Check for updates

OIKOS

Research Article

Familiarity and aggression shape long-term associations and mortality risk in a solitary ungulate

Rachel M. Stein and Adrian M. Shrader

Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

Correspondence: Rachel M. Stein (rstein2556@gmail.com)

Oikos

2026: e12226

doi: 10.1002/oik.12226

Subject Editor: Hillary S. Young
Editor-in-Chief:
Paulo R. Guimaraes
Accepted 5 March 2026

Periodic social interactions are important to animal fitness, even in solitary species. For solitary species, these interactions can be unexpected and shaped by previous encounters. Despite being aggressive and largely solitary, black rhinoceroses *Diceros bicornis* are commonly seen in groups, suggesting they may engage in more social behaviours than previously recognised. However, their social behaviour, and how those behaviours influence survival, are largely unknown. We evaluated association behaviour of black rhinos at different life stages (i.e. calf, subadult, adult) from 69 920 sightings from 14 reserves in southern Africa. Associative behaviours varied significantly by age class and sex, with subadult males associating with specific individuals at the highest rate and adult females associating with the greatest number of individuals. Rate of association was influenced by previous association (i.e. familiarity). However, our results illustrate that social associations can be costly for black rhinos. Specifically, mortality risk was higher for calves that associated at higher rates, and higher for adults that associated with more males, or more individuals close in age, likely due to aggressive interactions since fighting conspecifics is a common cause of death. In contrast, association might provide benefits. In adults that associated with at least one unrelated conspecific, males displayed lower mortality risk than females. To our knowledge, this is the first study documenting long-term association behaviour in a solitary ungulate, providing evidence that social interactions in solitary species are more common, and more important with regards to the impact on long-term survival, than previously thought.

Keywords: black rhinoceros, *Diceros bicornis*, fitness, groups, offspring, social, solitary living

Introduction

As adults, solitary animals mainly forage and sleep alone (Makuya and Schradin 2024a). Nevertheless, fitness of these species might be influenced by periodic social interactions with conspecifics during courtship and breeding, as well as social interactions outside breeding contexts (Clutton-Brock 2021). Life history, genetic lineage and environmental constraints result in a spectrum of social organisations in solitary

© 2026 The Author(s). Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

species from obligately solitary, in which all individuals are solitary, to facultatively solitary, in which many individuals live in pairs or even groups (Bearder 1999, Makuya and Schradin 2024a). When solitary species do engage in social interactions, those interactions can be unexpectedly nuanced. For example, pumas *Puma concolor* form social networks that influence the nature of their interactions as a function of reciprocal kill sharing, territorial overlap, and sex of the individuals (Elbroch et al. 2017). Despite the growing body of evidence that solitary species engage in such social interactions (Makuya and Schradin 2024b), social behaviour outside breeding is rarely documented.

The benefits of group living, such as reduction in predation risk and easy access to potential mates (Silk 2007, Clutton-Brock 2021) are more regularly documented than the benefits of solitary living. However, it may be inferred that the benefits of solitary living mitigate the costs of group living, for example by lessening disease risk, conflict, and competition for resources (Makuya and Schradin 2024a). Social behaviour in solitary species is likely context-dependent. For instance, Indian black scorpions *Heterometrus fulvipes* disperse and dig burrows soon after birth. However, dry soil conditions prevent young from digging, increasing predation risk and prompting offspring to form communal nests with their mothers and siblings. In these nests, individuals divide labour (i.e. nest expansion and foraging), share food, and do not cannibalise one another although cannibalism is common in the species (Shivashankar 1994).

An important determinant of social behaviour in many species is the behaviour of an individual's mother. Maternal interactions with the offspring and conspecifics during the time when an offspring is being cared for may influence affiliative behaviours with conspecifics later in life (Branchi et al. 2013, Thompson and Cords 2020). For example, only house mice *Mus musculus* that were exposed to both maternal and peer interactions, rather than one or the other, developed advanced adult social behaviours such as immediate assessment and acknowledgement of social status (Branchi et al. 2013). The social interactions of mothers can also affect offspring survival. In chacma baboons *Papio cynocephalus ursinus*, offspring live significantly longer if their mothers form strong rather than weak bonds with other females (Silk et al. 2009). Although rarely documented, there is some evidence that maternal relationships may have similar long-term effects on offspring in solitary species. For example, young female brown bears *Ursus arctos*, establish home ranges that not only overlap with their mother's, but also with familiar females whose home ranges overlapped with their mother's during rearing (Hansen et al. 2022). However, studies documenting maternal effects on offspring social behaviour in solitary species typically focus on long-term relationships between mothers and offspring rather than on how maternal behaviour affects offspring relationships with others (Makuya et al. 2024). Results like this suggests more attention should be devoted to evaluating maternal effects on social behaviours in solitary species.

The critically endangered black rhinoceros *Diceros bicornis* (hereafter black rhino) is a long-lived solitary and polygynous megaherbivore (i.e. ≥ 1000 kg) that exhibits maternal care (Berger 1994). Although adults are usually seen alone or with a calf, groups of 3–4 individuals have been observed regularly and larger groups, of even up to 13 animals, have been reported (Goddard 1967, Frame 1980). Subadults (i.e. males and females that have left their mother but are not old enough to breed), are so commonly seen in the company of other subadults or with an unrelated adult female with a calf, that the subadult period is often regarded as the most social stage of a black rhino's life (Klingel and Klingel 1966, Goddard 1967). Why subadults are so social is unknown. But, like dispersing subadult white rhinos *Ceratotherium simum*, subadult black rhinos may make exploratory excursions outside their home ranges in the company of other subadults or adult females with older calves, lessening the costs of dispersal (Shrader and Owen-Smith 2002). Thus, although solitary, black rhinos may engage regularly in social interactions. Nevertheless, black rhinos can be aggressive towards conspecifics and mortalities from fighting are common (likely stemming from territorial or mating disputes; Brett 1998, Linklater and Swaisgood 2008, Greaver et al. 2014). Multiple studies and conservation programmes report that mortality from fighting was a common cause of death for black rhinos in their populations, especially for subadult and adult males, probably from encountering aggressive territorial males (Du Toit and Emslie 2006, Greaver et al. 2014). Indeed, aggression is so common in black rhinos that it has been cited as a primary mechanism by which density-dependence influences their populations (Greaver et al. 2014). A lack of understanding about the subtle social interactions of solitary species can cause managers to overlook their social needs when making management decisions (Olivier et al. 2022), which, in the case of black rhinos, may change or lessen the effect of conservation actions such as translocation.

Here, we evaluate the associative behaviour, and the effects of that behaviour on mortality risk of black rhinos in multiple breeding populations at different life stages (i.e. calf, subadult, adult). We predicted that associations would be more likely to occur between individuals that already know each other, similar to other solitary animals (Elbroch and Quigley 2017, Hansen et al. 2022), which may lessen the risk of aggression. We expected this pattern to be more prevalent if interactions were tolerated by the mother (i.e. subadults and adults should associate at higher rates with a conspecific if they were allowed to interact when they were a calf). Additionally, we predicted that the influence of associative behaviour on mortality risk would be dependent on the life stage in which individuals engaged in the behaviour. Specifically, that association rate during the vulnerable calf and aggressive adult stages (Greaver et al. 2014) would have negative effects on survival due to fighting, but increased associative behaviour during the more social subadult life stage (Klingel and Klingel 1966, Goddard 1967) would decrease risk. However, because black rhinos are aggressive to

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ehk.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

conspecifics, we predicted that associating with higher numbers of conspecifics would increase mortality risk regardless of age.

Material and methods

Study sites

We utilised sightings and demographic data collected in 14 reserves that have had black rhinos between 2 and 20 years (2004–2024). One of these reserves was Liwonde National Park in Malawi, which is managed by African Parks, and the others were in four provinces in South Africa: Buffalo Kloof Private Game Reserve in the Eastern Cape, Dinokeng Game Reserve in Gauteng, Balule Nature Reserve, Makalali Game Reserve, and Selati Game Reserve in Limpopo, and Babanango Game Reserve, Manyoni Private Game Reserve, Mpilo Nature Reserve, Munyawana Conservancy, Nambiti Private Game Reserve, Pongola Game Reserve, Somkhanda Game Reserve and Thanda Mduna Private Game Reserve in KwaZulu-Natal. All the reserves experience two seasons (wet, dry), but the precise timing and severity of these seasons varied by location and year (Department of Forestry Fisheries and the Environment 2025). The sites also encompass a large elevational gradient ranging from 130 to 1430 m a.s.l. As a result, the vegetation communities varied widely across the sites. However, black rhinos were historically widespread throughout sub-Saharan Africa and are resilient to a range of environmental conditions (Rookmaaker and Antoine 2012).

Data collection

At each site, black rhino sightings were recorded by the site's monitoring team as part of regular management protocol, resulting in 1–81 (median = 2, mean = 3.7) sightings of each individual every month following translocation or birth, with some sites using VHF and/or GPS tracking devices to assist with these efforts. From these, the sites collectively provided 69 920 sightings of 542 black rhinos. Each animal was identified from a unique ear notching pattern previously applied as a routine part of each site's management activities (Goodman 2013). Individuals were considered to be within a group if they were within 50 m of other black rhinos. If a female was seen with a new calf, the calf's birth date was estimated using the last sighting of the mother prior to birth, the first sighting of the calf, and the calf's body size (Hitchins 1978). Calves were immobilized by their second birthday to apply ear notches (Goodman 2013) and any tracking devices. Prior to that, they were identified by their mother's ear notches.

The approximate birth dates of all black rhinos born on the sites were known, whereas birth dates of translocated individuals were estimated based on observations prior to capture and translocation. With the exception of some young calves, the sex of all individuals was also known. If an animal died during the study period, the site provided the approximate date and cause of death. We have not provided site-specific information for security reasons. The study was approved by the University of Pretoria Animal Ethics Committee and awarded the reference no. (NAS301/2024).

Data processing

We assigned the individual rhinos in each sighting to age classes. Individuals were defined as calves from birth until the point when they moved away from their mother (ca 2.5 years), as subadults until they were seven years old, and as adults after seven years (Goddard 1967, Du Toit and Emslie 2006). Sites collectively provided data on 542 individuals (range 12–76 individuals). However, we removed individuals whose sex was unknown (n = 43; Fig. 1), which were mainly young calves, because we tested for sex-specific differences in behaviour. Thus, our dataset comprised 499 individuals across the 14 sites (Fig. 1).

For every focal-associate dyad within every life stage of the focal, we calculated half-weight index (HWI), an established index of association rate (Cairns and Schwager 1987). We selected HWI because it is more robust than other association indices to situations in which individuals are more likely to be seen alone than together and is utilised in field studies to account for imperfect observation conditions and varying observation effort (Cairns and Schwager 1987, Delmé et al. 2023). Black rhinos are largely solitary, and a majority of the sightings (69%, n = 48 382) were of single individuals. We calculated HWI relative to the age class of the focal individual in every age class in which it was observed as:

$$\frac{x}{x + 0.5\left(y_a + y_b\right)}$$

where x was the number of sightings of the focal and associate together when the focal was in the target life stage, y_a was the number of sightings of the focal without the associate while it was in the target life stage, and y_b was the number of sightings of the associate without the focal while the focal was in the target life stage (regardless of the age of the associate). Thus, although HWI is usually not directional, to better address our questions, we calculated HWI directionally based on the dates when the focal was in a specific age class. For every focal-associate dyad, we also calculated absolute age difference (Fig. 1) based on the estimated birth date of the individuals to understand if black rhinos in each age class associate at greater rates with same or differently aged individuals.

For each focal animal in each age class in which they were observed, we calculated additional association metrics (Fig. 1). First, we calculated mean HWI from the calculated HWI in each dyad for which they were the focal to determine the overall rate at which an individual associated with others while within an age class. Next, we used dyad age difference to calculate average associate age difference for every focal within every age class. As we were interested in the risks of associating with males versus females, for every focal within each age class, we calculated associate sex ratio as the number of males a focal was seen with divided by the total number of male and female associates a focal was seen with. We did not apply any site-level adjustment to associate sex ratio (i.e. adjust associate sex ratio relative to site-specific sex ratios) because we accounted for site using a random intercept in all analyses. Additionally, we calculated degree, a social network

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ele.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

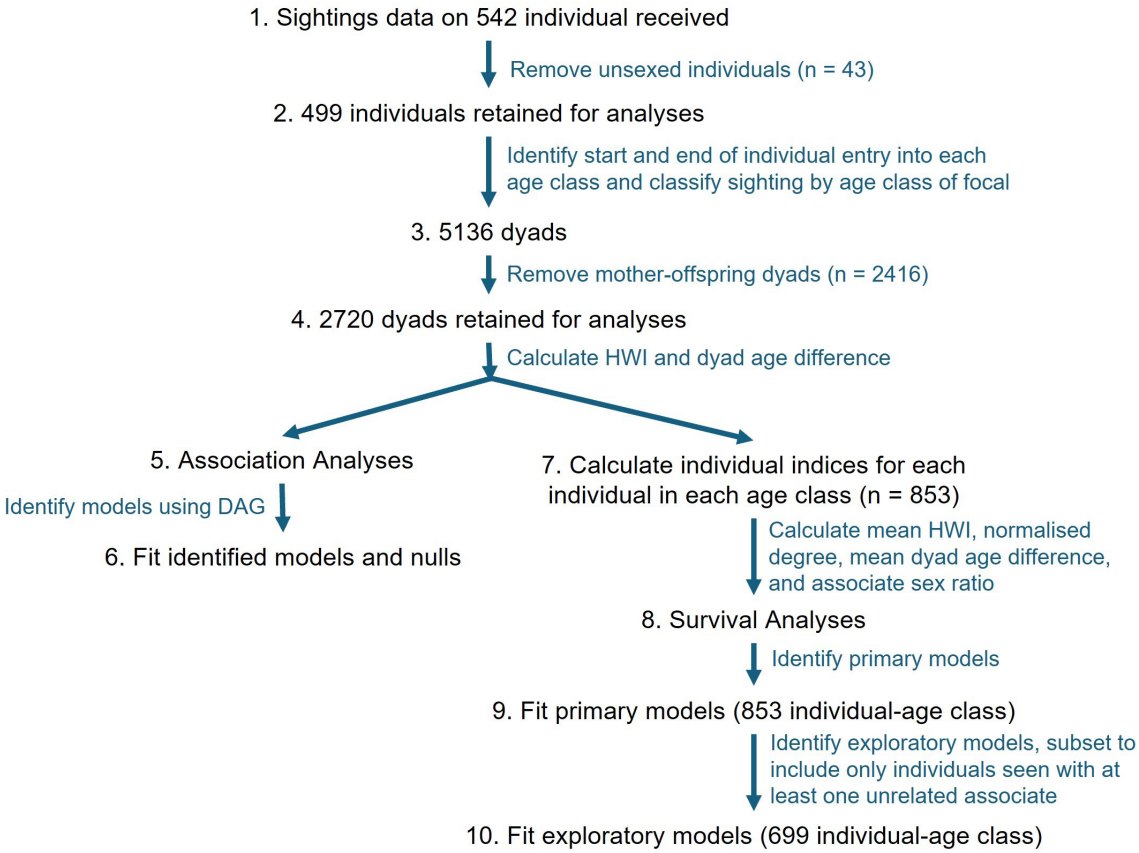


Figure 1. Data processing and analysis workflow. The workflow displays how individuals and dyads were filtered for analyses from the raw sightings data to dyadic association metrics, aggregation into individual-age class level indices, and the subsequent association and survival analyses. Dyad metrics were calculated directionally based on the age class of the focal in each focal-associate dyad. Individuals were removed between steps 9 and 10 if they were never seen during a given age class with an unrelated individual because the metrics used in the exploratory models could only be calculated for individuals observed with at least one unrelated associate.

metric, as the count of associates a focal was seen with during each age class (Wey et al. 2008). Because of the large differences in population sizes amongst sites, we calculated normalised degree, which was the number of associates the focal was seen with during the age class divided by the number of possible associates, which we defined as all living individuals at the site. Calculation of these metrics did not include associations between a focal and their mother or their calf.

We did not calculate other network metrics such as centrality or conduct full network analyses because sampling effort varied across sites and, within any given site, we cannot be certain that every network connection was observed. Incomplete observations of a social network can destabilize analyses and create spurious trends, particularly if individuals are usually seen alone (Wey et al. 2008, Farine and Whitehead 2015).

General analyses

We evaluated the differences in association metrics (HWI, associate age difference, normalised degree, associate sex ratio) between age and sex classes by running linear mixed-effects models using the 'lme4' package in R (Bates et al. 2015, www.r-project.org) with metric as the response, age-sex class as the predictor, and a random intercept for site. We did not separate age and sex as separate predictors because we expected an interactive effect of the two in which these behaviours varied across age classes and within age class, by sex. For these analyses, we split the age classes by sex because males tend to be more aggressive than females (Du Toit and Emslie 2006, Greaver et al. 2014) and so likely engage in associative behaviours at different rates, even within the same age class. For the HWI and associate age difference models, we also included random intercepts for focal and associate. We evaluated whether the metrics were significantly different by age-sex class by running the models through ANOVAs, evaluating the differences using Tukey's HSD, and calculating the estimated marginal means. Because of violations of the assumption of homoscedasticity, we applied a log transformation to HWI, normalised degree, and associate sex ratio prior to running those models. To aid in interpretation, we back-transformed the estimated marginal means.

Association analyses

To evaluate factors influencing HWI within each age class we first constructed a directed acyclic graph (DAG; Borger and Ramesh 2025), enabling us to define models to determine

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ehk.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

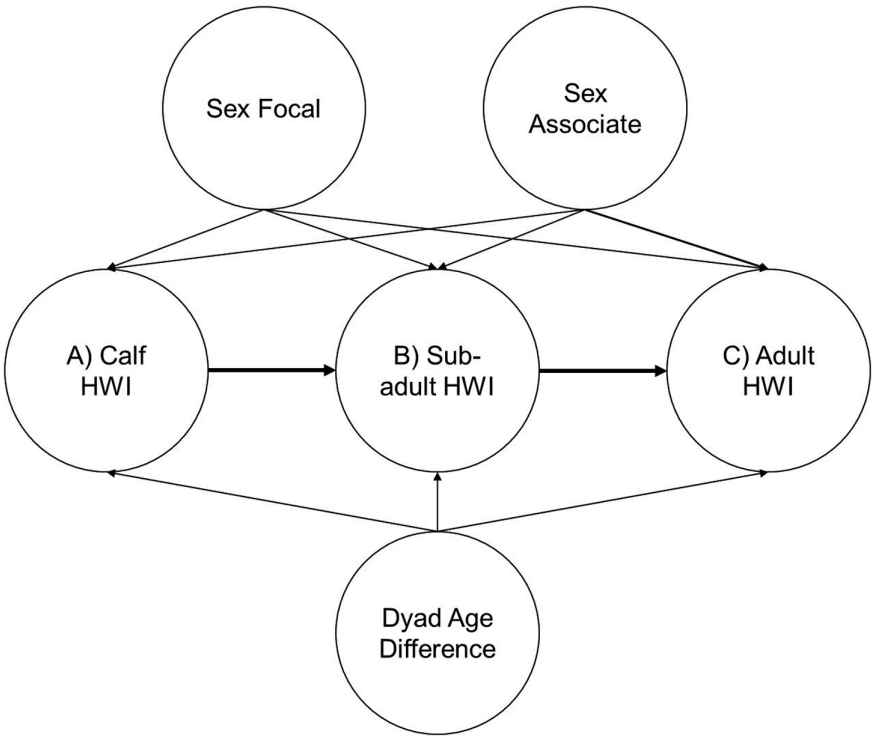


Figure 2. A directed acyclic graph (DAG) of the factors we expected to influence the half-weight index (HWI) of dyads within each focal age class. Arrows represent one variable acting on another. The variables of primary interest were labelled with A), B) and C) for later reference. Thin arrows represent the effect of intrinsic variables (sex of the focal, sex of the associate, and the age difference between the two). Thick arrows display the effects we were primarily testing, how HWI of a previous age class influences HWI of subsequent age classes.

the influence of familiarity (i.e. HWI in the previous age class) on associations (Fig. 1). Using the DAG (Fig. 2), we identified five models to address our hypotheses about the factors influencing HWI of each focal's observed association rates in each life stage (Table 1). Each model included the intrinsic variables that we expected to affect association rates regardless of previous familiarity: sex of the focal, sex of the associate, and dyad age difference, but varied by which HWI variable(s) were included (Table 1). We defined three different models with adult HWI as the response to understand the effects of recent familiarity (subadult HWI) and long-term familiarity (calf HWI) which could point to potential maternal effects. Based on our DAG (Fig. 2), we expected subadult HWI to mediate the effect of calf HWI on adult HWI and so ran model 5 to understand the relative magnitude of the mediating effect of subadult HWI in comparison to the direct effects of calf HWI in model 3 and subadult HWI in model 4 (Table 1).

We used the 'glmmTMB' package in R to fit the identified models as generalized linear mixed models with a beta distribution (Brooks et al. 2017). We restricted analyses to focal-associate dyads observed during the response life stage which ensured that inference focused on our primary question, about how association of observed dyads was influenced by

Table 1. Selected association models. We defined each model based on the DAG (Fig. 2). Our primary hypotheses were about the effects of HWI in one life stage on HWI in subsequent life stages and show the hypothesis being tested by each model (letters correspond to the letters in Fig 2). We display the response variable for each model, the fixed effects, and the variable(s) randomised in the model permutations we ran to define the null distribution. For every model, and their associated null, we included random intercepts for focal ID, associate ID and site.

Model	Primary link tested (DAG)	Response	Fixed effects	Randomised variable
1	A only affected by intrinsic variables	calf HWI	dyad age difference, sex focal, sex associate	–
2	A→B	subadult HWI	calf HWI, dyad age difference, sex focal, sex associate	Calf HWI
3	B→C	adult HWI	subadult HWI, dyad age difference, sex focal, sex associate	Subadult HWI
4	A→C	adult HWI	calf HWI, dyad age difference, sex focal, sex associate	Calf HWI
5	A+B→C	adult HWI	calf HWI, subadult HWI, dyad age difference, sex focal, sex associate	Calf HWI, Subadult HWI

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ehk.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

association in previous age classes. This approach allowed the predictors to explain variation in association strength without introducing uncertainty from unobserved dyads. To verify the robustness of this approach, we reran the models using all dyads with zero-inflated beta regression which resulted in models with same inference (Fig. 1, Supporting information). In addition to the fixed effects (Table 1), we included random intercepts for focal, associate, and site to each model. Although there were no true zeros in our response variables because of the focus on observed dyads, a large proportion of observations were still very close to zero (e.g. in model 1, 52% of calf HWI observations were < 0.05) which resulted in modelling errors because of beta regression assumptions. To overcome this problem, we employed Smithson and Verkuilen's (2006) transformation for beta regression using $\varepsilon = 0.5$. We verified the robustness of this epsilon value by rerunning the models with $\varepsilon = 0.001$, which produced negligible differences (Supporting information). We scaled and centred the numeric predictors prior to running the models. Our null hypothesis for each model was that the HWI of the target age class was not influenced by HWI of the previous age class better than random. To generate a null distribution, we ran 1000 permutations of each model in which we randomised the HWI predictor (Table 1, Supporting information). We did not randomise the intrinsic variables or random effects because their structure is biologically fixed and the random effects reflect the repeated structure of the data (Croft et al. 2011). Thus, we did not generate a null distribution for model 1 because the only predictor variables were intrinsic (Fig. 2, Table 1).

Survival analyses

To evaluate the effects of social behaviour in each life stage on mortality risk, we ran Cox proportional hazards models with the 'coxme' R package (Cox 1972, Therneaur 2023). Entry was designated as birth in the calf analyses, 981 days following estimated birth date (i.e. one day older than 2.5 years) in the subadult analyses, and 2556 days following estimated birth date (i.e. one day older than seven years) in the adult analyses. Events were defined as date of death. Most animals were still alive at the end of the study and were right-censored. Because we did not expect an effect of social rate on risk of death from poaching or other human causes, we censored those animals as well (28 individuals: 20 poached, 4 euthanised or died following a management complication, 4 vehicle collisions). We collapsed causes of death from non-human causes into three categories: natural (diseases, natural accidents, predation, old age), fighting, and unknown.

Our primary hypotheses were focused on the effects of social association rate (i.e. mean HWI) and number of individuals interacted with (i.e. normalised degree), and so our primary cox proportional hazard models contained only those variables and sex of the individuals (i.e. an intrinsic variable which might influence risk). Due to the small number of mortalities during the calf and subadult stages (4 and 5 respectively), we only ran models focused on the influence of life-stage specific association metric on overall mortality risk (i.e. to the end of the study period: 1 November 2024) rather than considering mortality risk within a life stage. Thus, we ran one model for each life stage (Table 2). In addition to the variables of interest, we controlled for the varying number of observations of each individual by including the number of observations of the individual during the age class as an additional fixed effect. Additionally, we included site as a random effect to control for site-specific factors. We did not add age as a time varying covariate to these models because of limits associated with our data and analysis structures (Supporting information).

In addition to the primary survival analyses, we were also interested in evaluating mortality risk to individuals associating with same and differently aged associates and those associating with different proportions of males and females. However, we could not calculate these metrics for individuals that were never observed associating with an unrelated individual. Thus, we ran exploratory models using a subset which included only individuals which were observed associating with an unrelated individual (i.e. n = 699 individual-age class; Fig. 1). In each age-class model, we included mean associate age difference and associate sex ratio as the primary fixed effects, number of observations of the individual included as a control fixed effect, and site as a random effect. We ran three models, one for each age class for which these variables were calculated (Table 2).

Results

Association rates

Of the 69 920 sightings, 69.2% were of individuals, 22.7% were pairs, 6.2% were groups of 3, 1.5% were groups of 4, and 0.4% were groups larger than 4, with the largest groups comprising 7 individuals (n = 5). From our ANOVAs and Tukey HSDs, we found that all association metrics significantly

Table 2. Cox proportional hazard models. For both the primary and secondary analyses, we ran one model per age class using the variables calculated during that age class. Exploratory analyses only included a subset of individuals that were seen socialising with at least one unrelated conspecific because the variables could not be calculated for individuals that were never observed with another. Every displayed model also included the number of observations of the individual during the age class as a fixed effect and a random effect for site.

	Age class	Variables
Primary	calf	Mean HWI
		Normalised degree
	subadult	Mean HWI
		Normalised degree
	adult	Mean HWI
		Normalised degree
Exploratory	calf	Mean age difference
		Associate sex ratio
	subadult	Mean age difference
		Associate sex ratio
	adult	Mean age difference
		Associate sex ratio

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ehk.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

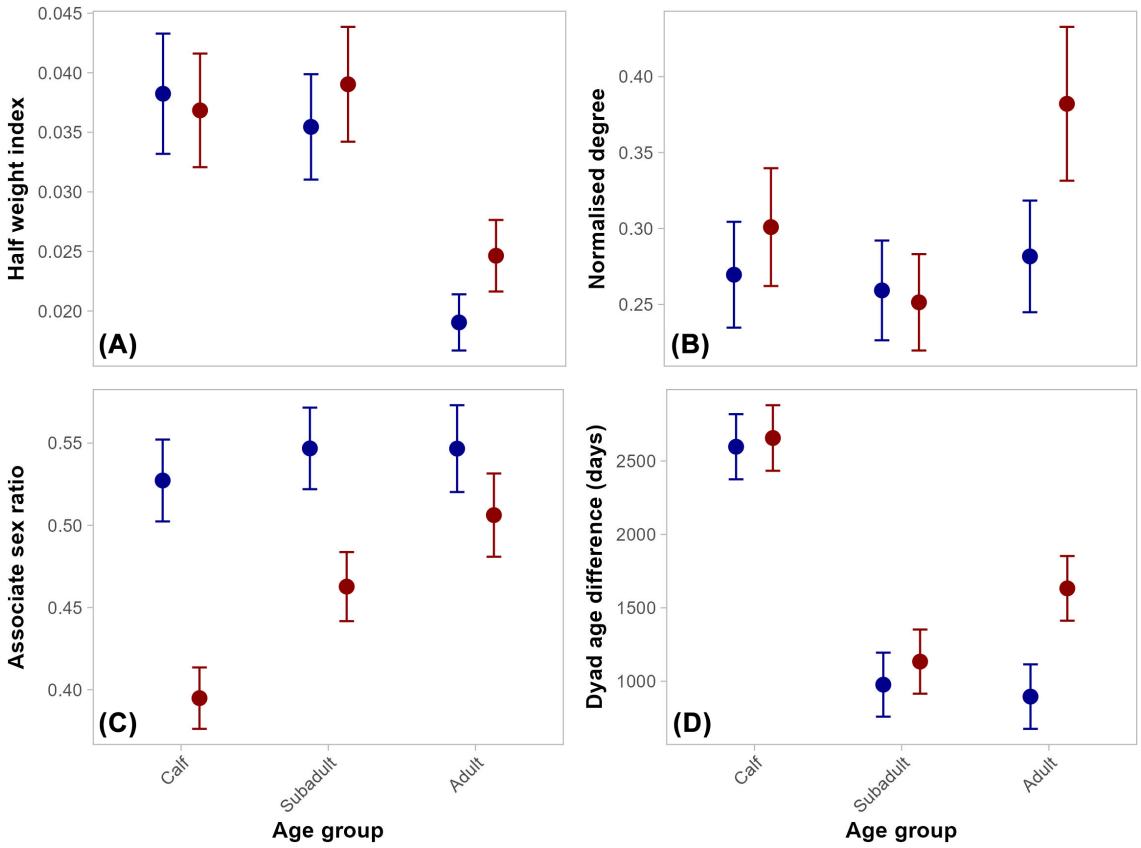


Figure 3. Estimated marginal means and standard errors of the association metrics by age class (x-axis) and sex (blue/left = male; red/right = female). (A) Half-weight index is an estimate of association rate between a focal and associate based on the focal's age class. (B) Normalised degree refers to the number of associates a focal has been seen with divided by the potential number of associates. (C) Associate sex ratio displays the sex ratio (i.e. males/(males + females)) of the associates of each focal. (D) Dyad age difference displays the absolute age difference between a focal and an associate.

varied by age-sex class (Fig. 3). Half-weight index (HWI) was significantly different between age-sex classes (ANOVA: $F_{5,829.83} = 25.651$, $p < 0.001$). However, the results of the Tukey tests showed that although the differences were significant between age classes, within age class, there was no significant difference between the sexes except for adults. Male subadults had the highest HWI (estimated marginal mean = 0.039 ± 0.005) and female adults the lowest HWI (mean = 0.025 ± 0.003). We also found significant differences in normalised degree by age-sex class ($F_{5,441.33} = 6.213$, $p < 0.001$). However, adult females (mean = 0.382 ± 0.051) were the only group with significantly different normalised degree than the others. We also found significant differences in the associate sex ratios by age-sex class ($F_{5,417.1} = 17.057$, $p < 0.001$). Interestingly, there were consistent differences between males and females within age classes where males associated with more males, and females associated with more females (although the difference was not significant in adults). This trend was most marked in calves, where male calves associated with more male associates (mean = 0.530 ± 0.025) and female calves associated more with females (mean = 0.395 ± 0.019). Average age difference between focals and their associates was strongly and significantly influenced by age-sex class ($F_{5,528.21} = 117.64$, $p < 0.001$) where calves associated more with differently aged individuals from themselves than other age classes. Female calves associated with individuals that were on average 2657 ± 223 days older (~ 6.7–7.9 years older). In contrast, adult males associated with individuals that were similar in age, 895 ± 220 days older or younger (~ 1.8–3.0 years difference). Thus, calves regularly associated with individuals that were in a different age class, but adult males associated with individuals that were likely in the same age class. Adult females associated more with individuals in different age classes compared to adult males (mean = 1632 ± 220 days; ~ 3.9–5.1 years), likely reflecting associations with other females with calves.

Association analyses

As predicted, HWI (i.e. association rate) of later age classes was predicted by HWI of the previous age class. However, the effects of intrinsic variables on HWI varied (Supporting information). The intrinsic variables did not influence calf HWI although there was a marginal effect of sex of the focal where male focals had a higher HWI ($\beta = 0.121$, $p = 0.062$). Yet, age difference significantly influenced subadult HWI where HWI was greater when the focal and dyad were close

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ehk.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

in age (β = −0.157, p <0.001). Calf HWI also significantly and positively influenced subadult HWI and had a greater effect size than age difference (β = 0.337, p <0.001). The model results for the effect of calf HWI on subadult HWI were significantly different from those obtained from the null distribution (two-sided empirical p < 0.001).

The effect on adult HWI varied depending on which previous HWI was included in the model (Supporting information). Including only subadult HWI resulted in a significant and positive effect on adult HWI (β = 0.172, p < 0.001) and significantly exceeded the null distribution in permutation testing (two-sided empirical p < 0.001). Moreover, we also found significant effects of sex of the focal (β = −0.185, p = 0.022) and sex of the associate (β = −0.144, p = 0.029), where HWI was lower if the focal or the associate was male. When calf HWI was a predictor, it was not significant (β = 0.074, p = 0.118) and did not differ from the permutated null distribution (two-sided empirical p = 0.140). The only significant variable in that model was sex of the focal where HWI was lower if the focal was male (β = −0.254, p = 0.043). Yet, there was a marginally insignificant effect of age difference, where HWI was marginally lower when associates were closer in age (β = −0.176, p = 0.090). When we included both calf HWI and subadult HWI, subadult HWI was significant (β = 0.190, p <0.001) and more significant than the permutated null distribution (two-sided empirical p = 0.015). However, calf HWI was not significant (β = −0.033, p = 0.579) and did not differ from the null distribution (two-sided empirical p = 0.641). This model points to a strong mediating effect of subadult HWI and supports our original DAG model (Fig. 2).

Survival analyses

Numbers of deaths by the different causes varied by age class, but notably there were few deaths of calves and subadults reflecting both the high survival rate of black rhino and the removal of unsexed individuals from the analyses (Supporting information). In calves, unknown causes were the most common cause of death (n = 2), while for subadults, the most common causes of death were fighting and unknown (n = 2 respectively). By contrast, the most common cause of death in adults was human causes (n = 27), namely poaching. In adults, the most common cause of death not directly associated with humans was natural causes (n = 23).

In the primary analyses, neither mean HWI nor normalised degree during the specified age class significantly influenced long-term mortality risk in most age classes (Supporting information). However, we found that mean HWI during the calf stage did significantly influence mortality risk (HR = 1.554, CI = 1.113–2.171, p = 0.010; Fig. 4). This result indicates that as individuals associated at higher rates as calves, their long-term mortality risk also increased. In these analyses, number of observations within the age class (a control predictor) and sex of the individual were also never significant.

In the exploratory analyses, which included only individuals which were seen with an unrelated associate at least once, mean associate age difference and associate sex ratio during the calf and subadult life stages did not influence mortality risk (Supporting information). The exploratory calf model violated the proportional hazards assumption, the only violation by any model, and we conducted a robustness check by removing the problematic variable (i.e. number of

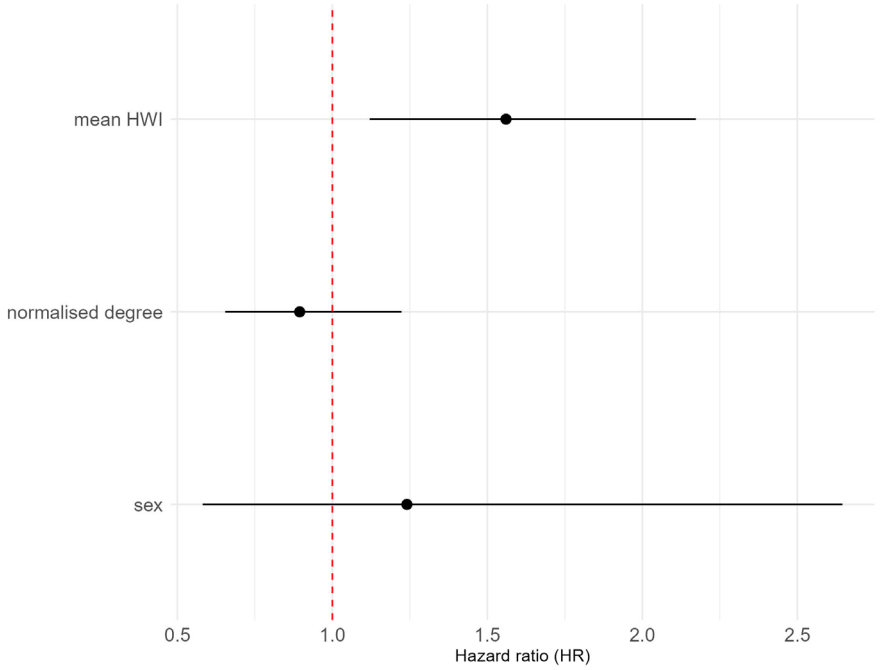


Figure 4. Hazard ratio plot displaying reslts for the primary calf survival model. The plot displays the modelled hazard ratios and confidence intervals of each predictor variable in the primary model evaluating the effects of calf associative behaviour on long-term mortality risk. The confidence intervals of all variables except mean HWI overlap 1, indicating that only mean HWI influenced mortality risk.

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ehk.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

observations; Supporting information). However, those metrics during the adult life stage did influence mortality risk (Supporting information). Increasing mean age difference was tied with lowered long-term mortality risk (HR = 0.198, CI = 0.097–0.401, $p < 0.001$), likely reflecting lower risk from associating with younger individuals. In contrast, increasing associate sex ratio (i.e. associating with a higher proportion of males) was tied to increased mortality risk (HR = 2.208, CI = 1.244–3.919, p = 0.007). Neither individual sex nor number of observations were significant in the calf or subadult models. However, they were both significant in the adult model. Adult males in this subset (which only included individuals observed associating with at least one unrelated individual) had substantially lower mortality risk than adult females in this subset (HR = 0.203, CI = 0.072–0.752, p = 0.003). Surprisingly, increasing number of observations of individuals in this subset was tied to increased mortality risk (HR = 2.889, CI = 1.714–4.869, $p < 0.001$), the only model in which this variable was significant.

Discussion

The social interactions of solitary animals can be highly context dependent being driven by multiple factors including familiarity with conspecifics (Elbroch et al. 2017), and maternal behaviour (Hansen et al. 2022). Our study provides additional evidence about how life stage, familiarity, and maternal behaviour influence association dynamics in an aggressive, solitary species, and how associative behaviour at specific life stages influences mortality risk.

Overall, associations were more likely to occur between animals that were already familiar. Specifically, we found that a subadult was more likely to be seen with an individual (i.e. had a higher HWI) if it had associated with that individual at a higher rate when the subadult was a calf, and that an adult was more likely to be seen with an individual if they had associated at a higher rate when the adult was a subadult. However, we did not find evidence that calf HWI influenced adult HWI and the effect of calf HWI on adult HWI was strongly mediated by subadult HWI.

When an individual is a calf, its mother determines if a conspecific will be allowed to move with her and her calf (Goddard 1967). Thus, a mother's tolerance of specific associates may be a key factor affecting the social associations of her calf, but only through the subadult years. If subadults group to aid dispersal and lower risk of aggression from others, similar to white rhinos (Shrader and Owen-Smith 2002), it could be that by allowing her calf to associate with similar-aged individuals, she helps establish associations for her calf that could aid dispersal and reduce aggression. Yet, we did not find evidence that associative behaviours during the subadult stage significantly influenced survival (Supporting information). However, this raises a question as to why these calf associations do not continue into adulthood. A potential explanation is that during the subadult stage, individuals disperse away from their mother's home range (Lent and Fike 2003) and in doing so, disperse away from some individuals they associated with as calves. As they form associations with the subadults in their new location, they then maintain these more recent subadult associations into adulthood.

Our results also support the second of our alternative predictions about age of associates on subadult association rates, specifically that subadults preferentially associate with peers that are similar in age. The relatively lower rate of aggression by subadults (relative to adults; Greaver et al. 2014) may make fellow subadults safer companions, and their company could still lessen the risks associated with dispersal such as reducing the risk of being attacked by dominant territorial males (Shrader and Owen-Smith 2002).

With regards to the influence of social interactions on mortality, we found support for our prediction that the more calves associated with others, the greater their risk of mortality through the end of the study period. Calves are especially vulnerable to attacks by older aggressive conspecifics (Greaver et al. 2014). However, black rhino mothers could mitigate this danger by lowering their own association rate or associating more with young individuals. But, we found that adult females associated at a significantly higher rate than adult males (Fig. 3). In our survival analyses, only four calves died during the calf stage (Supporting information). So, this higher rate of adult female association was probably not affecting short-term mortality risk of their calves, but may have increased long-term risk for by subjecting them to increased stress (Creel et al. 2013), suggesting that maternal association decisions may influence risk to their offspring.

We had also expected association rate and number of associates to negatively influence adult survival, but found no support for that expectation (Supporting information). Instead, we found that in individuals that associated with unrelated conspecifics, associating with more males, or with similarly-aged adults, increased their mortality risk. This was presumably because associating with adults or males increased the chances that associates might be aggressive (Supporting information). Unexpectedly, we also found that males in this subset were subject to lower risk of mortality than females which may reflect the observed differences in associative behaviours by sex (Fig. 3). Specifically, adult females associated with significantly more individuals than adult males (Fig. 1), which may be because they are associating with more cow–calf pairs, allowing their calves to establish networks, and importantly, because they were interacting with dominant males looking to breed, which might increase risk. Combined, our results suggest that associating with other black rhinos can be risky for adults but that risk is related to the intrinsic traits of the conspecifics (sex and age) rather than rate of association or number of associates.

In contrast to adults and calves, we expected that subadult survival might be positively influenced by social rate as they are regarded as the most social age class (Klingel and Klingel 1966, Goddard 1967). Surprisingly, our results did not show evidence that associative behaviours influenced mortality risk in subadults. Future studies may benefit from incorporation of full network analyses, which we were unable to build

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ehk.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

due to data limitations, to explain why subadults are seen in groups more often than individuals in other age classes (Klingel and Klingel 1966, Goddard 1967).

Although fighting injuries are a common cause of death in other studies (Du Toit and Emslie 2006, Greaver et al. 2014), fighting was not a key driver of mortality in our populations (Supporting information), which may be partly because the studied populations were generally at lower densities than more established populations in other studies. Nevertheless, fighting- or aggression-associated deaths were reported in every age class, even in calves and subadults where few deaths were reported. Our results seem to reflect a subtle effect of social behaviour on mortality risk, where risk of death from fighting is real, but may not be the only mechanism by which mortality risk is responsive to associative behaviour. Even if fighting does not directly cause mortality, a serious injury could decrease survival (Rennolds and Bely 2023). Furthermore, in solitary and territorial species, social interactions increase stress, which can decrease survival by decreasing resistance to disease or other limiting factors (Creel et al. 2013). Indeed, the most common cause of non-human death was natural causes (e.g. disease, old age, accidents). Thus, the nuanced effects on mortality risk from associating with conspecifics may not only be from direct fighting, but also from injury or increased stress.

Our results provide evidence that the solitary lifestyle of black rhinos may be partly maintained by aggression. For example, we found that black rhinos preferred to associate with known individuals, and associative behaviour can significantly influence mortality risk, particularly as a function of associative behaviour during the calf and adult life stages. The prevalence of aggression in black rhinos, despite the clear costs, indicates there must be a fitness benefit to the behaviour. Aggression is likely not associated with forage guarding because black rhinos are browsers that consume a variety of species and are more limited by seasonal water availability (le Roex et al. 2019). Instead, their aggression may be related to increasing reproductive potential. Adult males increase their chances of mating by establishing home ranges from which they largely exclude other adult males via aggression, but which overlap with multiple breeding females (Tatman et al. 2000). By contrast, maternal care of calves is an important mechanism by which females increase their reproductive potential. As our results illustrate, calves are vulnerable to aggressive conspecifics, while also being vulnerable to predation (Plotz and Linklater 2009). Thus, female aggression may have arisen to aid in calf protection.

The large sample size in our study gathered from multiple breeding populations provides strong evidence for our results, but we caution that our study was subject to some limitations. The sightings data only indicated if individuals were within 50 m of one another but did not include information about the nature of the interactions. We interpreted repeated sightings of the same dyads as being relatively unaggressive, but this may not always be the case, especially considering the aggressive tendencies of black rhinos. Additionally, although certain dyads were seen together regularly during specific life stages, our data does not provide information about whether those individuals moved together or were simply more likely to meet up after moving separately. Nevertheless, even if the animals typically moved separately, the fact that they consistently were found together suggests long-term associations. Further, our mortality risk assessments provide information about the relative level of mortality risk individuals were subject to as a function of the calculated association metrics but do not account for other risks such as resource access. Finally, although our sample size was large for the species, black rhino survival is so high, particularly when only accounting for death by non-human causes, that each survival model includes relatively few mortalities, limiting power and inference.

Overall, our results illustrate that black rhinos are largely solitary, but their associative behaviours, while uncommon, point to the importance of long-term associations, adding to the increasing body of literature documenting social behaviours in solitary species as diverse as primates (Bearder 1999), carnivores (Elbroch et al. 2017), rodents (Makuya et al. 2024), and invertebrates (Shivashankar 1994). Altogether, our results add further evidence that social behaviour in solitary species is more common than previously thought.

For black rhino conservation efforts, our results indicate that existing social relationships may be important when selecting individuals for translocation (Linklater and Swaisgood 2008). Thus, selecting animals with existing relationships may allow translocated individuals to safely engage in associative behaviours while minimising aggression. Further, when selecting individuals for translocation, managers may consider their existing populations from a social, rather than just a population dynamics position, wherein increasing the ratio of males could not only detract from population growth via population-level dynamics but also by increasing risk of fighting. Like black rhinos, many solitary species are threatened or endangered and lack of understanding about their social behaviours may lead to less effective conservation actions (Olivier et al. 2022). As such, we encourage future research into social behaviour and how it influences the survival of endangered solitary species.

Acknowledgements – We thank WWF South Africa, the Black Rhino Range Expansion Project, Ezemvelo KZN Wildlife, Eastern Cape Parks and Tourism Agency, and the teams at Babanango Game Reserve, Balule Nature Reserve, Buffalo Kloof Private Game Reserve, Dinokeng Game Reserve, Liwonde National Park and African Parks, Makalali 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 Mduna Private Game Reserve.
Funding – Our study was funded from a grant by the International Rhino Foundation (R-2023-5).
Conflict of interest – The authors declare no conflict of interest.

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ehk.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Author contributions

Rachel M. Stein: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Adrian M. Shrader**: Conceptualization (equal); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Because one of the primary threats to the critically endangered black rhino is poaching, we cannot provide our data to protect security of the study animals and reserve staff.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Bates, D., Mächler, M., Bolker, B. M. and Walker, S. C. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bearder, S. K. 1999. Physical and social diversity among nocturnal primates: a new view based on long term research. – Primates 40: 267–282.

Berger, J. 1994. Science, conservation, and black rhinos. – J. Mammal. 75: 298–308.

Borger, M. J. and Ramesh, A. 2025. Let's DAG how directed acyclic graphs can help behavioural ecology be more transparent. – Proc. R. Soc. B 292: 20250963.

Branchi, I., Curley, J. P., D'Andrea, I., Cirulli, F., Champagne, F. A. and Alleva, E. 2013. Early interactions with mother and peers independently build adult social skills and shape BDNF and oxytocin receptor brain levels. – Psychoneuroendocrinology 38: 522–532.

Brett, R. 1998. Mortality factors and breeding performance of translocated black rhinos in Kenya: 1984–1995. – Pachyderm 26: 69–82.

Brooks, M. E., Kristensen, K., Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M. and Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – R J. 9: 378–400.

Cairns, S. J. and Schwager, S. J. 1987. A comparison of association indices. – Anim. Behav. 35: 1454–1469.

Clutton-Brock, T. 2021. Social evolution in mammals. – Science 373: eabc9699.

Cox, D. R. 1972. Regression models and life-tables. – J. R. Stat. Soc. 34: 187–202.

Creel, S., Dantzer, B., Goymann, W. and Rubenstein, D. R. 2013. The ecology of stress: effects of the social environment. – Funct. Ecol. 27: 66–80.

Croft, D. P., Madden, J. R., Franks, D. W. and James, R. 2011. Hypothesis testing in animal social networks. – Trends Ecol. Evol. 26: 502–507.

Delmé, C., Jackson, N., Class, B., Strickland, K., Potvin, D. A. and Frère, C. H. 2023. Adaptive significance of affiliative behaviour differs between sexes in a wild reptile population. – Proc. R. Soc. B. 290: 20230805.

Department of Forestry Fisheries and the Environment 2025. South African weather service. – Republic of South Africa.

Du Toit, R. F. and Emslie, R. 2006. Guidelines for implementing SADC rhino conservation strategies. – WWF-SARPO.

Elbroch, L. M. and Quigley, H. 2017. Social interactions in a solitary carnivore. – Curr. Zool. 63: 357–362.

Elbroch, L. M., Levy, M., Lubell, M., Quigley, H. and Caragiulo, A. 2017. Adaptive social strategies in a solitary carnivore. – Sci. Adv. 3: e1701218.

Farine, D. R. and Whitehead, H. 2015. Constructing, conducting and interpreting animal social network analysis. – J. Anim. Ecol. 84: 1144–1163.

Frame, G. W. 1980. Black rhinoceros sub-population on the Serengeti Plains, Tanzania. – Afr. J. Ecol. 18: 155–166.

Goddard, J. 1967. Home range, behaviour, and recruitment rates of two black rhinoceros populations. – Afr. J. Ecol. 5: 133–150.

Goodman, P. 2013. Ezemvelo KZN wildlife monitoring plan: black rhinoceros (*Diceros bicornis minor*). – Department of Environmental Affairs, South Africa.

Greaver, C., Ferreira, S. and Slotow, R. 2014. Density-dependent regulation of the critically endangered black rhinoceros population in Ithala Game Reserve, South Africa. – Austral Ecol. 39: 437–447.

Hansen, J. E., Hertel, A. G., Frank, S. C., Kindberg, J. and Zedrosser, A. 2022. Social environment shapes female settlement decisions in a solitary carnivore. – Behav. Ecol. 33: 137–146.

Hitchins, P. M. 1978. Age determination of the black rhinoceros. – S. Afr. J. Wildl. Res. 8: 71–80.

Klingel, H. and Klingel, U. 1966. The rhinoceroses of Ngorongoro crater. – Oryx 8: 302–306.

le Roex, N., Dreyer, C., Viljoen, P., Hofmeyr, M. and Ferreira, S. M. 2019. Seasonal space-use and resource limitation in free-ranging black rhino. – Mamm. Biol. 99: 81–87.

Lent, P. C. and Fike, B. 2003. Home ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa. – S. Afr. J. Wildl. Res. 33: 109–118.

Linklater, W. L. and Swaisgood, R. R. 2008. Reserve size, conspecific density, and translocation success for black rhinoceros. – J. Wildl. Manage. 72: 1059–1068.

Makuya, L. and Schradin, C. 2024a. Costs and benefits of solitary living in mammals. – J. Zool. 323: 9–18.

Makuya, L. and Schradin, C. 2024b. The secret social life of solitary mammals. – Proc. Natl Acad. Sci. USA 121: e2402871121.

Makuya, L., Pillay, N., Sangweni, S. P. and Schradin, C. 2024. Tolerant mothers: aggression does not explain solitary living in the bush Karoo rat. – Proc. R. Soc. B 121: e2402871121.

Olivier, C. A., Schradin, C. and Makuya, L. 2022. Global change and conservation of solitary mammals. – Front. Ecol. Evol. 10: 906446.

Plotz, R. D. and Linklater, W. L. 2009. Black rhinoceros (*Diceros bicornis*) calf succumbs after lion predation attempt: implications for conservation management. – Afr. Zool. 44: 283–287.

Rennolds, C. W. and Bely, A. E. 2023. Integrative biology of injury in animals. – Biol. Rev. 98: 34–62.

Rookmaaker, K. and Antoine, P.-O. 2012. New maps representing the historical and recent distribution of the African species of

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ele.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

rhinoceros: *Diceros bicornis*, *Ceratotherium simum* and *Ceratotherium cottoni*. – Pachyderm 52: 91–96.
Shivashankar, T. 1994. Advanced sub social behaviour in the scorpion *Heterometrus fulvipes* Brunner (Arachnida). – J. Biosci. 19: 81–90.
Shrader, A. M. and Owen-Smith, N. 2002. The role of companionship in the dispersal of white rhinoceroses (*Ceratotherium simum*). – Behav. Ecol. Sociobiol. 52: 255–261.
Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. – Philos. Trans. R. Soc. B 362: 539–559.
Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. and Cheney, D. L. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. – Proc. R. Soc. B 276: 3099–3104.
Smithson, M. and Verkuilen, J. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. – Psychol. Methods 11: 54.
Tatman, S. C., Stevens-Wood, B. and Smith, V. B. T. 2000. Ranging behaviour and habitat usage in black rhinoceros, *Diceros bicornis*, in a Kenyan sanctuary. – Afr. J. Ecol. 38: 163–172.
Therneaur, T. 2023. coxme: mixed effects cox models. – R package, https://cran.r-project.org/web/packages/coxme/index.html.
Thompson, N. A. and Cords, M. 2020. Early life maternal sociality predicts juvenile sociality in blue monkeys. – Am. J. Primatol. 82: e23039.
Wey, T., Blumstein, D. T., Shen, W. and Jordán, F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. – Anim. Behav. 75: 333–344.

16000706, 2026, 8, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/ecj.12226 by Spanish Cochrane National Provision (Ministerio de Sanidad), Wiley Online Library on [24/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License