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Intrinsic and extrinsic factors affecting the spatiotemporal interactions within a black rhinoceros population

Anne Pandraud [a, *, 1], Haemish Melville [a, b], Kerry Slater [a], Craig Sholto-Douglas [c], Willem Maartin Strauss [a, d]

[a] *Applied Behavioural Ecology and Ecosystem Research Unit (ABEERU), Department of Environmental Sciences, Florida Campus, University of South Africa, Johannesburg, South Africa*
[b] *School of Animal and Veterinary Sciences, University of Adelaide, Australia*
[c] *Kwandwe Private Game Reserve, Eastern Cape, South Africa*
[d] *School of Biological Sciences, University of Canterbury, New Zealand*

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Animal space use is influenced by their intrinsic characteristics (e.g. age, sex) and their extrinsic environment (e.g. social environment and resource accessibility). Understanding the links between social behaviour and movement ecology may be crucial in isolating the factors impacting a population's space use. Black rhinoceroses, *Diceros bicornis*, are territorial animals and are now largely confined to fenced protected areas because of increased security concerns as a consequence of poaching. In this study, we investigated the spatiotemporal interactions within an established black rhinoceros population and the intrinsic (age, sex, maternal state and dominance) and extrinsic factors (season, vegetation type, bush cover and intraspecific interactions) influencing these interactions. We used location data from 21 black rhinoceroses fitted with Global Positioning System collars to explore the spatial distribution and the spatiotemporal interactions between and within sexes. Our results revealed that males shared their seasonal ranges with four females, while the seasonal ranges of females overlapped with that of at least one male. Females showed strong spatial fidelity to males' ranges; however, they remained at a mean distance of 3.1 km from the males with no influence of the age of males, females or calves on this proximity. The ranges of males overlapped in relation to both the overall and core ranges, with the older males having the largest ranges and the greatest access to females. Minta's analysis revealed that only older males were attracted to the overlap zone with the ranges of the younger males. However, access to forage did not differ between younger and older males. Finally, we found that males regularly transgress the borders of their own and neighbouring males' ranges. Our findings highlight the complex link between the spatiotemporal distribution and the social interactions among black rhinoceroses.

Animal space use is influenced by their environment (i.e. extrinsic factors) and their intrinsic characteristics, such as their age and sex (Bauder et al., 2016; Bracken et al., 2024). Extrinsic factors typically include resource accessibility, climate and social environment (Smit et al., 2007; Vander Wal et al., 2014; Viana et al., 2018; Webber et al., 2023). He et al. (2019) suggested that social variables (e.g. the presence of young, mates and competitors) may influence animal movements by making specific areas more or less attractive and, thus, may shape their spatial distribution. Consequently, linking concepts from animal movement ecology, that is, where and why animals move (Nathan et al., 2008), with social behaviour (i.e. which animals interact where, when and with whom) may improve our understanding of the factors influencing population space used (Vander Wal et al., 2014).

Territorial animals defend a delimited area and/or monopolize limiting resources such as food, water and mates, which restricts conspecific interactions and limits home range overlap (Kamath & Wesner, 2020; Schlichting et al., 2022). Ultimately, understanding

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* Corresponding author.
E-mail address: pandraudanne@gmail.com (A. Pandraud).
[1] Present address: Zuka Private Game Reserve, Munywana Conservancy, Hluhluwe, KwaZulu-Natal, South Africa.

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social and spatial behaviour of species and how these influence movement patterns is critical because it may directly influence population dynamics. This is particularly true in areas where space is limited, including fenced protected areas. Indeed, on such protected areas, animals have limited space to establish their ranges and are therefore more likely to have overlapping ranges with other individuals. These conditions might lead to increased antagonistic behaviour and ultimately result in increased mortality and reduced birth and growth rates (e.g. Gaillard et al., 2000; Tanner, 1966).

The black rhinoceros is critically endangered throughout its remaining distribution range (Emslie, 2020). Because of the implementation of conservation programmes, intensive monitoring and increased security, the majority of wild black rhinoceroses in Africa occur in South African, Namibian, Zimbabwean and Kenyan protected areas (Emslie, 2020). Fencing is used extensively as a wildlife management tool in protected areas, especially in Southern Africa (Trinkel & Angelici, 2016). However, support for, and implementation of, conservation fencing is increasing across the African continent (Pekor et al., 2019). Inevitably, the fencing of protected areas results in habitat fragmentation, limiting natural dispersal, which may result in increased social pressure and aggression among male black rhinoceroses (Nhleko et al., 2017).

Male black rhinoceroses are territorial and display aggressive behaviour towards conspecific males (R. N. Owen-Smith, 1988), whereas females are more tolerant of one another and occupy overlapping ranges (Adcock, 1994). The size and location of black rhinoceros ranges are influenced by the individuals' age (i.e. intrinsic characteristic), vegetation type, forage quality and availability of water and food (i.e. extrinsic factors; le Roex et al., 2019; Reid et al., 2007; Tatman et al., 2000). Larger ranges are expected during seasons with high resource (food and water) availability and quality (le Roex et al., 2019; Reid et al., 2007). However, past studies have not considered the potential impact of aggressive male behaviour on female spatial distribution or potential links between male—male dominance relationships and their movement patterns. Indeed, dominance typically refers to antagonist behaviour, which at a dyadic level results in a dominant—subordinate relationship (Drews, 1993). However, Wittemyer et al. (2007) found that dominance interactions between elephant, *Loxodonta africana*, herds is displayed by dominant herds having the highest access to preferred resources. N. Owen-Smith (1971) identified a dominance hierarchy among male white rhinoceroses, *Ceratotherium simum*, where subordinates are tolerated within the territories of dominant males but have no access to females. Male black rhinoceroses may have similar dominance hierarchies where access to resources is ordered among individuals and ultimately influences their space use. Most previous studies exploring black rhinoceros social interactions have been limited to daytime observations (e.g. Lent & Fike, 2003; Odendaal-Holmes et al., 2014) and direct observations that may disturb the animals and result in irregular, inaccurate (Plotz et al., 2017) and potentially biased data. Hence, despite several studies (Göttert et al., 2010; Plotz et al., 2016; Reid et al., 2007; Tatman et al., 2000) investigating the spatial behaviour and habitat selection of black rhinoceroses, our knowledge of their socio-spatial behaviour is limited.

To improve our understanding of black rhinoceros social dynamics and how that might affect their space use, we investigated the spatiotemporal interactions within an established black rhinoceros population on a fenced protected area. We focussed on intrinsic (age, sex, maternal state and dominance) and extrinsic factors (resources and conspecifics) that might influence black rhinoceros spatiotemporal interactions. We hypothesized that spatial interactions among male black rhinoceroses conform to a dominance hierarchy that is characterized not only by the limitation of direct encounters but also by an ordered access to resources and potential mates. We also predicted that males and females would have overlapping ranges (Lent & Fike, 2003). Finally, we expected that females accompanied by a calf might avoid direct interactions with males.

METHODS

Study Area

Kwandwe Private Game Reserve (hereafter Kwandwe; 20 000 ha) is located in the Great Fish River Valley of the Eastern Cape province, South Africa (Fig. 1). Kwandwe comprises seven vegetation types dominated by *Portulacaria afra* thicket, short *Euphorbia bothae* thicket and karroid shrubland (Kwandwe Private Game Reserve, n.d.-a). Kwandwe sustains various herbivore species including elephant; black and white rhinoceroses; Cape buffalo, *Syncerus caffer*; and a variety of other ungulate species. Populations of small and large carnivores occur on Kwandwe; these include Cape grey mongoose, *Galerella pulverulenta*; brown hyaena, *Parahyaena brunnea*; leopard, *Panthera pardus*; and lion, *Panthera leo*. The climate is semiarid with a mean annual rainfall of 273 mm (SD = 96 mm; 2016—2023) and temperatures ranging from −2 °C to 48 °C (2016—2023; Kwandwe Private Game Reserve, n.d.-b). The wet season extends from December to April with a mean monthly rainfall of 34 mm (SD = 10; 2016—2023), whereas the dry season extends from May to November with a mean monthly rainfall of 14 mm (SD = 7; 2016—2023; Kwandwe Private Game Reserve n.d.-b). Water for animals is available year-round at pumped waterholes and in the perennial Great Fish River.

Prior to the 19th century, black rhinoceroses occurred in the Eastern Cape province but their populations declined because hunting and farming (Feely, 2007; Somerville, 2025). The first black rhinoceroses were reintroduced into Kwandwe in 2001. Kwandwe translocates black rhinoceroses to maintain a stable population and occasionally introduces new rhinoceroses to maintain a genetically diverse population. Given ongoing security concerns, we are not permitted to disclose the current black rhinoceros population density in Kwandwe or the location of their ranges.

Location Data

In 2022, prior to the commencement of our study, a subset of the Kwandwe black rhinoceros population were fitted with ankle-mounted Global Positioning System (GPS) collars (Rouxcel Technology Ptyd, Stellenbosch, South Africa). The collars were programmed to log locations every 4 h. We analysed the GPS data seasonally for six males (5—21 years old; Table 1), 13 females during the dry season (June to August 2023) and 15 females during the wet season (December 2023 to February 2024); females were aged between 3 and 33 years old (Table S1).

Rhinoceros monitoring is conducted daily on Kwandwe, where all individual rhinoceroses are identifiable by unique ear notch patterns. This monitoring enables the early detection of injured individuals and new calves. Using these data, we found that during the study period, nine adult females were accompanied by their calves and that several of monitored females were related (either as mother—daughter pairs or sisters; Table S1).

Ethical Note

Ethical approval for the use of secondary data from Kwandwe's ongoing rhinoceros monitoring programme was granted by the University of South Africa's Animal Research Ethics Committee

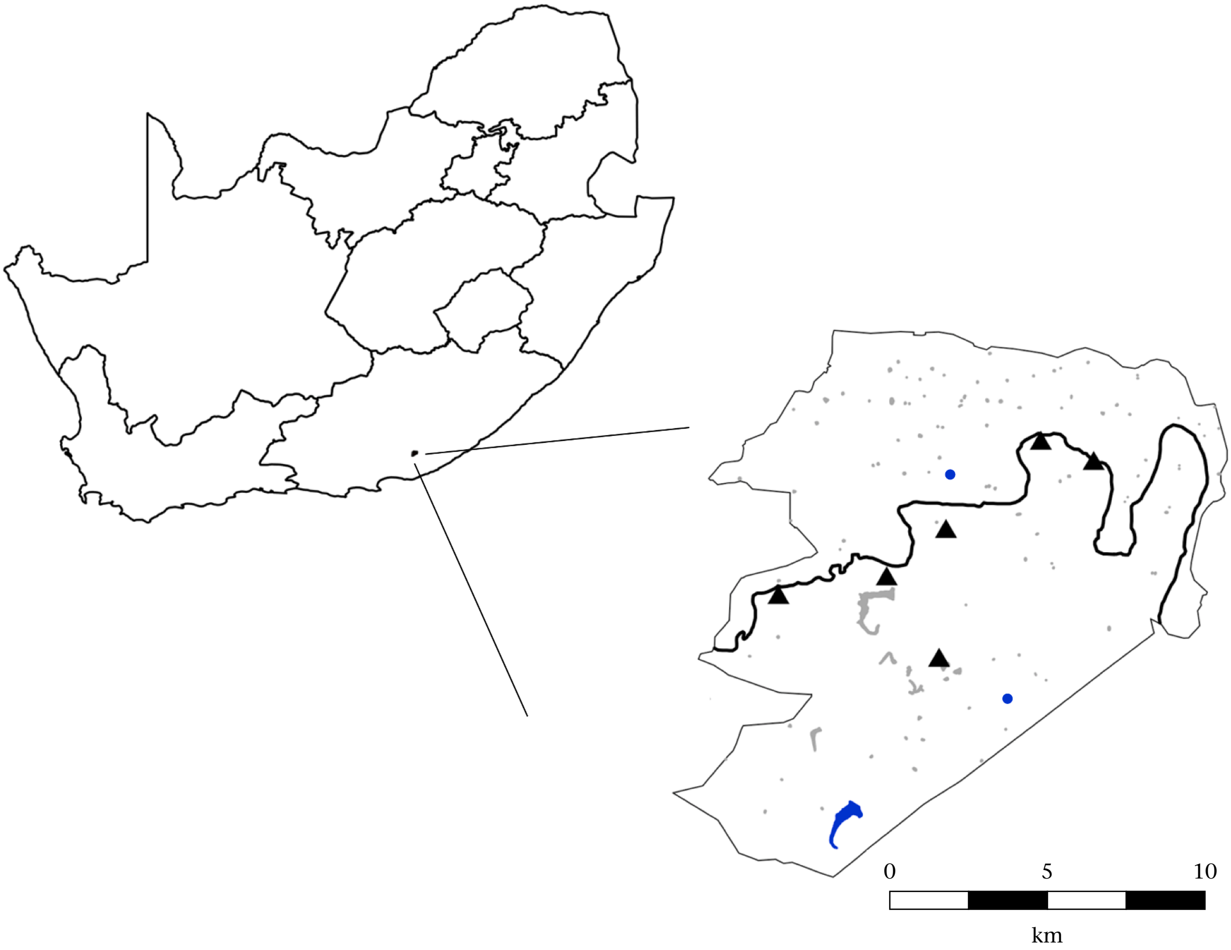

Figure 1. Location of Kwandwe Private Game Reserve (Kwandwe), in the Eastern Cape Province of South Africa. The exterior black outline represents Kwandwe boundary fence. The perennial Great Fish River (dark black line), the pumped waterholes (blue) and the nonperennial waterholes (typically available during the wettest months, grey) are displayed. The black triangles represent the location of the commercial lodges.

(Ethics number: 2024/CAES_AREC/3344). As part of Kwande's monitoring and management programme for rhinos, the rhinos are ear notched for individual identification purposes and equipped with ankle-fitted GPS collars for monitoring of movement. No rhinoceroses were immobilized, ear notched or collared for the purpose of our study. The reserve's protocol for ear notching and collaring was as follows. When rhinoceroses were between 18 and 24 months old, each rhinoceros was immobilized by an experienced veterinarian from a helicopter. For rapid immobilization, the veterinarian used etorphine mixed with hyalase to increase its absorption. Naltrexone was used to wake the rhinoceros up. The veterinarian cut unique triangular notches into the rhinoceros' ears and applied a local antiseptic to reduce risk of infection (permit number S09629 was granted by the Department of Environmental Affairs to Kwandwe). Each GPS collar weighed <700 g (i.e. less than 5% of the rhinoceroses' body weight [Manville et al., 2024]). During immobilization (for collaring and notching), a blindfold was fitted over the eyes, and ear stoppers were inserted into the ears of the immobilized rhinoceroses to reduce any potential stress. The responsible veterinarian monitored the vital signs of each rhinoceros for the duration of the procedure. None of the animals suffered any ill effects from the immobilization, collaring or notching. To date, 1300 GPS collars from Rouxcel Technology Pty (Stellenbosch, South Africa) have been deployed to black and white rhinoceroses across their distribution range with no collar-related injuries reported (S. le Roux, personal communication, 20 June 2025).

Spatial Distribution

To investigate the spatial distribution of the black rhinoceroses, we computed the dry and wet season ranges and core ranges of each collared black rhinoceros (hereafter seasonal ranges and core ranges when referring to both dry and wet season ranges and core ranges). As three of the males were subadults (<10 years old), we did not expect them to be territorial and, therefore, to avoid confusion between the terms 'home ranges' and 'territories', we used the term 'range' to refer to the areas (i.e. 90% isopleths) utilized by the collared individuals. Kwandwe is fenced, thus limiting the black rhinoceroses' movements, and consequently their space use. Thus, to allow for the hard boundaries in the ranges (Stark et al., 2017), we used the local convex hull nonparametric kernel method (LoCoH), and we followed the 'fixed number of points' approach (k-LoCoH) using the 'rule of thumb' process to choose *k* (Getz et al., 2007). The selected k values ranged between 33 and 64. We defined the seasonal ranges and seasonal core ranges as the areas within 90% and 50% isopleths, respectively (Börger et al., 2006). For each statistical analysis, we used Shapiro—Wilk tests to determine whether data were normally distributed. In the case that data deviated from normal distribution, we used

Table 1
Size (km^2) of the seasonal ranges and core ranges of black rhinoceros males of different ages in Kwandwe Private Game Reserve

	ID	Age (years)	Core range (km^2)	Range (km^2)
Dry season	BRM8	21	7.7	36.8
	BRM23	11	5.5	27.1
	BRM30	8	6.0	24.2
	BRM31	7	2.4	7.3
	BRM34	12	14.0	41.7
	BRM51	5	4.4	14.9
Wet season	BRM8	21	6.5	37.5
	BRM23	11	6.2	22.2
	BRM30	8	5.5	20.4
	BRM31	7	0.4	1.8
	BRM34	12	9.0	36.2
	BRM51	5	1.9	12.9

nonparametric tests. We used Student's *t* test to investigate whether the size of the rhinoceros ranges varied between seasons and between and within sexes.

Males—Females

Range overlap

We investigated the spatial interactions between females and between female and male black rhinoceroses. To do this, we first overlaid the individual seasonal ranges to compute the overlap between the seasonal ranges of the females and between the seasonal ranges of the females and the males (Ramos-Fernandez et al., 2013). Then, we calculated the proportion of female seasonal ranges included in the seasonal ranges of the males. We used Wilcoxon's rank test to investigate whether related females (i.e. mother—daughter, sisters) had higher levels of overlap between their seasonal ranges than those of unrelated females.

Proximity

We quantified the affinity between females and males that had overlapping seasonal ranges. First, as core ranges represent high-use areas within an animal's range, we calculated the overlap between females' and males' seasonal core ranges to investigate whether females and males spatially avoided or were attracted to one another (Holmes et al., 2019).

Second, we investigated whether males and females spent time together using proximity analysis (Bertrand et al., 1996). We considered a female and a male to be together when their individual locations, acquired within 30 min of one another, were less than 30 m (10 m + 20 m GPS error) apart (Pandraud et al., 2020; Schauber et al., 2015). As a 30 m threshold can be restrictive, we conducted the same analysis, with a threshold of 100 m (Buderman et al., 2021). This did not influence the outcome of the analyses, and we therefore only present the results from our finer scale (30 m) analysis. Finally, we quantified the proximity between males and females with overlapping seasonal ranges by measuring the distance between their proximal simultaneous locations (i.e. locations acquired by the collars less than 30 min apart).

We isolated the intrinsic factors (i.e. age of the male, female and calf and sex of the calf) that could influence the proximity between male and female black rhinoceroses. We computed the mean proximity for each pair (i.e. male and female with overlapping ranges) as the proximity between males and females did not vary seasonally (see 'Results'). We used linear models and model selection (we chose the model with the lowest Akaike information criterion; Table S2) as this is likely to best explain the proximity of males and females to one another. We confirmed the models' performance using the distribution of the residuals.

Males—Males

Range overlap

We visually inspected the overlap between seasonal ranges and the seasonal core ranges of black rhinoceros males to determine if they had exclusive-use ranges (Schlichting et al., 2022). As each male's seasonal ranges overlapped that of at least one other male (Fig. 2), we investigated how dominance manifests between males with overlapping seasonal ranges.

Dominance

To compare the dominance interactions between males, we grouped them into dyads (i.e. two males with overlapping seasonal

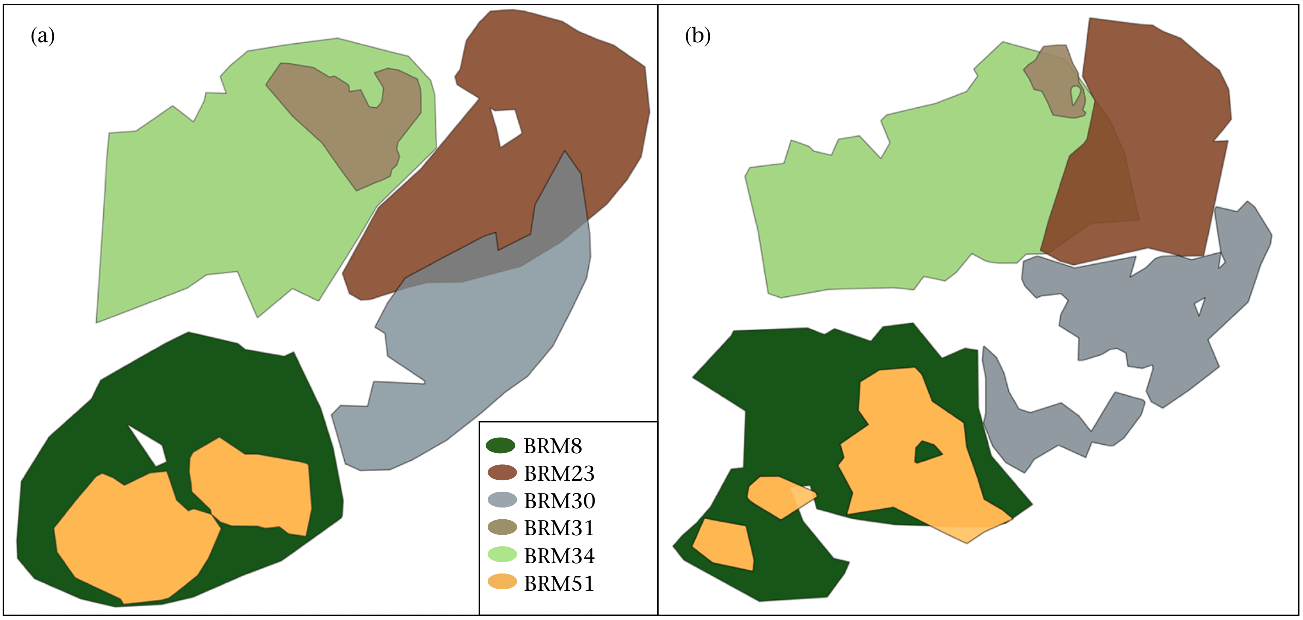

Figure 2. Dry (a) and wet (b) season ranges (90% isopleth) of each collared rhinoceros male. Ranges were obtained using the k-LoCoH method.

ranges; Boyd & Silk, 1983; Büttner et al., 2019). We expected that the dominant male within each dyad would restrict access of the other, putatively subordinate, male to resources such as food and mates (Morgan et al., 2009). To test these assumptions, within each dyad, we identified the dominant male and subordinate male by computing the size of their respective seasonal ranges and core ranges; we also quantified their access to females and forage and explored their use of the overlap zone of their seasonal ranges. We did not quantify their access to water as all the male seasonal ranges included permanent water sources (artificial waterholes and/or the perennial river).

To evaluate individual male access to females, we determined the number of seasonal ranges of females overlapping the seasonal ranges of each member of each male dyad. We also investigated where females concentrated their activity by quantifying the proportion of overlap between the seasonal core ranges of females and the seasonal ranges of each member of the dyad, separately. We used Wilcoxon's rank tests to compare dyad members.

We quantified each male in a dyad's access to forage by estimating the proportion of each vegetation type included in the seasonal range and core range of each male. Furthermore, we extracted the proportion of bush cover for each male's seasonal ranges and core ranges using the MODIS (Moderate Imaging Spectroradiometer) Vegetation Continuous Field (VCF) product (MOD44B Version 6.1) produced at a resolution of 250 m annually (Hansen et al., 2003). We only used the nontree cover layer (i.e. canopy height <5 m) to represent the vegetation potentially available to black rhinoceroses as forage (Ganqa et al., 2005). We used Wilcoxon's rank tests to determine whether the proportion of bush cover varied between dyad members' ranges and core ranges.

Finally, we explored the behaviour of dyad members in relation to the overlap zone of their seasonal ranges. We used Minta's statistics (Minta, 1992) to determine whether they were attracted to or avoided the overlap zone and whether they used it simultaneously. We defined simultaneous locations as locations acquired less than 30 min apart. In addition, as the Minta's analysis does not account for the distance between the individuals, we used proximity analysis to determine whether males had direct encounters while within the overlap zones. To do this, we used locations acquired less than 30 min apart that were within 30 m of one another (Schauber et al., 2015). We conducted the same analysis using a 100 m threshold (Buderman et al., 2021), but this did not impact the results. Therefore, we present the results from our finer scale, 30 m, analysis.

Movements beyond seasonal ranges

We investigated the behaviour of males while outside their seasonal ranges (Owen-Smith, 1975; Pandraud et al., 2022). For each male, we measured the following: the distance travelled beyond the extent of their ranges, the proportion of time spent outside their ranges and the regularity of the forays out of their ranges. We also determined whether, while outside their seasonal ranges, a male crossed into another male's range (beyond the overlap zone). In such cases, we measured the distance between the nonresident and the resident male.

RESULTS

Males—Females

Range overlap

We found that the collared black rhinoceroses are distributed through the reserve. There was no significant difference in the size of the seasonal ranges between female and male black rhinoceroses during our study (Student's *t* test: $t_{15.58} = -1.96$, $P = 0.067$, $N_1 = 12$, $N_2 = 28$). In addition, there was no seasonal variation in the range size of individual females (mean ± SD = 15.5 ± 8.8 km^2, $N = 28$; paired Student's *t* test: $t_{12} = 0.88$, $P = 0.39$, $N_1 = N_2 = 13$) or males (mean ± SD = 23.5 ± 12.8 km^2, $N = 12$; Student's *t* test: $t_5 = 0.65$, $P = 0.62$, $N_1 = N_2 = 6$; Table 1, Table S1).

Males shared their seasonal ranges with a mean of 4.4 (SD = 2, $N = 12$) females (Tables S3 and S4). The seasonal ranges of the females overlapped those of at least one male (mean ± SD = 1.5 ± 0.8, $N = 28$) by 4%—100% (Tables S3 and S4). During the dry season, nine of the 13 females had their ranges overlapping with the ranges of two males from the same dyad (Table S3), whereas overlap was observed in six of the 15 females during the wet season (Table S4). The seasonal range of females always overlapped with the range of at least one of the males, with which its range had overlapped in the previous season (Tables S3 and S4).

The seasonal ranges of a female overlapped with the seasonal ranges of a mean of five (SD = 2, $N = 28$) other females (Tables S5 and S6). Related females (i.e. mother—daughter, sisters) had higher levels of overlap between their seasonal ranges than unrelated females (Mann—Whitney's *U* test: $W = 6382$, $P = 0.005$, $N_1 = 336$, $N_2 = 30$).

Proximity

When female and male black rhinoceroses had overlapping seasonal ranges, the overlap between their ranges did not vary seasonally (Wilcoxon's signed rank test: $W = 235$, $P = 0.19$, $N_1 = N_2 = 24$). In addition, the seasonal ranges of males and females overlapped significantly more than their seasonal core ranges (Wilcoxon's signed rank test: $W = 1076$, $P = 5.56\ 10^{-7}$, $N_1 = N_2 = 49$). Indeed, the median overlap between the seasonal ranges of male and female black rhinoceroses was 63% (IQR 42%, $N = 49$), whereas the median overlap between their seasonal core ranges was 20% (IQR 54%, $N = 49$; Tables S3 and S4). Females and males with overlapping seasonal ranges maintained a distance of 2.8 km (IQR = 2.9, $N = 7182$) between each other with no seasonal effect (Mann—Whitney's *U* test: $W = 5\ 238\ 936$, $P = 0.12$, $N_1 = 4934$, $N_2 = 2248$) and spent a mean of 3.9% (SD = 3.8, $N = 49$) of their time together. Only BRM31 and BRM23 did not spend any time with the collared females. Our model revealed that the proximity between males and females was not influenced by the age of males, females or calves (Table S2).

Males—Males

Range overlap

We found that the seasonal ranges of each male black rhinoceros of a given dyad (i.e. two males with overlapping seasonal ranges) overlapped one another between 15% and 100% (Fig. 2, Table S7). Two dyads, BRM31—BRM34 and BRM51—BRM8, also had overlapping seasonal core ranges (Table S7). BRM51—BRM8 had the highest overlap between their seasonal core ranges (26%—87%).

Dominance

Within each dyad, we found that the older male had significantly larger seasonal ranges (Student's *t* test: $t_{10.08} = 5.82$, $P = 0.0002$, $N_1 = N_2 = 6$; Fig. 3a) than the younger male. In addition, for each dyad, the proportion of the younger member's range included in that of the older member's was significantly larger than the proportion of the older member's range in that of the younger member (Wilcoxon's signed rank test: $W = 4$, $P = 0.030$, $N_1 = N_2 = 6$; Fig. 3b).

The number of seasonal ranges of females overlapping the seasonal ranges of the males did not differ significantly between members of a dyad (Wilcoxon's signed rank test: $W = 19$, $P = 0.93$, $N_1 = N_2 = 6$; Fig. 3d). However, females spent significantly more

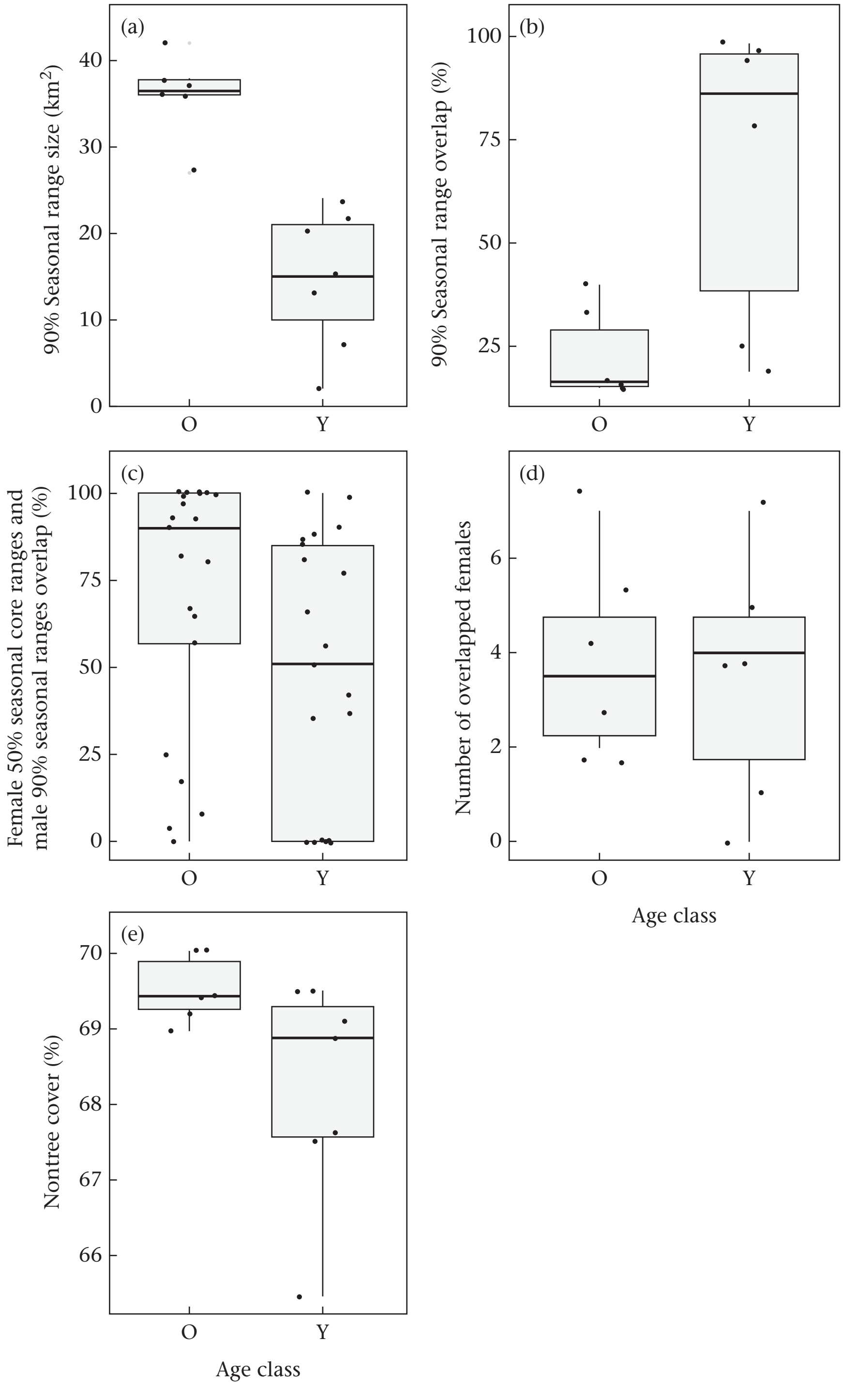

Figure 3. Comparison of black rhinoceros dyads (i.e. two males with overlapping seasonal ranges) in Kwandwe Private Game Reserve with regards to (a) their estimated seasonal range size, (b) the proportion of overlap between their seasonal ranges, (c) the proportion of overlap between the seasonal core ranges of the females and the seasonal ranges of the dyad members, (d) the number of seasonal ranges of females overlapping the seasonal ranges of the dyads and (e) the proportion of bush cover within the seasonal ranges of the dyad members (i.e. nontree, canopy height <5 m). Per dyad, we classified the older member (O; 11–21 years) and the younger member (Y; 5–8 years). The horizontal lines inside each box represent the median of the sample, the lower and upper hinges correspond to the first and third quartiles (i.e. 25th and 75th percentiles), and the lower and upper whisker extends from the hinge to the smallest and largest value no more than 1.5 × IQR from the hinge.

time in the seasonal ranges of the older dyad members than in the ranges of the younger dyad members (Wilcoxon's signed rank test: $W = 315$, $P = 0.017$, $N_1 = N_2 = 21$; Fig. 3c). Indeed, where females occurred within the ranges of both members of a dyad, a mean of 33% ($SD = 35$, $N = 42$) of the females' core range overlapped the older male's seasonal range, whereas there was a mean of 23% ($SD = 22$, $N = 42$) overlap with the younger males' seasonal range. BRM30 was the only younger dyad member to have more females spending time in his dry season range than in the older member's (BRM23) dry season range (Fig. S1).

The ranges and core ranges of the males were all dominated by three vegetation types: bushclump karroid thicket, karroid shrubland and short *Euphorbia* thicket. In addition, the proportion of bush cover in the seasonal ranges and core ranges was not significantly different between both dyad members ([ranges: Wilcoxon's signed rank test: $W = 33$, $P = 0.099$, $N_1 = N_2 = 6$]; [core ranges: Wilcoxon's signed rank test: $W = 23$, $P = 0.48$, $N_1 = N_2 = 6$]; Fig. 3e).

Minta's spatiotemporal interaction indicated that the older males of each dyad were significantly attracted to the overlap zone with the range of the younger dyad member (Table 2) and that simultaneous use of the overlap zone was random (i.e. there was no avoidance nor attraction between dyad members; Table 2). However, the dyadic members were never recorded having direct encounters while in the overlap zones.

Movements beyond seasonal ranges

All the males moved out of their seasonal ranges, every 2.2 (SD = 1.0, $N = 12$) days (Table 3). They all spent, between 7 and 13% of their time in any season, outside of their seasonal ranges. When outside their seasonal ranges, males travelled between 306 m and 1.2 km (Table 3), at a mean of 0.5 km/h (SD = 0.2, $N = 12$). When within their seasonal ranges they moved, males travelled at a mean of 0.2 km/h (SD = 0.1, $N = 12$). These seasonal movement speeds were not different (Wilcoxon's signed rank test: $W = 29$, $P = 0.070$, $N_1 = N_2 = 6$). During these excursions, males moved into the seasonal range of another male but remained at a mean of 2.8 km (SD = 1.2, $N = 77$) from the range occupier. We did not record any direct encounters between males during these forays. We found that, during most trips outside its range, a male moved into the range of another male when the resident was outside of its own range. For example, BRM30 was observed mating with BRF52 (C. Sholto-Douglas, personal observation, 10 October 2024) in BRM8's range, whereas BRM8 was out of his own range. However, when BRM31 and BRM51 went into BRM34 and BRM8's seasonal ranges, respectively, BRM34 and BRM8 were still within their own ranges. However, BRM34 and BRM8 were observed chasing BRM31 and BRM51 (C. Sholto-Douglas, personal observation, 12 December 2024).

DISCUSSION

In this study, we investigated the spatiotemporal interactions within an established population of critically endangered black rhinoceroses. We explored the extrinsic (resources and conspecifics) and intrinsic (age, sex, maternal state and dominance) factors influencing their spatial distribution, the interaction between males and females and the dominance hierarchy among males. We revealed similarities between black and white rhinoceros sociospatial behaviour and isolated factors that may be shaping the spatial behaviour of black rhinoceroses.

Table 2
Results of Minta's spatiotemporal interaction statistics

	Dyad	L_A	L_B	L_{ixn}
Dry season	BRM8 (a)	1.0	0.3	1.6
	BRM51 (b)	$P = 6.5 \times 10^{-4}$*	$P = 0.78$	$P = 0.18$
	BRM34 (a)	NA[1]	NA[1]	NA[1]
	BRM31 (b)			
	BRM23 (a)	0.8	0.4	0.1
	BRM30 (b)	$P = 7.4 \times 10^{-4}$*	$P = 0.099$	$P = 0.61$
Wet season	BRM8 (a)	1.2	−1.0	−1.4
	BRM51 (b)	$P = 6.1 \times 10^{-10}$*	$P = 0.26$	$P = 0.26$
	BRM34 (a)	0.5	1.6	0.2
	BRM31 (b)	$P = 0.017$*	$P = 8.1 \times 10^{-8}$*	$P = 0.59$
	BRM34 (a)	1.9*	−0.3	−0.8
	BRM23 (b)	$P = 1.1 \times 10^{-7}$	$P = 0.56$	$P = 0.051$

For each dyad (i.e. males with overlapping seasonal ranges), the members are displayed together. The coefficients L_A and L_B represent whether the males were significantly attracted (>0) to the overlap zone or whether they significantly avoided it (<0). The temporal interaction coefficients, Lixn, represent whether the males used the shared area simultaneously (>0), whether they avoided one another (<0) or whether the use of the shared area was random (=0). A coefficient was considered significant when the *P* value (*P*) of the chi-square test was less than 0.05 and is represented by *.

[1] The range of BRM31 was completely overlapped by that of BRM34. Therefore, no estimation of their temporal interaction within the overlap zone of their ranges was possible.

Previous studies have demonstrated that the size of black rhinoceros ranges is primarily influenced by water and food availability resulting in smaller winter (i.e. dry season) ranges because of limited resources (water: le Roex et al., 2019; forage: Reid et al., 2007). This contrasts with our results as the size of ranges of the Kwandwe rhinoceroses did not vary seasonally. Earlier studies were conducted in the Kruger National Park (le Roex et al., 2019) and Hluhluwe-Imfolozi Park (Reid et al., 2007), respectively, where the vegetation is dominated by *Vachellia* and *Senegalia* (formerly included in the genus *Acacia*), *Combretum* and *Terminalia* species. The vegetation in Kwandwe is dominated by *Portulacaria* thicket and short *Euphorbia* thicket, vegetation types rich in succulents with high water content that are resistant to drought and low temperatures (Griffiths & Males, 2017). Moreover, in Kwandwe, water is available year-round at pumped waterholes and in the perennial river. Black rhinoceroses in Kwandwe, therefore, likely have greater access to resources (forage and water) during the driest months and, unlike the black rhinoceroses in Kruger National Park and Hluhluwe-Imfolozi Park, do not need to limit their movements during the dry season.

Black and white rhinoceros adult males are territorial but may tolerate females in their territories (Adcock, 1994; Owen-Smith, 1975). The ranges of female white rhinoceroses can overlap the ranges of more than seven males (White et al., 2007). Our results confirm that this is also the case in black rhinoceroses, as we found that the seasonal ranges of black rhinoceros males were overlapped by four females. We also found spatial fidelity between females and males during both the wet and the dry seasons. Indeed, the ranges of all females overlapped with that of one or more males, with a similar level of overlap during both seasons. In addition, all females remained with the same males from season to season. We suspect that females might use males for protection. Black rhinoceros males display aggressive behaviour towards male and female conspecifics (R. N. Owen-Smith, 1988). However, it is possible that a male may be more tolerant of females that have ranges that overlap with his (Kamath & Wesner, 2020). Hence, a female may receive protection against other adult males, as the resident male is likely to defend his range and resources, including mates, from potential competitors (e.g. Hutchins & Kreger, 2006; N. Owen-Smith, 1971). Irrespective of their age, related females (i.e. mother–daughter, sisters) often maintained close spatial proximity and ultimately shared space with the same male. In the long term, this may negatively affect black rhinoceros populations through inbreeding (Kretzschmar et al., 2020), as daughters could potentially breed with their biological fathers because of the territorial-based mating system. This calls for increased genetic monitoring in resident populations to determine if inbreeding occurs and potentially adapt management strategies to allow for increased translocation of young females.

The seasonal core ranges of female and male black rhinoceroses overlapped significantly less than their seasonal ranges, which suggests a level of spatial separation between sexes (Holmes et al., 2019; Schlichting et al., 2022). In fact, males and females that had overlapping seasonal ranges, remained at a mean distance of more than 3 km apart and spent less than 4% of their time together. This highlights the predominately solitary behaviour of black rhinoceroses (R. N. Owen-Smith, 1988). Our results did not support our first hypothesis as neither the age of females nor the age of her calf

Table 3
Male black rhinoceros movement out of their seasonal ranges

Season	ID	Proportion of time out of the range (%; locations out/ total locations)	Mean (± SD) return time within an area out of the range (days)	Mean (± SD) distance travelled out of the range (m)	Where to and how many times	
Dry	BRM8	11 (24/222)	3.2 ± 3.5	1000 ± 800 max = 2990	BRM34	5
	BRM34	6.9 (29/417)	3.2 ± 3.6	925 ± 442 max = 1800	BRM8	1
	BRM23	6.7 (24/356)	1.3 ± 2.3	1200 ± 100 max = 2700	BRM30	2
	BRM30	8.8 (39/444)	2.2 ± 3.1	940 ± 417 max = 1700	BRM8 BRM51/BRM8	2 1
	BRM31	9.7 (50/512)	3.6 ± 13	306 ± 177 max = 781	BRM34	23
	BRM51	7.6 (35/459)	2.2 ± 3.6	508 ± 310 Max = 1300	BRM8	14
Wet	BRM8	9.1 (48/502)	1.8 ± 2.0	860 ± 548 max = 2627	BRM34	7
	BRM34	10.3 (65/701)	2.4 ± 3.6	984 ± 610 max = 2320	BRM8 BRM30	2 2
	BRM23	10 (28/283)	1.5 ± 2.4	1068 ± 681 max = 2350		
	BRM30	12.6 (87/923)	1.2 ± 1.5	886 ± 673 max = 3509	BRM23 BRM8	3 3
	BRM31	9.3 (56/601)	1.6 ± 3.1	874 ± 1280 max = 5424	BRM34	12
	BRM51	8.6 (44/496)	1.9 ± 3.5	924 ± 442 max = 2476	BRM8	17

The movements are reported as the proportion of time spent out of their ranges, the return time out of their ranges and the distance travelled while out. The identity of the range holder (i.e. resident) into which the nonresident ventured and the frequency of such intrusions. During the dry season, BRM23 did not enter another male's range.

influenced the dynamics of this spatial relationship. However, the low resolution of GPS fixes (4 h) in the current study may have influenced these results, and future studies with finer resolution data would therefore be necessary to confirm this finding.

We found that adult males (>10 years; Odendaal-Holmes et al., 2014) had nonoverlapping seasonal core ranges. However, adult male black rhinoceroses can have overlapping ranges but exclusive-use core ranges (Odendaal-Holmes et al., 2014), as was observed for BRM34 and BRM23. This supports the contention that black rhinoceros males, as territorial animals, may have overlapping ranges but exclusive core ranges (Schlichting et al., 2022). Of the four male dyads in our study, three were composed of an adult male (>10 years) and a subadult male. Both black (Lent & Fike, 2003) and white (N. Owen-Smith, 1971) rhinoceros adult males may share parts of their territories with subordinate males. In accordance with our second hypothesis, the dominance interactions among males appear to be governed not only by direct interactions but also by an ordered access to potential mates. Indeed, comparison of males within the same dyad revealed that the older male in each dyad generally had a larger seasonal range, had greater access to females and shared a small proportion of his range with the younger member of the dyad. Only BRM51, though not sexually mature at 5 years old, had similar access to females as BRM8 (the older, mature male within the dyad) did.

Dominance interactions among white rhinoceros males (N. Owen-Smith, 1971) and elephant herds (Wittemyer et al., 2007) have been described as a system for ordering reproductive competition and access to preferred resources (i.e. food and water), where subordinates may have limited opportunities to reproduce and fewer resources in their ranges. As previously suggested, because of a dominance hierarchy among individuals, dominant black rhinoceroses may also limit subordinates' access to resources (Morgan et al., 2009) and potential mates. This may explain why the younger black rhinoceros males within a dyad in our study had limited access to females. The male, BRM51, had not reached sexual maturity so, we assume that BRM8 did not need to restrict BRM51's access to females. In contrast, BRM30 (8 years old) had more access to females than the older member of the dyad, BRM23 (11 years old). It is likely that BRM30 had started to establish his own territory by increasing his access to potential mates and by excluding BRM23 from his own range (nonoverlapping wet season ranges). Moreover, the seasonal ranges of BRM23 were the only ones to include commercial lodges, which might have resulted in human disturbance making his seasonal ranges less attractive to females (Mukinya, 1973). In addition, we found that the bush cover did not differ between dyad members' range. However, additional fieldwork may be necessary to quantify palatable plants in males' ranges to confirm whether dyad members have the same access to forage. Finally, we demonstrated that all the older members of any dyad were significantly attracted to the overlap zone between their ranges and those of the other dyadic members' ranges (Table 2). However, dyad members did not use the overlap zones simultaneously. White rhinoceroses share information relating to territorial status via volatile organic compounds in their dung (Marneweck et al., 2017). They use this system to assert dominance and delineate territorial borders. This strategy appears to limit frequent direct conflicts with other territorial males (Owen-Smith, 1975). Black rhinoceros males may also communicate indirectly using chemosensory mechanisms to limit direct interactions and reduce the risk of injuries.

Based on our results, dominant territorial black rhinoceros males have the largest ranges and thus, the greatest access to females (Fig. 3a–c). They also tolerate subordinate males in their ranges but, affirm their dominance by limiting subordinates' access to space and females and by patrolling the overlap zone between ranges. Dominance is often defined as aggressive direct encounters that result in a winner and loser (Drews, 1993). Given the low resolution of GPS fixes and the lack of observation data, we could not investigate the direct interactions between the dyad members. Direct observations may provide a more complete understanding of the dominance interactions between black rhinoceros males.

During the study period, all males travelled beyond the borders of their seasonal ranges. Owen-Smith (1975) reported that dominant white rhinoceros males, on rare occasions, move out of their territories to access water, but no further than 100 m. We found that the adult black rhinoceros males moved out of their seasonal ranges and could travel more than 1 km. However, all the males had seasonal ranges that included artificial waterholes and/or the perennial river, it is thus likely that they did not venture out of their ranges to access water. We found that the males transgressed the ranges of other males while the resident males were 'distracted' by being either outside of their ranges or in another male's range. The transgressing males might be considered to be 'sneakers' as they enter other male's ranges and attempt to mate with resident females that share space with the resident male (Kamath & Wesner, 2020; Taborsky, 1994). In addition, during these events, we did not record any direct encounters between black rhinoceros males, which suggest that the 'sneaker' avoided interacting with the resident male. Only BRM51 and BRM31 went into BRM8 and BRM34's ranges, when these resident males were not outside their ranges or in another male's range. It is likely that BRM51 and BRM31 were too young (5 and 7 years old, respectively) and inexperienced to have learned to avoid the resident male. Future studies would be necessary to isolate the cues that the sneakers use to know when the resident males are distracted.

We have provided new information on black rhinoceros social and spatial behaviour by demonstrating that social behaviour and space use are closely linked. We have shown that like white rhinoceros males, black rhinoceros males seem to have age-related rank hierarchy within their territorial structure. Moreover, the seasonal ranges of males are not very restrictive as males move beyond the borders of their own ranges. Males tolerate multiple females in their ranges and females show a strong spatial fidelity to males' seasonal ranges. Overall, we isolated extrinsic and intrinsic factors that, according to the sex and age of the individual, may influence black rhinoceros spatiotemporal distribution and interactions. Ultimately, the approach we followed in this study has broader applicability and could provide new insights into the sociality of many social mammals.

Author Contributions

Anne Pandraud: Writing – review & editing, Writing – original draft, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Haemish Melville:** Writing – review & editing. **Kerry Slater:** Writing – review & editing. **Craig Sholto-Douglas:** Writing – review & editing. **Willem Maartin Strauss:** Writing – review & editing.

Data Availability

Because of ongoing security concerns, we are bound by nondisclosure agreements with Kwandwe Private Game Reserve and are embargoed from sharing data.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123444.

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