such observations suggest that solitary species might be subject to the effects of the resource dispersion hypothesis (RDH). The RDH states that in territorial or home-range holding species, if resources are abundant and distributed heterogeneously, multiple individuals may satisfy their resource needs in a shared area without imposing large costs on one another. Thus, these ecological conditions may lower grouping costs regardless of whether individuals receive any other benefits of group membership (Carr & Macdonald, 1986; Macdonald & Johnson, 2015; Macdonald & Newman, 2022).

To date, explorations of the RDH in vertebrates have most commonly focused on carnivores (Geffen et al., 1992; Nel et al., 2013; Valeix et al., 2012), but it is likely to apply to herbivores as well (Jarman, 1974; Macdonald & Johnson, 2015). In herbivores, home range or territory establishment is generally linked to reproduction rather than resource access (Carranza et al., 1990; Roberts & Dunbar, 2000). Typically, herbivores cannot defend all potential food sources in their range or territory from intra- and inter-specific competitors even during periods of more limited availability. Moreover, when resources are abundant, the costs of trying to defend a territory from incursion by intra- and inter-specific competitors likely outweigh the benefits (Carpenter, 1987). Thus, the ecology of herbivores likely meets a key assumption of the RDH, that there is at least some excess of the resource within a territory or home range, which lowers the cost of tolerance for the holder, increasing the likelihood of group formation (Carr & Macdonald, 1986; Macdonald & Johnson, 2015; Macdonald & Newman, 2022). Herbivores are often limited by seasonal forage availability (Hempson et al., 2015) and so grouping responses relevant to the RDH could involve seasonal resource pulses. The hypothesis may be especially applicable to solitary herbivores that probably do not receive additional benefits from grouping. However, to the best of our knowledge, only social herbivores have been assessed (Peignier et al., 2019; Verdolin, 2009).

Despite observations of solitary species grouping around concentrated resources, adults in solitary species usually forage alone because the costs outweigh any benefits (Makuya & Schradin, 2024a). For instance, individuals in solitary species may be aggressive to conspecifics and so grouping behaviour can be associated with significant costs in the form of stress, injury or even mortality (Baxter-Gilbert & Whiting, 2019; Creel et al., 2013; Elbroch & Quigley, 2017). Social networks based on familiarity between group members may be important for mitigating these potential costs. For example, the interactions of mountain lions grouping around a large kill are dictated not only by access to the clumped and highly valuable resource, but also by familiarity with group members, particularly based on previous kill-sharing (Elbroch et al., 2017). Thus, although grouping behaviour may be primarily driven by resource access, in aggressive solitary species, group size and composition may be driven, at least partly, by within-group familiarity.

In solitary species, most groups are ephemeral in time and space (Makuya & Schradin, 2024b; Twining et al., 2024). Yet, for solitary species that exhibit maternal care, mother-offspring pairs or groups may persist for months or even years (Goddard, 1967; Van De Walle et al., 2018). Larger groups of usually solitary species are probably more likely to occur when multiple mother-offspring groups come together, or other conspecifics temporarily join the group. For example, in an evaluation of the variation in social behaviour of 13 species of otters, Lodé et al. (2021) demonstrated how flexible social lifestyles and occasional grouping in more solitary species likely originates partly from mother–cub relationships, such as when a breeding male temporarily joins a mother–cub group.

The critically endangered black rhino (*Diceros bicornis*) is a solitary and aggressive megaherbivore that forms solitary home ranges and engages in long-term maternal care (Berger, 1994; Goddard, 1966, 1967). Black rhinos are somewhat selective browsers that will consume a variety of forage based on seasonal (usually rainy vs. dry) abundance and quality, so are rarely limited by forage quantity (Ferreira et al., 2019; Ganqa et al., 2005; le Roex et al., 2019). As such, the defence of food resources is unlikely, particularly during periods of abundance, and so the RDH may play a role in the formation of black rhino groups. However, aggression towards other conspecifics is common, especially male aggression, such that injury from fighting is one of the most important sources of mortality (Brett, 1998; Linklater & Swaisgood, 2008). Despite this aggression, black rhinos are commonly spotted in groups of 2–3 individuals, occasionally more. One study reported a group of 13 individuals

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(Goddard, 1967). Black rhinos preferentially associate with familiar conspecifics and avoid males, which might lower the risk from aggression (Stein & Shrader, 2026). The most common social unit in black rhinos is the cow–calf dyad and groups may form around these dyads. During the subadult phase, individuals usually disperse away from their mother's home range and are often seen in the company of other subadults or cow–calf pairs (Goddard, 1967; Klingel & Klingel, 1966).

We evaluated whether black rhino grouping behaviour is driven primarily by principles of the RDH or by the unique behavioural ecology of the species. To test these drivers, we formulated a series of predictions about the influence of vegetation quality and heterogeneity as well as season on group formation, and we also developed predictions about group demographics as a function of group size (Table 1). To the best of our knowledge, this is the first study to evaluate the applicability of the RDH in a solitary herbivore and only the second to apply those principles to any ungulate.

2 | MATERIALS AND METHODS

2.1 | Study sites

We received data from 13 fenced reserves in southern Africa that had black rhinos for 3–20 years (2004–2024). Twelve of the reserves were located in four provinces in South Africa: Babanango Game Reserve, Manyoni Private Game Reserve, Mpilo Nature Reserve, Munywana Conservancy, Nambiti Private Game Reserve, Pongola Game Reserve, Somkhanda Game Reserve, and Thanda Safari Private Game Reserve in KwaZulu-Natal, Greater Makalali Private Game Reserve and Selati Game Reserve in Limpopo, Buffalo Kloof Private Game Reserve in the Eastern Cape, and Dinokeng Game Reserve in Gauteng. The final reserve, Liwonde National Park was located in Malawi. Although widespread, most of the reserves were subject to distinct rainy and dry seasons that shifted slightly by location and year (Department of Forestry Fisheries and the Environment, 2025). One site, Buffalo Kloof, in the Eastern Cape, did not have seasons distinct by rainfall, but rather by temperature (i.e. summer vs. winter). Elevation of the sites varied widely ranging from 130 to 1430 m a.s.l. (Farr et al., 2007). The variable seasonal precipitation, latitude and elevations of these reserves have resulted in different vegetation types and communities including savanna, thicket and forest (Cowling et al., 1997). The historic range of black rhinos includes much of sub-Saharan Africa, enabling them to thrive in these diverse environments (Rookmaaker & Antoine, 2012).

2.2 | Data collection

As part of their regular monitoring practices, each reserve has maintained detailed records on each individual rhino since they were reintroduced. Individual black rhinos at each reserve were identifiable by unique ear notch patterns that were applied by the reserve staff. Calves were identified by the presence of their mother and their own ear notches applied by the age of 2 years, so they would be identifiable once they dispersed away from their mother (Goodman, 2013).

The reserve monitoring teams documented every sighting of black rhino(s) including whether the rhinos were in a group (i.e. within ~50 m of one another), identification of each individual, and GPS location. Most individuals did not have GPS or VHF tracking devices (although some did) and so GPS coordinates were primarily gathered at the location of the observers. On average, observers were approximately 50–100 m from the animal(s), close enough to enable identification but far enough to reach safety if an animal decided to charge. In this way, each individual black rhino in the different populations was documented 1–81 (mean = 3.3) times per month, alone or in groups. The reserves each had 12–81 black rhinos on which they provided data from 59,271 sightings. For security reasons, we are unable to provide site-specific sample sizes and population metrics. The study was approved by the University of Pretoria Animal Ethics Committee (reference no. NAS301/2024).

We gathered data on vegetation productivity and heterogeneity from the MODIS Terra Vegetation Indices 16-day 250 m global product (MOD13Q1, Version 6) using Google Earth Engine (Descloitres et al., 2002; Gorelick et al., 2017). First, we removed 3174 sightings because they had incomplete or invalid GPS coordinates (e.g. coordinates that placed the sighting outside the reserve) resulting in 56,907 sightings retained. Next, we placed 100 m buffers around each point to account for the spatial error we expected to be present due to the data collection method in which GPS coordinates were taken at the location of the observers (Frair et al., 2010; Jin & Sader, 2005). For each sighting date and reserve, we filtered for the nearest image either 16 days before or after the observation and extracted the composite normalised difference vegetation index (NDVI) product, as an index of vegetation productivity (Huete et al., 2002). NDVI indexes photosynthetic productivity and has been linked to herbivore biomass in many systems, including in African herbivores (Ryan et al., 2012). If there were no NDVI MODIS images available for the reserve within the date range, we removed the sighting from further analyses because images taken further from the sighting date were less likely to reflect conditions when the rhinos were spotted. This resulted in a 13% reduction in sample size to 48,678 sightings of 405 black rhinos retained for analysis. Using these images, we extracted NDVI from the pixel intersecting the buffered sighting location to index vegetation productivity at the location. For each sighting, we also extracted the mean NDVI of the pixels intersecting the full reserve as well as the standard deviation of NDVI, then used those values to calculate the coefficient of variation of NDVI for the reserve, as an index of vegetation heterogeneity (i.e. patchiness).

Because seasonal variation significantly influences forage access for black rhinos (Ganqa et al., 2005), we designated each month as being either in the rainy or dry season using rainfall and temperature data from the nearest South African Weather Service Station to the reserve (Department of Forestry Fisheries and the Environment, 2025). For Liwonde National Park, we used rainfall

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TABLE 1 Predictions about group formation, size and demographics.

Name	Prediction	Explanation	Citations
Vegetation RDH	Increasing vegetation productivity and heterogeneity will be associated with higher likelihood of group formation and larger groups	A central prediction of RDH is that group formation and size are driven by both patch quality and heterogeneity	Carr and Macdonald (1986) and Macdonald and Johnson (2015)
Vegetation BRE	Increasing vegetation productivity will not increase likelihood of a group forming or group size	BR are usually not limited by forage but are at risk from conspecifics and the lowered resource costs of grouping may not overcome the costs of aggression	Brett (1998) and le Roex et al. (2019)
Season RDH	Groups will be more common, and larger in the rainy season than the dry season	Increased vegetation availability during the rainy season lowers the cost of grouping (particularly competition)	Carr and Macdonald (1986) and Macdonald and Johnson (2015)
Season BRE	Groups will be less common, and smaller, in the rainy season than the dry season	The prevalence of high-quality forage during the rainy season will allow solitary BR to spread out more during the rainy season than the dry season, avoiding potentially aggressive conspecifics	le Roex et al. (2019)
Familiarity RDH[a]	Larger groups will be associated with decreasing within-group familiarity	Animal groups may form regardless of social structure/familiarity if the principles of RDH are met	Carr and Macdonald (1986) and Macdonald and Johnson (2015)
Familiarity BRE[a]	Larger groups will be associated with no change or increasing within-group familiarity	BR are solitary and aggressive, and socialise more with familiar individuals, to lower the costs of socialisation	Stein and Shrader (2026)
Sex Ratio RDH[a]	Group size will be associated with an increasingly unbiased sex ratio	Under the RDH, animal groups form on the basis of resources, not necessarily demographics	Carr and Macdonald (1986) and Macdonald and Johnson (2015)
Sex Ratio BRE[a]	Increasing group size will be associated with no change or an increasingly female-biased sex ratio	Male BR are highly territorial and aggressive so they may not tolerate being a part of larger groups, and females may avoid them	Brett (1998)
Cow–Calf RDH[a]	Increasing group size will be associated with a decreasing proportion of cow–calf dyads	Animals form groups based on resources and may not necessarily group around females with young	Carr and Macdonald (1986) and Johnson et al. (2002)
Cow–Calf BRE[a]	Increasing group size will be associated with no change or an increasing proportion of cow–calf dyads	Because BR are solitary, cow–calf dyads are the most common and stable social unit, so groups are likely to form around them	Goddard (1967) and Stein and Shrader (2026)
Age RDH[a]	Increasing group size will be associated with a decrease in the proportion of subadults	Animal groups form around resources, and may not reflect expected demographic trends	Carr and Macdonald (1986) and Johnson et al. (2002)
Age BRE[a]	Increasing group size will be associated with no change or an increasing proportion of subadults	Subadults are commonly seen in groups of two or more, which might aid in dispersal. They also tend to be seen in groups with cow–calf dyads	Goddard (1967) and Klingel and Klingel (1966)

Note: The acronym following each name indicates if that prediction is associated with the resource dispersion hypothesis (RDH) or black rhino ecology (BRE). The RDH may still affect grouping behaviour even if group composition primarily reflects species ecology (Macdonald & Johnson, 2015; Macdonald & Newman, 2022). But it provides a potential explanation of grouping when composition does not follow expected species ecology.

[a]The composition predictions are not direct alternatives.

data provided by the reserve. We designated rainy months as those with monthly rainfall exceeding the annual median for that site and dry months as those less than the median for that site. We reviewed the designation of months for every site-year to adjust for anomalous months. For example, if we found a 'rainy' month between otherwise 'dry' months within a site-year, we reassigned the month as dry, and the same for 'dry' months within otherwise 'rainy' months.

Such distinct rainy and dry seasons generally did not occur at Buffalo Kloof. In the Eastern Cape, rainfall occurs at relatively similar amounts throughout the year. In the sites with rainy-dry season

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cycles, rainy seasons, which occur in the summer, are associated with high-vegetation growth and resource availability, and the dry winter season with low-resource availability. To identify similar seasons of higher and lower resource availability, 'rainy' and 'dry' seasons for Buffalo Kloof were designated using monthly temperature where 'rainy' months were defined as those with monthly temperatures above the site median (i.e. summer) and 'dry' months were defined as those with monthly temperatures below the site median (i.e. winter). Although the transitional months varied from year to year, there were no anomalous months within the seasons. This process resulted in every sighting month at every reserve designated as either 'rainy' (i.e. climactic variables associated with higher vegetative growth) or 'dry' (i.e. climactic variables associated with lower vegetative growth).

In addition to environmental variables, we were interested in composition of the groups formed as a function of size, and so calculated multiple composition metrics. First, we used individual birth date and sighting date to determine the age of each rhino in each sighting. We defined animals as a calf from birth to 2.5 years, as subadults from 2.5–7 years old, and individuals older than 7 as adults (Du Toit & Emslie, 2006; Goddard, 1967). Next, we adapted the Half Weight Index (HWI; Cairns & Schwager, 1987) to quantify how often specific dyads were seen together (i.e. how 'familiar' they were). We selected HWI because it accounts for situations in which animals are more likely to be seen alone than together and may also lessen effects from variation in sampling effort (Cairns & Schwager, 1987; Delmé et al., 2023). We calculated this as:

$$\mathrm{HWI} = \frac{x}{x + 0.5 \times \left(y_a + y_b\right)}$$

where x = number of joint sightings of rhino a and b up to that sighting; y_a = the number of sightings of rhino a up to that time, and y_b = the number of sightings of rhino b up to that time. By calculating the index for a sighting of a dyad only based on that and previous sightings, we incorporated the potential effects of increasing familiarity over time. We also identified dyads that were composed of cows with their calf and used that to calculate the proportion of cow–calf dyads within each sighting group as cow–calf dyads/all dyads. We used age class to calculate the proportion of calves, subadults and adults in each sighting, but because they were highly correlated, focused on subadults as our predictions pertained to them. Finally, we calculated group sex ratio as number of males/(number of males+ number of females). The sex of a small number of individuals (almost exclusively young calves) was not known. We did not include those individuals in the sex ratio calculation when they were sighted (only 55 out of the 48,678 sightings included an unsexed individual). All data processing besides NDVI extraction was completed in program R (R Core Team, 2024).

2.3 | Data analysis

We first evaluated the factors influencing whether a sighting was of an individual or a group of any size. Because calves were always seen with their mothers, regardless of the predictors, in this analysis, we excluded sightings in which groups of two consisted solely of a cow with her calf, which could have biased the results. Using the *lme4* package in R (Bates et al., 2015), we ran binomial generalised linear mixed-effects models (GLMMs) with a binary 'group' variable as the response (0 = individual, 1 = any size group), NDVI at the sighting location, coefficient of variation (CV) of NDVI of the reserve, and season as the predictors, and random intercepts for site and year. Although there were multiple sites within some provinces, we did not nest site within province because in most, there was only one site, the sites were fenced with no movement of black rhinos between them, and province was not necessarily an indicator of biological hierarchy (see Supporting Information). We considered including mean NDVI at the reserve, but it was correlated with NDVI at the sighting location, and sighting location NDVI was a better index of vegetation quality at the sighting location. We scaled and centred all numeric predictors then ran all combinations of the predictors, including two-way interactions, and a null random-intercept-only model. We ranked the models using Akaike's Information Criterion (Akaike, 1974).

Next, we evaluated factors influencing group size. We created a subset of the data which included only sightings of groups, including groups of two composed of cow–calf dyads. Using the *glmmTMB* package (Brooks et al., 2017), we fit truncated negative binomial GLMMs modelling group size as a function of season, NDVI at the sighting location, and CV of NDVI at the reserve as predictors, and random intercepts for site and year. Before fitting the models, we transformed the response by subtracting one, enabling us to use *glmmTMB*'s standard zero truncation. We scaled and centred all numeric predictors and ran all combinations, including two-way interactions, of the predictors, fit a random-intercept-only null and ranked models using AIC. We also ran a series of models to evaluate whether these environmental factors influenced whether a group was above a specific group size using binomial GLMMs (Supporting Information). Additionally, because individuals were included in multiple sightings which likely affected observation independence, and the irregular fluid group structure prevented simple modelling approaches within our main analyses, we ran a series of sensitivity tests to evaluate the relative effects of repeated observations of individuals on our group formation and size results (Supporting Information).

Finally, we evaluated group social characteristics (i.e. within-group HWI, sex ratio, proportion subadults, proportion cow-calves) as a function of group size. Running a typical ANOVA resulted in violations of model assumptions, largely because the variables were bounded from 0 to 1. Instead, we ran beta regression models with social characteristic as the response, group size as the predictor, and random intercepts for site and year. Before running the models, we used Smithson and Verkuilen (2006)'s transformation for beta regression using $\varepsilon = 0.001$ because the data included values of 0 and 1. This transformation applies a minor adjustment to the response values so that all fall between, rather than on, 0 and 1, as required by beta regression. For each response variable, we also ran a null random-intercept-only model and evaluated whether sighting group

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size predicted the variable better than the null using a chi-squared test. We used the model results to calculate estimated marginal means and conducted post hoc pairwise comparisons using Tukey's honestly significant difference test to evaluate specific differences in the variables by group size. All interpreted models across all analyses were assessed for adherence to their respective model assumptions and fit.

3 | RESULTS

In total, we used data from 48,678 sightings of 405 black rhinos. Of the sightings, 45.2% ($n=21{,}981$) were in the dry season and 54.8% ($n=26{,}697$) in the rainy season. Unsurprisingly, most sightings (68.36%, $n=33{,}277$) were of individuals. Groups of 2 comprised 23.50% ($n=11{,}441$) of the sightings; 6.27% ($n=3053$) were groups of 3, 1.54% ($n=752$) were groups of 4, 0.25% ($n=121$) were groups of 5, and only 0.07% were groups of 6 or 7 ($n_6=31$, $n_7=3$).

In the model set in which we evaluated factors influencing whether a sighting was of a group or an individual, the top-ranked model included NDVI at the sighting location, the coefficient of variation (CV) of NDVI at the reserve, and season (Table S1). There were no models competing with the top-ranked model, which was ranked 232.41 ΔAIC above the null. In the top model, increasing NDVI at the sighting location was associated with an increasing likelihood that the sighting would be a group rather than an individual ($\beta=0.127$, p-value <0.001). Similarly, increasing CV of NDVI was associated with an increasing likelihood of a group rather than an individual ($\beta=0.114$, p-value <0.001). Season (rainy vs. dry) did not predict whether a sighting was an individual or group ($\beta=0.036$, p-value = 0.244). The sensitivity analysis in which we reevaluated this model at the individual scale resulted in the same qualitative results, except season was significant and indicated that an individual was more likely to be seen within a group in the rainy season relative to the dry season (Table S2).

In the model set evaluating factors influencing group size, the highest ranked model also included NDVI at the sighting location, CV of NDVI, and season (Table S3). There were four competing models which all included season and either NDVI or CV of NDVI. The top model was ranked significantly higher than the null (ΔAIC = 50.48). In the top model, NDVI at the sighting location was marginally insignificant ($\beta=-0.032$, p-value = 0.073), although it was significant in competing models where increasing NDVI was associated with decreasing group size. Increasing CV of NDVI was associated with increasing group size ($\beta=0.074$, p-value = 0.037). Season was also significant ($\beta=0.163$, p-value <0.001), where groups were larger in the rainy season than in the dry season. In the sensitivity analysis in which we iteratively removed observations containing the most observed individuals, the direction of all predictors was the same as in the main analysis; season was significant, but significance of the NDVI predictors was variable (Table S4). In the threshold group size models, season, NDVI, and CV of NDVI significantly predicted group size in the 2–3 threshold in the same direction as the main results and sensitivity analyses, but season was the only significant predictor of the other thresholds (Tables S5–S7).

Group composition, including within-group familiarity (i.e. mean group HWI), sex ratio, proportion of subadults and cow–calf dyads, varied by group size (Figure 1). Within-group familiarity significantly improved model fit ($\chi^2_{(5)}=2613.9$, p-value <0.001) where increasing group size was associated with decreasing familiarity (Figure 1a). In the pairwise comparisons, larger groups tended to have significantly lower HWI than smaller groups, except in comparisons between groups of 7 to groups of 4–6 and in the comparison of groups of 6 to groups of 5.

Group size better explained sex ratio than the null ($\chi^2_{(5)}=715.23$, p-value <0.001). However, in pairwise comparisons, only groups of 2 and 3 had significantly different estimated sex ratios than other groups; specifically, groups of 2 were more female-biased than groups of 3–5, and groups of 3 were more female-biased than groups of 4 and 5. Estimated marginal means indicated that although groups of 2–3 were female-biased, other groups were statistically unbiased (Figure 1b).

Proportion of subadults also varied by group size, where group size explained proportion of subadults better than the null ($\chi^2_{(5)}=424.91$, p-value <0.001). Although the proportion of subadults appeared to increase with increasing group size (Figure 1c), only groups of 2 and 3 contained significantly fewer subadults than larger groups (i.e. 4–7 individuals). Finally, the proportion of cow–calf dyads was explained by group size better than the null ($\chi^2_{(5)}=112.79$, p-value <0.001), but only groups of 2 had an estimated marginal mean significantly different than the others where groups of 2 had fewer cow–calf dyads than groups of 3 and 4. Of the observed groups of 2, only 72% were a cow–calf dyad whereas >90% of other groups contained at least 1 cow–calf dyad (Figure 1d). The dependence structure associated with these data containing multiple sightings of the same individuals may have influenced these results similarly to the group formation and size results. However, the sensitivity analyses for those model sets generally supported the conclusions of the main analyses.

4 | DISCUSSION

The RDH provides a useful framework for understanding the importance of resources on grouping behaviour, and our results illustrate how the RDH may predict grouping, but the composition of those groups may be influenced by species-specific context rather than only resources. Our group formation and size results aligned with the RDH predictions, while group composition followed both RDH predictions and predictions based on black rhino ecology.

As expected by the RDH (Table 1; Vegetation RDH), whether black rhinos were seen in groups was driven by vegetation productivity (NDVI) at the sighting location and heterogeneity (CV of NDVI across the reserve) where an increase in either was associated with a higher probability of a group forming. Although increasing heterogeneity was also associated with increasing group size, increasing productivity at the sighting location was somewhat associated

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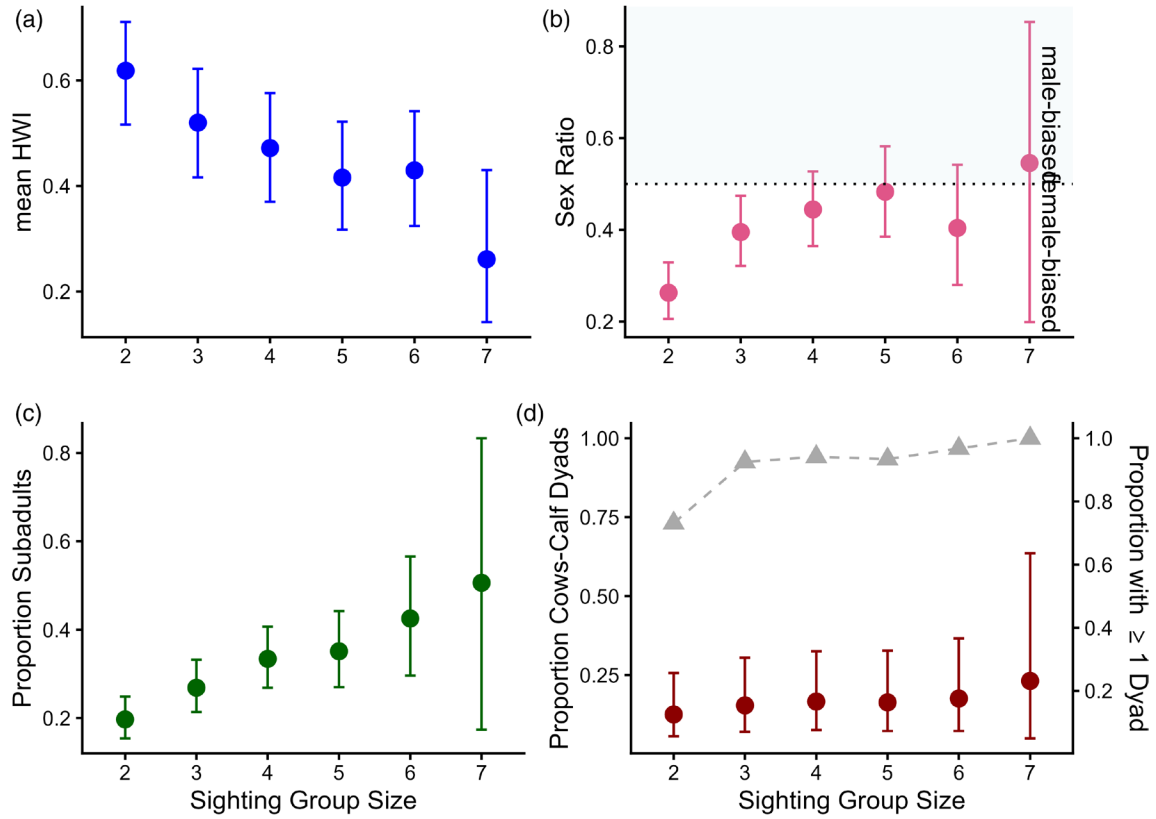


FIGURE 1 Estimated marginal means of within-group composition by group size. (a) Within-group familiarity displayed as mean HWI within the groups. (b) Sex ratio of the groups displayed as males/(males+females) such that sex ratio below 0.5 indicates more females than males in a group and above 0.5 indicates more males than females. (c) Proportion of subadults by group size as number subadults/group size. (d) Proportion of cow–calf dyads by group size as number of dyads/group size (red dots). The grey triangles display the proportion of groups observed with at least one cow–calf dyad.

with smaller groups which may reflect the costs of grouping in this solitary species (Greaver et al., 2014; Stein & Shrader, 2026). Unexpectedly, season did not significantly predict whether a group would form, but it did predict group size where groups were likely to be larger in the rainy season, supporting the Season RDH prediction over the Season BRE prediction in terms of group size but not formation (Table 1). We had expected groups might be more common and larger in the dry season because the prevalence of high-quality vegetation in the rainy season could allow black rhinos to avoid potentially aggressive conspecifics. Instead, as predicted by the RDH (Carr & Macdonald, 1986; Macdonald & Johnson, 2015), it is likely that the increased quality and abundance of resources in the rainy season lowers the costs of grouping such that tolerance of conspecifics is higher than during the dry season.

Social composition of groups generally varied by group size. The Familiarity RDH prediction was supported, where groups were generally less familiar with one another as group size increased (Table 1; Figure 1a), indicating that although black rhinos preferentially associate with familiar individuals (Stein & Shrader, 2026), the environmental drivers of the RDH may increase tolerance for strangers. We found that in pairwise comparisons, sex ratio was not significantly different between most group sizes, but groups of 2 and 3 were significantly more female-biased than larger groups which were unbiased. These results support our Sex Ratio RDH prediction (Table 1) where sex ratio became less biased with group size. Because males tend to be more aggressive than females and can increase risk to other black rhinos (Stein & Shrader, 2026), we had expected groups to be female-biased regardless of size. Instead, the female bias in the smaller groups probably reflects the presence of cow–calf dyads relative to group size. Indeed, we found that a majority of groups, including groups of 2, contained cow–calf dyads and so it is unsurprising that the smaller groups were female-biased even though the larger groups were not. Although most groups of all sizes, and especially larger groups, had at least one cow–calf dyad, the proportion of groups composed of cow–calf dyads remained largely constant with increasing group size, supporting our Cow–Calf BRE prediction (Table 1). Further, the proportion of groups with at least 1 cow–calf dyad was more than 90% for groups larger than 2 (Figure 1d). Together these findings support the importance of the cow–calf dyad as the most common social unit in the species. Finally, we found that, as expected by our Age BRE prediction (Table 1), an increasing number of subadults was associated with increasing group size, pointing to the increased social behaviour of subadults (Goddard, 1967; Klingel & Klingel, 1966). Overall, our group composition results show how both the RDH and species-specific context may be necessary in understanding group composition.

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Our study is the first evaluation of principles of the RDH in a solitary herbivore, and only the second in an ungulate. Moreover, it adds to the literature documenting the importance of species-specific context in evaluations of the RDH (Macdonald & Johnson, 2015; Macdonald & Newman, 2022). The mother-offspring social unit is the primary social unit in many solitary species (Lodé et al., 2021; Van De Walle et al., 2018). Similarly, in black rhinos, we found cow–calf pairs in nearly every group larger than two. Although principles of the RDH clearly drive black rhino grouping behaviour, cow–calf dyads still appear to be the basis for most of those groups, and we expect similar results in other solitary species that engage in maternal care.

Surprisingly, given the prevalence and severity of aggression in black rhinos (Brett, 1998; Goddard, 1967), the effects of aggression on grouping behaviour were limited. Familiarity lowers the risk of aggression in solitary aggressive species and subsequently is important not only to black rhinos (Stein & Shrader, 2026), but also to mountain lions (Elbroch et al., 2017), brown bears (Hansen et al., 2022), and giant kangaroo rats (*Dipodomys ingens*; Randall et al., 2002). In black rhinos, males tend to be more aggressive than females, so much so that associating with males at a high rate can increase individual mortality risk (Brett, 1998; Stein & Shrader, 2026) and so we expected groups to be largely female-biased. However, we found that increasing group size was associated with decreasing within-group familiarity and largely unbiased sex ratios. Simultaneously, groups were larger in the rainy season (i.e. the season of higher vegetation productivity) than the dry season. These results support an important aspect of the RDH, that the resource access and distribution that facilitates grouping, may do so by lowering the costs of grouping (Carr & Macdonald, 1986; Macdonald & Johnson, 2015; Macdonald & Newman, 2022). Aggression is a major cost of grouping in black rhino, yet, these results indicate that black rhinos may be more tolerant of unfamiliar or even unknown individuals, as well as males, during periods of resource abundance.

Translocation of black rhinos to establish new populations or supplement existing populations is one of the most important conservation interventions for the species but is also risky partly because of aggression by conspecifics (Linklater et al., 2011). As our results indicate that local individuals may be more tolerant of conspecifics, even unfamiliar strangers, during periods of higher resource availability and heterogeneity, introductions of translocated individuals may be more successful during these periods. Further, we also found that larger groups were largely unbiased with regards to sex. Because of the higher rates of aggression in males, and the risk they impose on others (Brett, 1998; Stein & Shrader, 2026), we had expected groups to be largely female-biased (Table 1; Sex Ratio BRE). But our results imply that periods of higher resource availability may also increase male tolerance. Thus, introductions during periods of higher resource availability, such as the rainy season, may lessen the risk of male aggression.

Despite the novel nature of our results, our study was subject to several limitations. First, we could not confidently calculate home ranges because we were using sightings, rather than GPS collar data, precluding a true empirical test of the RDH, which is based on territory- or home-range holding behaviour. However, because black rhinos establish home ranges in which they tolerate some overlap with neighbours (Goddard, 1967; Lent & Fike, 2003), and because grouping behaviour largely adheres to predictions following the RDH, we expect that a true empirical test would support the RDH. Because black rhinos do establish home ranges, they may be using spatial memory to select locations with quality resources although we did not account for that in the analyses. But spatial memory of resource distribution does not negate the RDH. Rather, it reinforces RDH's importance in explaining home range formation and distribution. An additional limitation is that black rhinos have access to forage resources year-round, but the more important limiting resource is likely access to water (Ferreira et al., 2019). Most of the study sites did not have water bodies large enough to be reliably detectable by the remote sensing products (i.e. at least 30 m) that were readily available across the full region and study period. Consequently, we could not include access to water as one of the environmental factors. We encourage future research that measures the effect of water on grouping behaviour and expect that water access will likely play a stronger role in driving black rhino grouping behaviour than forage. Additionally, the data did not include information on the nature of within-group interactions. We assumed dyads and groups with higher HWI, as well as larger groups were relatively unaggressive, but we cannot be sure that was always the case. Finally, because of the fluid group structure, we were unable to fully account for the non-independence of the data inherent in using multiple sightings of the same individuals. Our results were generally supported by the sensitivity analyses despite this problem, but the results should still be interpreted cautiously.

In addition to being ideal subjects for empirical tests of the RDH, it is likely that the unexpectedly nuanced social dynamics of solitary species also significantly influence grouping behaviour. Our study adds to evidence supporting the RDH and illustrates how species-specific context interacts with resource needs in shaping grouping behaviour.

AUTHOR CONTRIBUTIONS

Rachel M. Stein led conceptualisation, data curation, formal analysis, methodology, validation, writing and editing. She also contributed to project administration. Adrian M. Shrader led funding acquisition, project administration, resources and supervision. He also contributed to conceptualisation, formal analysis, writing and editing. All authors contributed to all drafts and gave final approval for publication.

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Dinokeng Game Reserve, Liwonde National Park which is managed by African Parks, Greater Makalali Private Game Reserve, Manyoni Private Game Reserve, Mpilo Nature Reserve, Munyawana Conservancy, Nambiti Private Game Reserve, Pongola Game Reserve, Selati Game Reserve, Somkhanda Game Reserve and Thanda Safari Private Game Reserve.

CONFLICT OF INTEREST STATEMENT

We declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Black rhinos are critically endangered and one of the primary threats is poaching. To protect the security of the study animals and reserve staff, we cannot make our data publicly available.

STATEMENT ON INCLUSION

Our study uses data gathered by local managers and monitoring teams from reserves in South Africa and Malawi. Both authors were based at the University of Pretoria in South Africa for the duration of the study.

STATEMENT ON USE OF AI

We used OpenAI's ChatGPT to assist with troubleshooting our R code, specifically to identify the causes of error messages and to resolve them. All suggested code was manually reviewed, tested and edited by the authors prior to use. No AI tools were used for study design, interpretation or writing.

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Table S1. Factors influencing whether a sighting was likely to be a group or an individual. We provide the top five models ranked by AIC as well as the null, with model weights displayed. Models could include NDVI (i.e. index of resource availability at the sighting location), CV_NDVI (i.e. coefficient of variation of NDVI at a reserve during a sighting as an index of patchiness), season (rainy vs. dry), and one-way interactions. In each listed model, variables that are significant within the model according to the *p*-value are bolded.

Table S2. Individual rhino sensitivity test. To evaluate how the patterns in the top group or single model were influenced by the repeated observations of the same animals, we conducted a sensitivity test. In the test, for every group, we added an observation for each individual present to enable an additional focal individual random effect. The table displays the results of both (main vs. sensitivity) for easy comparison. Season is coded as the likelihood of a group being spotted in the rainy versus the dry season.

Table S3. Model set evaluating the effects of environmental factors on group size. We list the top five models and the null. Bolded variables are significant within the model.

Table S4. Sensitivity test removing the most observed individuals. To evaluate the potential influence of animals with more observations, we progressively removed groups containing individuals with the most observations. We then reran the model with each reduced dataset.

Table S5. Factors influencing whether a group sighting was likely to be of more than 2 individuals. We display the top ranked models and null. Bolded variables are significant predictors in the model.

Table S6. Factors influencing whether a group sighting was likely to be of more than 3 individuals. We display the top ranked models and null. Bolded variables are significant predictors in the model.

Table S7. Factors influencing whether a group sighting was likely to be of more than 4 individuals. We display the top ranked models and null. Bolded variables are significant predictors in the model.

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