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Original investigation

Seasonal space-use and resource limitation in free-ranging black rhino

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ABSTRACT

The spatio-temporal distribution of forage and surface water shapes space-use for many herbivore species. Herbivores must make trade-offs between critical resources such as water and forage under resource-limited conditions. The species-specific strategy employed to do so, however, varies with nutritional requirements, thermoregulation and body size. The black rhinoceros (*Diceros bicornis* (Linnaeus, 1758)) is a browsing megaherbivore that requires upwards of 50 kgs of forage per day and is considered water-dependant. Contrasting evidence regarding surface water dependence and forage selectivity in black rhino, however, makes it unclear which exerts the primary influence on space-use under resource-limited conditions. We used telemetry data to calculate and compare seasonal home range sizes, utilisation overlap and site fidelity for black rhino in the Kruger National Park, South Africa, and use the results to infer the primary limiting resource in a semi-arid savanna ecosystem. Our findings demonstrate seasonal differences in space-use by black rhino, both in home range size and utilisation. Smaller home ranges and higher site fidelity in the dry season suggest that surface water is the primary resource driving these differences, i.e. black rhino restrict their range rather than expand it under resource-limited conditions. This has management implications for understanding the limitations of black rhino re-introduction programmes and the population capacity of small reserves.

Introduction

Resource availability and variability (Grainger et al., 2005), the density of conspecifics (Dahle and Swenson, 2003), breeding strategy (Fattebert et al., 2016) and predation risk (Crosmary et al., 2012; Valeix et al., 2009) influence the spatial organization and movement of terrestrial mammals. Maximising fitness necessitates a trade-off between acquiring the essential primary resources and the costs associated with the acquisition process (Mitchell and Powell, 2012). Forage and surface water function as primary resources, the spatio-temporal distribution of which shapes space-use for many herbivore species (Redfern et al., 2005; Smit, 2011). Spatial resource variability across a landscape occurs as a result of forage patches that vary in composition within an area and the irregular distribution of perennial water sources. Temporal variability occurs in areas with seasonal rainfall: forage biomass and quality decrease with decreasing rainfall (Coe et al., 1976) resulting in progressive forage depletion during the dry season, and the emergence of temporary pools and pans during the rainy season changes surface water availability. Water-dependant herbivores must make trade-offs between water and forage under resource-limited conditions (Cain et al., 2012; Redfern et al., 2003; Smit, 2011); the species-specific strategy employed to do so, however, varies with nutritional requirements, thermoregulation and body size (Cain et al., 2012; Redfern et al., 2003).

The interplay between surface water dependency and forage requirements can influence ranging behaviour by either: (i) driving animals to travel increasingly large distances to and from water during the dry season when surface water is reduced, in order to allow for selective forage requirements, or (ii) constraining animals to low-quality/bulk forage within a smaller area to minimise the distance travelled to meet regular water requirements. Travelling large distances to and from water expends energy and reduces forage and resting time (Cain et al., 2012), while remaining in the vicinity of perennial water intensifies forage depletion and increases intra- and inter-specific competition and predation risk (Cain et al., 2012; Crosmary et al., 2012). The species-specific approach employed is likely related to nutritional demands: if high forage quality is necessary to meet nutritional requirements,

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animals must expend extra energy travelling greater distances when forage resources are limited, but if low-quality bulk forage is sufficient, shorter distance to water may be energetically more productive, even with potentially increased competition and predation risk. Optimal foraging theory (Charnov, 1976) for herbivores predicts an energy-maximising approach, where individuals strive to maximise nutrient and minimise fibre intake through diet selection to achieve a maximum net benefit (Belovsky, 1997; Owen-Smith and Novellie, 1982). Foraging strategy ultimately has consequences at the population level, such as decreased survival rates when daily displacement increases in response to varying resource gradients (Young and van Aarde, 2010).

The black rhinoceros (black rhino; *Diceros bicornis*) is a browsing megaherbivore with an adult body mass of greater than 1000 kgs and requires upwards of 50 kgs of forage per day (Atkinson, 1995). Black rhino consume an extensive variety of plant species across numerous families; shrubs, herbs and young trees of the *Capparaceae, Euphorbiaceae, Fabaceae, Malvaceae, Zygophyllaceae* and *Solanaceae* families are often actively selected, although both preference and diet proportions vary between habitats and seasons (Anderson et al., 2018; Buk and Knight, 2010; Ganqa et al., 2005; Goddard, 1968; Mukinya, 1977). Evidence suggests that black rhino actively avoid plants heavily defended by volatile chemical compounds, such as phenols and alkaloids (Anderson et al., 2018; Buk and Knight, 2010; Muya and Oguge, 2000); outside of these nutritional constraints, however, browse frequency may be driven by availability (Mukinya, 1977; Muya and Oguge, 2000; van Lieverloo et al., 2009). This is in contrast with the expected energy-maximising optimal foraging theory for herbivores (Belovsky, 1997; Owen-Smith and Novellie, 1982). Black rhino are considered water-dependant and must drink every 24–48 hours (Emslie and Adcock, 2013; Joubert, 1971). Observations suggest that black rhino may select, and be faithful to, one or more permanent water sources within their home ranges, even if the water source is little more than a puddle in the dry season (Joubert, 1971). Contrasting evidence, however, has been reported that describes black rhino remaining within their home ranges even once all surface water dried up, and surviving purely on the water obtained by feeding on succulent vegetation (Goddard, 1968).

Black rhino show well-defined home ranges across most study systems. Reported home range sizes for black rhino are, however, highly variable (3–218 km^2) between areas and statistical methods employed, and the majority of studies report annual rather than seasonal estimates (Plotz et al., 2016). Differences in home range size between the wet and dry seasons should reflect the primary limitation experienced by black rhino when resources are scarce. Similarly, differences in within-season site fidelity within home ranges should support predicted limiting processes (van Beest et al., 2010; Wittmer et al., 2006). Site fidelity is a measure of the tendency of an individual to utilise the same area over time (White and Garrott, 1990), and within-season site fidelity can be described by the proportion of home range overlap seen over shorter time periods during each season (van Beest et al., 2010; Wittmer et al., 2006). If the primary driver of space-use in black rhino is forage selectivity, dry season home ranges should be bigger than wet season home ranges to increase forage availability, and site fidelity within the dry season should be lower than in the wet season, as preferred patches are depleted and animals must move accordingly. If the primary driver of space-use is surface water, dry season home ranges should be smaller than wet season home ranges as animals are restricted to a smaller proportion of their range where water is available, and site fidelity within the dry season should be higher than in the wet season, as surface water would be localised within that range. If resource limitation is an interplay between water and forage, dry season home ranges are likely to be smaller than the wet season, restricted by proximity to water, but site fidelity within the dry season would likely be lower than the wet season, as a result of movement between depleted forage patches within the restricted home range.

In the savanna ecosystem, distinct dry and wet seasons change both surface water and forage distribution substantially (Redfern et al., 2005; Smit, 2011; Smit and Grant, 2009). Contrasting evidence regarding surface water dependence and forage selectivity in black rhino makes it unclear which exerts the primary influence on space-use under resource-limited conditions. The Bell-Jarman principle proposes that large herbivores have greater tolerance for low-quality forage than medium-sized herbivores due to higher digestive efficiency and lower metabolic demands per unit body mass (Bell, 1971; Geist, 1974). Similarly, the wider feed quality spectrum for large herbivores means they may be able to utilize a larger proportion of the landscape/forage resources available. As such, black rhino may not be regulated by selective forage requirements under resource-limited conditions, and surface water availability may be the primary limiting resource for this species. We predict that black rhino will exhibit significant differences in seasonal home range size, utilisation and site fidelity between wet and dry seasons in a semi-arid savanna ecosystem, as a function of temporal (seasonal) resource variability. We used GPS tracking data collected across wet and dry seasons to (i) calculate and compare seasonal home range and core area sizes for black rhino, (ii) determine the utilisation overlap between seasonal home ranges, and (iii) estimate bimonthly site fidelity within the wet and dry seasons. Furthermore, we tested the influence of vegetation and water on dry season home range size in black rhino, and examined the effects of these resources on within-range movement. We used the results of these analyses to infer the primary limiting resource/s for black rhino in the savanna ecosystem.

Material and methods

Study area

The Kruger National Park (Kruger), South Africa (24°0′41″ S, 31°29′7″ E) is comprised of low-lying, semi-arid savanna located in north-eastern South Africa. The reserve extends for 19,485 km^2 and is comprised of 35 different landscapes classified according to soil, vegetation and geological characteristics (Gertenbach, 1983). Our study focused on the southern part of Kruger where major landscape types include thornveld, mountain bushveld, lowveld sour bushveld, river thicket, *Acacia* thicket, *Acacia* savanna, *Combretum* woodland, mixed woodland and Lebombo south, primarily dominated by varying combinations of *Acacia*, *Combretum* and *Terminalia* species. Winters are warm and dry (mean maximum temperature: 26.1 °C) and summers are hot and humid (mean maximum temperature: 32.4 °C). Annual rainfall across the park ranges from 440 to 750 mm (north to south), with higher average rainfall in the southern region and the majority of rain falling from October to March (Gertenbach, 1980). Surface water occurs in the form of major rivers, artificial waterholes and natural pans. For this study, we defined seasons as 'dry' (April to September), 'wet' (October to March), and annual (April to March). Black rhino were re-introduced into the Kruger National Park from 1971, and the population grew from 81 founders to an estimated population size of 507 (95% CI: 427–586; Ferreira et al., 2019) in 2017. The population has experienced size fluctuations in recent years, primarily as a result of illegal offtake, but remains one of the largest free-ranging populations of black rhino in the world. This makes this population an ideal study system for understanding the natural processes shaping seasonal black rhino movement.

Fig. 1. Immobilised black rhino with a satellite leg collar fitted on the right front lower leg.

Tracking data

Female black rhinos were fitted with satellite GPS tracking collars (African Wildlife Tracking, Pretoria, South Africa; Fig. 1) in southern Kruger as part of scientific support to management from February 2016 to April 2018. Independent female black rhino were randomly selected in southern Kruger, where the majority of black rhino occur, to visualise movement behaviour and support security initiatives. Rhino captures were performed in accordance with South African National Parks (SANParks) Wildlife Capture Standard Operating Procedures. During capture, additional demographic data such as age, presence and age of calf, and visible injuries were recorded. GPS fix frequency was collected every four hours from February 2016 to August 2017, and every hour from August 2017 to April 2018. Location data per individual rhino were collated and cleaned. Data points that met the following criteria were removed: missing GPS location, predicted location error of >20 m, location outside park boundaries, and locations within 24 h of immobilisation. Season and diel period (day vs night) were assigned to each GPS fix. For home range calculations, individual data was sub-sampled to two fixes per 24 h (one fix per day and one fix per night). To model the effect of environmental covariates on within-range movement, individual data was subsampled to four fixes per 24 h period (2 per day and 2 per night), the highest resolution possible for all animals across both seasons.

Seasonal space-use

Home range estimation is typically limited by number of locations per rhino, and approximately 30 seasonal and 50 annual locations have been calculated as the minimum threshold required for accurate home range determination (Plotz et al., 2016). We used animals collared for at least 160 days per season (out of the maximum 180 days) to calculate the number of daily locations needed to determine home range within 95% of the maximum estimate (accumulation curve; supplementary Figure S1). The curve reached an asymptote at approximately 95 days, suggesting that after this time period black rhinos have essentially covered the extent of their home range for that season. Consequently, we included all animals that had been collared for a minimum of 100 days per season in the seasonal home range analysis.

We calculated 90% home range and 50% core (Samuel et al., 1985) fixed bivariate kernel utilisation distributions (KUDs; Worton, 1989) with the reference bandwidth for each black rhino per season. KUD estimation is a two dimensional probability density function that represents the probability of finding an animal within a particular area (Worton, 1989). For home range estimation, 90% KUDs were identified as better approximations of animal space-use than 95% KUDs (Börger et al., 2006). We thus used 50% and 90% KUDs to describe seasonal space-use for black rhino in this study. We used paired t-tests to test for significant differences in both core and home range size between wet and dry seasons, and calculated the ratio of core to home range for each season. This ratio indicates how uniform utilisation is across the full home range. Ratios closer to zero indicate the importance of patches/areas within the home range, while ratios closer to one suggest that areas are similar in importance. Annual home range and core KUDs were calculated using the combined wet and dry season data described above. We also calculated 95% KUD and 95% minimum convex polygon (MCP) home ranges, as well as 50% KUD to 95% KUD ratios to enable comparison with previous black rhino home range studies.

Utilisation overlap and site fidelity

We used Bhattacharyya's Affinity (BA; Bhattacharyya, 1943) statistic to calculate intra-individual and mean seasonal overlap between home ranges and cores. The BA statistic is a useful measure for comparing the overall similarity of two utilisation distributions (Fieberg and Kochanny, 2005), and ranges from zero (no overlap) to 1 (identical utilisation distributions), allowing meaningful comparison of statistical means. Within-season site fidelity was investigated by calculating bimonthly home range overlap within each season using the BA statistic, for all animals retained in the sample set with more than 100 days per season, in order to examine temporal trends. The overlap between home ranges for each month and the following month were calculated, starting from the first month of each season. Mean bimonthly site fidelities between seasons were compared using paired t-tests. All home range and overlap calculations were performed using the package *adehabitatHR* (Calenge, 2006) in R v3.5.1 (R Core Team, 2018).

Home range size and within-range movement

We fitted linear models to test the effects of environmental covariates on the home range size of black rhino under resource-limited conditions during the dry season. Covariates included in the models as fixed effects were: Enhanced Vegetation Index (EVI; MODIS satellite sensor, NASA, CSIR), woody cover (Bucini et al., 2009) and distance to perennial water (SANParks aerial distribution survey, unpubl. data 2018). Dry season EVI, included as a proxy for vegetation quality, was averaged across five years prior to this study and mean dry season EVI across the home range of each individual was extracted. Percent woody cover was included as a proxy for vegetation quantity from which we calculated mean percent woody cover across each home range. Distance to perennial water was calculated from the centre of each individual home range. The presence/absence of a dependent calf was included as a fixed effect.

To investigate the influence of vegetation and water on within-home range movements, an equal number of random points as GPS fixes were generated within each individual's dry season home range. GPS fixes and random points were coded as '1' and '0', respectively, and used as the binary response variable of generalised linear mixed models (GLMM, Bolker et al., 2009). Percent woody cover, EVI and distance to perennial water were included as environmental covariates. Diel period was included as an interaction term with all covariates, as evidence suggests that feeding and drinking behaviour of black rhinos may show diel differences (Joubert, 1971). Individual ID was included as random effect. Models were fitted using the R package *lme4* (Bates et al., 2015), and the most parsimonious models were selected using Akaike's Information criterion for small sample sizes (AICc) using all possible combinations of covariates in the R package *MuMIn* (Barton, 2018). Where top candidate models were within ΔAICc < 2, model averaging was performed to estimate unbiased coefficients.

Table 1
Seasonal and annual kernel utilisation distribution (KUD) home range and core statistics. SE = standard error.

	Dry Season		Wet Season		Annual	
	50% KUD (km^2)	90% KUD (km^2)	50% KUD (km^2)	90% KUD (km^2)	50% KUD (km^2)	90% KUD (km^2)
Mean	10.24	33.36	14.19	46.45	13.84	45.14
Range	3.47–18.94	11.58–67.46	5.25–34.21	17.61–126.31	4.05–24.11	15.9–88.4
SE	1.3	4.68	2.17	7.76	1.79	6.53

Results

Seasonal space-use

Meeting the criteria of data for a minimum of 100 days out of the possible 183 per season, for both wet and dry seasons, resulted in a final dataset that included 14 female black rhino with an average of 303.9 locations per rhino in the dry season, 284.3 in the wet season and 588.2 per annum. Dry season home ranges (33.36 ± 4.68 km^2) were significantly smaller than wet season home ranges (46.45 ± 7.76 km^2; paired t-test: t = -2.49, p = 0.03; Table 1). Similarly, dry season cores (10.24 ± 1.3 km^2) were significantly smaller than wet season cores (14.19 ± 2.17 km^2; paired t-test: t = -2.66, p = 0.02). The ratio of 50% to 90% core to home range KUDs, however, remained consistent across seasons (dry season: 0.32 ± 0.01, wet season: 0.32 ± 0.01). This means that black rhino spent half of their time in approximately 32% of their seasonal home range. Mean annual home range (45.14 ± 6.53 km^2) and core (13.84 ± 1.79 km^2) sizes were not significantly different from wet season home range and core sizes (home range: paired t-test, t = 0.31, $p > 0.05$; core: paired t-test, t = 0.29, $p > 0.05$). Dry season, wet season and annual 95% MCP home range size estimates were smaller than those obtained from 90% and 95% KUD methods; the same seasonal patterns were, however, still reflected. Mean 95% KUD and MCP home range estimates are presented in supplementary Table S2. The ratio of 50% core to 95% KUD home range was 0.24.

Utilisation overlap and site fidelity

The mean intra-individual seasonal overlap indices were 0.19 ± 0.03 (range: 0.00–0.42) and 0.64 ± 0.05 (range: 0.11–0.85) for core and home ranges, respectively. Two-dimensional examples of seasonal comparisons of core and home ranges are shown in Fig. 2. Bimonthly home range overlap (site fidelity) increased with the progression of the dry season (0.56–0.69), and decreased with the progression of the wet season (0.69–0.49; Fig. 3). Mean bimonthly overlap between seasons, however, was not significantly different (dry season: 0.62 ± 0.02, wet season: 0.61 ± 0.03; paired t-test: t = 1.03, p > 0.05).

Home range size and within-range movement

The top linear model of dry season home range size for black rhino included none of the environmental covariates tested (top model: Home range size ~ 1 + Dependant Calf; r-squared = 0.51). The presence of a dependant calf, however, decreased the size of the dry season home range significantly (Dep.Calf: coef = -25.04, s.e. = 7.15, $p = 0.004$). For within-range movement, the full model including all environmental covariates and interactions was the top-ranked model (supplementary Table S3); all other candidate models showed ΔAICc > 2 and thus no model-averaging was performed. During the day, black rhino were more likely to be found with increasing woody cover and distance to perennial surface water. At night, black rhino were found closer to perennial water and in areas with higher EVI. Visual representations of these effects can be seen in supplementary Figure S2.

Discussion

Seasonal patterns in home range size and site fidelity suggest that surface water is the primary limiting resource for female black rhino in the savanna ecosystem. Dry season home range size was significantly smaller than wet season home range size, i.e. black rhino restrict their range rather than expand it under resource-limited conditions. Bimonthly site fidelity increased with the progression of the dry season and decreased with the progression of the wet season, further supporting surface water availability as the limiting resource for black rhino in this system. It is clear from the seasonal differences in home range size, utilisation and fidelity that seasonal home range analyses provide a more informative portrayal of black rhino space-use at the individual level than annual home range estimates.

Comparing home range sizes calculated using different methodologies, between different habitats or within the same habitat, can result in misleading findings as noted previously with black rhino (Lent and Fike, 2003; Plotz et al., 2016; Reid et al., 2007). Home ranges are also typically reported as annual rather than seasonal ranges (Plotz et al., 2016). Management bodies often infer habitat suitability and/or carrying capacity for black rhino based on these results (e.g. Reid et al., 2007), although meaningful inference should not be drawn from such comparisons (Linklater et al., 2010; Plotz et al., 2016). The findings of this study should therefore be interpreted as pertinent to free-ranging female black rhino in a semi-arid savanna, where space constraints are absent, allowing resource gradients and social factors to potentially play significant roles. Our results showed average dry and wet season home ranges of 33 km^2 and 46 km^2, respectively, for adult female black rhino in the Kruger National Park. Annual home range sizes were similar to wet season estimates. While the seasonal home ranges were significantly different in size, the effect size was not large. This may be related to the relatively even distribution of permanent water across southern Kruger (Redfern et al., 2003). MCP estimates were smaller than KUD range sizes, again demonstrating the dissimilar size estimations produced by these two methods and highlighting the need for consistent methodology within and between ecosystems.

Black rhino home ranges vary across African habitats, with smaller sizes typically reported in wetter areas and larger sizes reported in more arid areas (Plotz et al., 2016). The home range sizes determined in our study are substantially larger than most published estimates (e.g. Lent and Fike, 2003; Plotz et al., 2016), consistent with reports that black rhino exhibit larger home ranges in savanna vegetation types compared to thicket vegetation (Hitchins, 1969). Göttert et al. (2010) calculated annual and seasonal home range sizes in a small, newly established population of black rhino in a semi-arid system in Namibia. They found a mean home range size of 89.9 km^2 (range: 7.1-220.2 km^2; 95% KUD), with no difference between dry and wet season home ranges for females. However, the behaviour of a newly-reintroduced population is unlikely to be stable for some time, and a comparison of the ranging behaviour in the first season post-release (dry season) with the subsequent season (wet season) is unlikely to be an ecologically meaningful comparison and more likely to reflect initial exploratory behaviour. Increased location errors as a result of triangulations may also have contributed to large home range

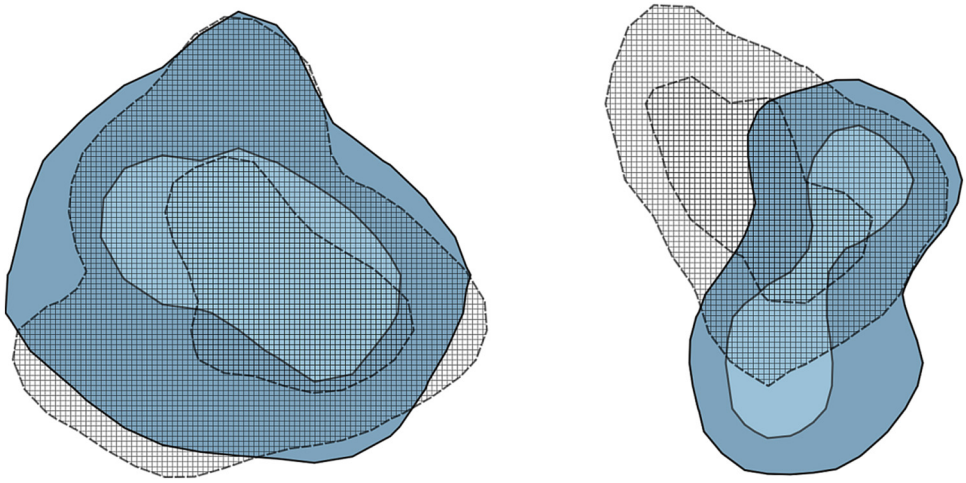

Fig. 2. Examples of high (left; core overlap: 0.42, home range overlap: 0.85) and low (right; core overlap: 0.09, home range overlap: 0.52) seasonal overlap of core and home ranges (90% and 50% KUD isopleths) from two black rhino within our sample set. Solid fill represents wet season ranges and hatched fill represents dry season ranges.

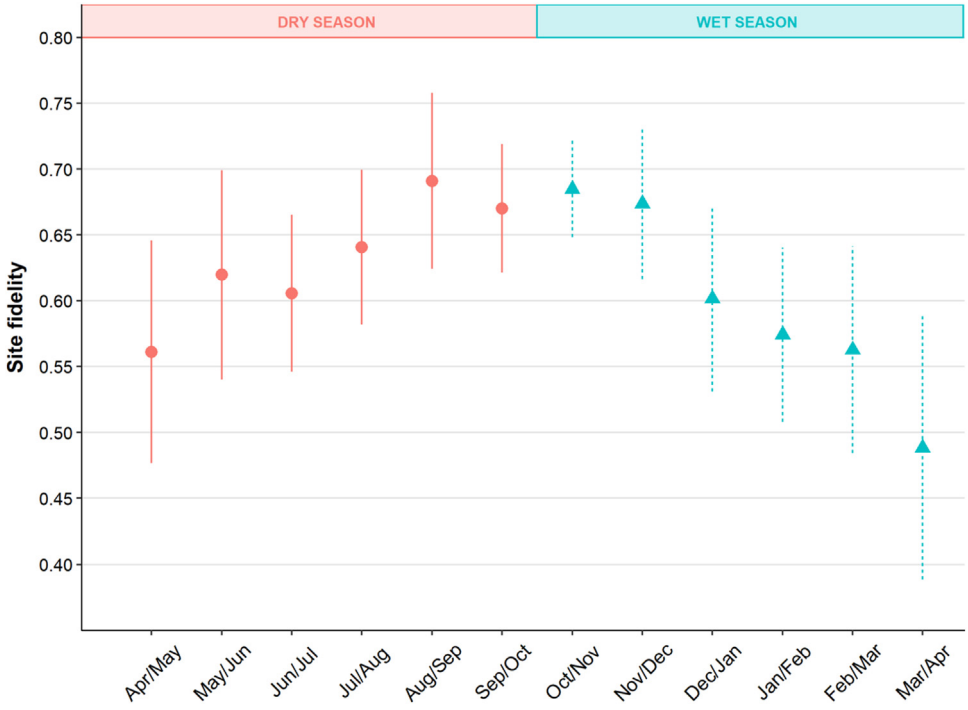

Fig. 3. Mean bimonthly home range overlap as an index of site fidelity during the dry and wet seasons. Bimonthly overlap was calculated using the BA statistic (Bhattacharyya, 1943). Error bars depict standard error.

estimates (Plotz et al., 2017). Plotz et al. (2016) and Lent and Fike (2003) found considerably smaller mean home ranges of 16.2 km^2 (90% KUD; subtropical ecosystem) and 11.7 km^2 (95% MCP; thicket biome), respectively. Interestingly, the ratio of 50%–95% KUD areas in our study was 0.24, compared to 0.21 and 0.24 found by Lent and Fike (2003) and Plotz et al. (2016), respectively. This suggests that although home range sizes may be considerably different between habitat types, the proportion of heavily utilised to peripheral area appears to be maintained across ecosystems.

We found a significant difference in seasonal home range size for female black rhino, with dry season home range size smaller than wet season range size. Thus, black rhino contract their range under resource-limited conditions during the dry season. This suggests that surface water availability rather than selective foraging drives seasonal space-use in this system. While we recognise that our study pertains to female black rhino in one ecosystem, these findings support the position of Linklater et al. (2010), who caution that an increase in range size should not be used to infer habitat quality change. At the very least, a detailed, seasonal study within the habitat in question using consistent methodology should be undertaken before any management action. Although mean site fidelity between seasons was not significantly different, bimonthly site fidelity increased with the progression of the dry season and decreased with the progression of the wet season, further supporting surface water as the limiting resource under these conditions. Mean intra-individual seasonal overlap was 0.19 and 0.64 for core and home ranges, respectively, with substantial variation between individuals. This means that not only were the sizes of the black rhino seasonal ranges significantly different, but utilisation within each range also changed with season. This is particularly true for core areas, where black rhino spend half their time.

The influence of surface water on the landscape-scale distribution and movement of other herbivores in semi-arid landscapes has been well-documented. Within Kruger, Smit et al. (2007) showed that landscape-scale herbivore distribution during the dry season was influenced by artificial waterholes, rivers or both, depending on species and/or feeding behaviour. Redfern et al. (2003) showed association between surface water and both grazer and browser distribution during the dry season in Kruger. Furthermore, their results suggested that body size and gut morphology influenced the trade-off that species experienced between nutrition and water constraints. The Bell-Jarman hypothesis predicts that large herbivores can survive on lower quality forage than medium or small-bodied herbivores due to higher metabolic efficiency (Bell, 1971; Geist, 1974). In addition, hindgut fermenters are able to process small amounts of low-quality forage all day long and thus survive in resource-limited conditions where ruminants may not be able to obtain sufficient nutrition (Cromsigt, 2006; Iason and van Wieren, 1999). As large body-sized, hindgut fermenters, black rhino should therefore be able to process and extract sufficient nutrients from large quantities of low-quality forage. Under resource-limiting conditions, where trade-offs between water, energy-expenditure and nutritional demands must be made, it may be more beneficial to remain close to water if nutritional demands can be met by consuming low-quality bulk forage in the vicinity. In resource-plentiful conditions during the wet season, the greater home ranges and lower site fidelity suggest that black rhino may be more discriminatory in their forage selection and make use of an energy-maximising foraging strategy as increased surface water availability enables greater movement. This suggests that water is the primary limiting resource for black rhino.

We found no influence of EVI, woody cover or perennial water on home range size under resource-limited conditions. This may be for a few reasons: (i) home range size may be predominantly influenced by social factors, such as local black rhino density and/or individual relatedness, (ii) the resolution of the environmental covariates may not have been sufficient to capture effects at this scale, or (iii) EVI and/or woody cover may not be good proxies for forage quality and quantity for black rhino. Alternatively, if home ranges are established within a maximum distance to surface water, this may explain the absence of detectable effect of surface water on home range size. While social factors such as density, among-individual relatedness or breeding-associated behaviours may influence baseline home range size for black rhino (Lent and Fike, 2003), we were unable to account for such factors due to a paucity of social data. For the purpose of comparing individual seasonal ranges, however, we do not expect density or relatedness to vary between seasons and thus should not confound the results. Similarly, no evidence of breeding or birth peaks in black rhino in this system has been reported and thus breeding behaviours are also unlikely to influence our findings. The presence of a dependant calf was the only covariate with a significant effect; home range size decreased when a dependant calf was present, likely to further reduce travelling distances and consequently decrease risk of calf predation. Young black rhino calves are at their most vulnerable (particularly to spotted hyenas *Crocuta crocuta*; Hitchins and Anderson, 1983) when left alone while their mothers travel to water. Thus the less time a cow spends away from her calf, the lower the predation risk. Within-range movement during the dry season was influenced by EVI, woody cover and distance to perennial water. Black rhino were more likely to be found in areas of higher woody cover and further from perennial water during the day. At night, black rhino occurred closer to perennial water and in areas of higher EVI. These diel patterns support reported black rhino movements, with resting/refuge behaviour in highly wooded areas during the day, and drinking and feeding behaviour in more open areas at night (Lent and Fike, 2003).

Our findings demonstrate seasonal differences in space use by female black rhino, both in home range size and utilisation. Smaller home ranges and higher site fidelity under resource-limited conditions suggest that surface water is the primary resource driving these differences in this semi-arid savanna. This has management implications for understanding re-introduction limitations and the black rhino capacity of small reserves. Fine-scale exploration into movement patterns, including distance travelled under seasonal/diel conditions and site visitation, would further elucidate the drivers of resource acquisition in black rhino and clarify the minimum requirements for home range establishment under resource-limited conditions.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.mambio.2019.11.001.

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