

## Research Article

# Effect of rainfall on white rhino calf survival depends on home range choice of the mother

Christoffel J. de Lange<sup>1,\*</sup>, Olivier Bonnet<sup>2</sup>, Adrian M. Shrader<sup>1</sup>

<sup>1</sup>Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag X28, Pretoria 0028, South Africa

<sup>2</sup>School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa

\*Corresponding author: Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag X28, Pretoria 0028, South Africa. Email: [christoffeldelange@gmail.com](mailto:christoffeldelange@gmail.com)

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### Abstract

Within African savannas, seasonal rainfall influences the survival of mammalian grazers by determining the availability and quality of food. The strength of these effects may, however, vary depending on the availability of reserve and buffer resources within the home range of an individual. From 1999 to 2019, 24% of the white rhino (*Ceratotherium simum simum*) calves born in Ithala Game Reserve died without a known cause. To explore this, we investigated the impacts of seasonal rainfall on calf survival, and whether these relationships were modified by the availability of woodlands (i.e., reserve resources) and bunch grasslands (i.e., buffer resources) within the home ranges established by the mothers. We found that nearly all of the deceased calves died during their first dry season after weaning had commenced. The likelihood of a calf surviving this period was positively influenced by rainfall during the dry season and negatively influenced by its duration. However, these effects were more pronounced when the availability of woodlands within the home range of the mother was high. Ultimately, calf deaths were caused by a combination of low dry season rainfall, long dry seasons, and the selection of home ranges with insufficient bunch grasslands by some mothers. With climate change models predicting increased dry season durations and a reduction in dry season rainfall, our results highlight future challenges for the conservation of white rhinos and other large herbivores.

**Key words:** African savannas, *Ceratotherium simum simum*, climate change, food availability and quality, habitat selection, large herbivore demography, reserve and buffer resources.

Seasonal rainfall often regulates the production and maintenance of food for mammalian grazers in African savannas, and is thus an important determinant of their survival (Mduma et al. 1999; Dunham et al. 2004). During the wet season, when grass growth peaks, rainfall promotes the production of large amounts of high-quality forage (Grunow et al. 1980; Deshmukh 1984). However, during the dry season, grass growth stops, plants shift their nutrients to underground reserves, and leaves senesce and become fibrous (Grunow et al. 1980; Codron et al. 2007). As the dry season continues, grazers quickly deplete the remaining high-quality grass within their home ranges and rely on fat reserves to meet their energetic requirements, resulting in a loss of body condition (Fryxell 1987; Shrader et al. 2006). Prolonged dry seasons may therefore lead to high risks of starvation and death (Fryxell 1987; Mduma et al. 1999). Yet, sufficient rainfall during this time maintains grass growth, and hence the availability of high-quality forage, which benefits grazer survival (Dunham et al. 2004; Bonnet et al. 2010).

The strength of rainfall effects on grazer survival, however, may vary depending on the availability of reserve (i.e., forage of acceptable quality that can sustain herbivores in the absence of

high-quality food) and buffer (i.e., forage with little nutritious value that herbivores can utilize when all other food sources have been exhausted) resources within the home range of an animal (Illius and O'Connor 1999, 2000; Owen-Smith 2002). This is because reserve resources are often maintained despite low rainfall and can therefore support grazer survival throughout most of the dry season (Owen-Smith 2002; Yoganand and Owen-Smith 2014). Then, when reserve resources become depleted, grazers can shift and feed on buffer resources to alleviate starvation (Owen-Smith 2002; Hobbs and Gordon 2010). Together, these resources reduce the vulnerability of a grazer during periods of low rainfall and food scarcity (Hobbs and Gordon 2010).

The southern White Rhinoceros (*Ceratotherium simum simum*) displays a strong seasonal pattern in its use of grassland types (Owen-Smith 1988; Shrader and Perrin 2006). During rainy summer months, they prefer to feed in highly nutritious short grass areas and grazing lawns (Owen-Smith 1988). However, at the start of the dry season, grass regrowth in these grasslands stops (Bonnet et al. 2010). In response, white rhinos shift their foraging to woodlands containing reserve resources such as *Panicum maximum*, where grass greenness is perpetuated by the microclimate

beneath the canopy (Owen-Smith 1988; Shrader et al. 2006). Then, as the dry season progresses and woodland grasses are depleted, white rhinos become reliant on buffer resources, such as *Themeda triandra*, in bunch grasslands (Owen-Smith 1988; Shrader and Perrin 2006).

Yet, the availability of reserve and buffer resources to an individual depends on the location and size of its home range (Owen-Smith 1988; Hebbelmann 2013). Unlike males, whose territories are largely determined through conflict and exclusion by other males, females choose where to establish their home ranges based on access to males and habitat types (Owen-Smith 1988; White et al. 2007a). By selecting areas with an adequate availability of woodlands and bunch grasslands, females are not only likely to protect themselves against low rainfall conditions, but also their offspring (McLoughlin et al. 2007). This is crucial because white rhinos give birth aseasonally, typically peaking near the end of the wet season or within the dry season (Owen-Smith 1988; Skinner et al. 2002). Until the age of 2 months, the calves nurse exclusively. However, weaning commences shortly after this, with calves dramatically increasing their reliance on grass when they are 4 months old (Owen-Smith 1988). Due to the timing of births, this stage of weaning often coincides with the first dry season of a calf. Unfortunately, calves are still small (200 to 250 kg; Wagner and Edwards 2002) at this age compared to adults (1,600 to 2,300 kg; Owen-Smith 1988) and are therefore less capable of tolerating food limitations (Munn and Dawson 2006). Interactions between the home range choice of a mother and seasonal rainfall are thus likely to be critical determinants of calf survival during this time.

From 1999 to 2019, 24% of the white rhino calves born in Ithala Game Reserve, South Africa, died. Yet, the cause of these deaths remained unknown. To address this, we investigated the impacts of different rainfall parameters (i.e., dry season rainfall and duration, and preceding wet season rainfall and duration) on white rhino calf survival, and whether these relationships were modified by the availability of woodlands and bunch grasslands within the chosen home range of the mother. We predicted that dry

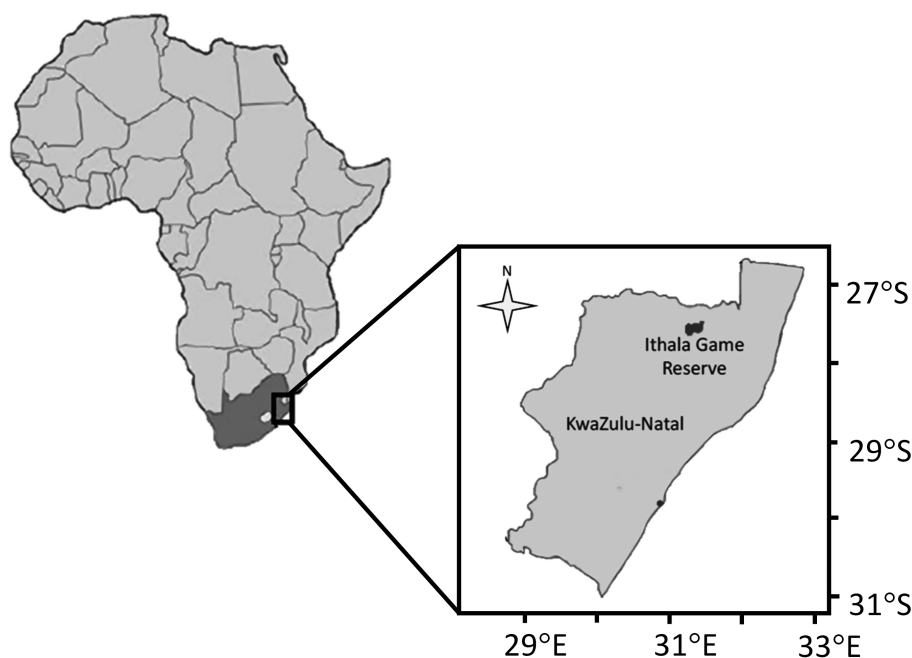
season rainfall would positively affect calf survival by maintaining the availability of nutritious short grass during the dry season. However, an increase in the availability of woodlands, and hence reserve resources, would weaken this effect by allowing calves to meet their dietary needs irrespective of rainfall during this time. In addition, we predicted that an increase in dry season duration would negatively affect calf survival by increasing the time that calves had to endure a shortage of high-quality food, but that an increase in bunch grasslands within the home range of the mother would help mitigate this effect by increasing the overall availability of buffer resources.

## Materials and methods

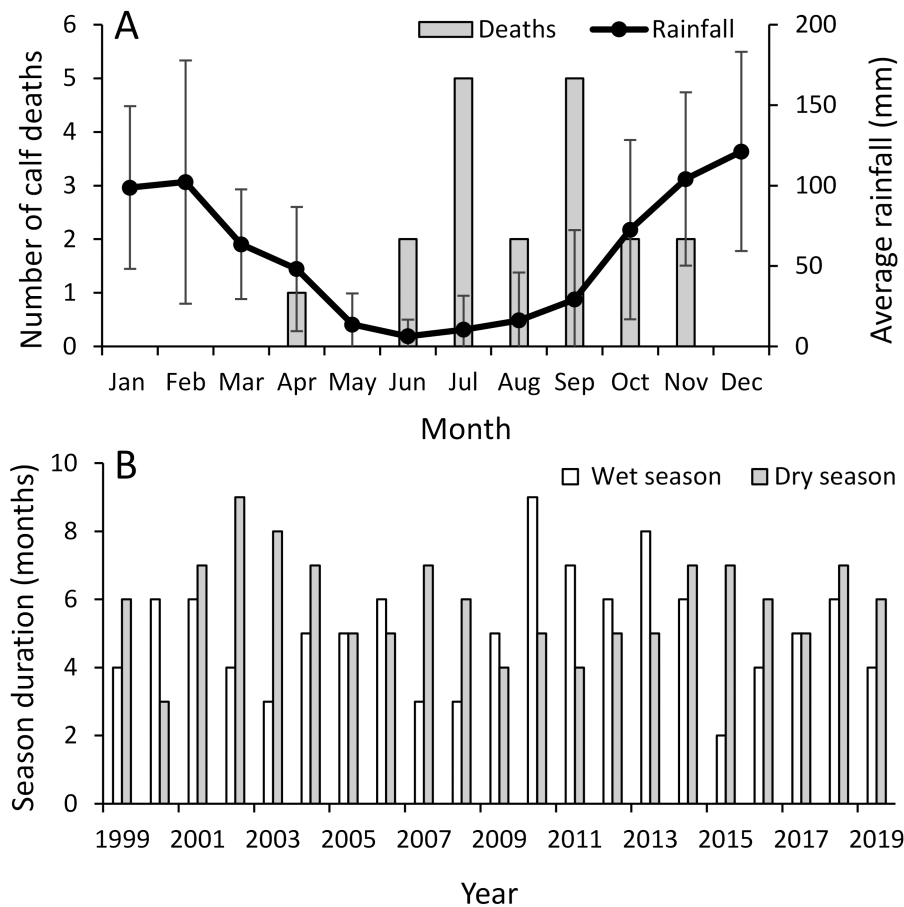
### Study site

We conducted our study in the 297 km<sup>2</sup> Ithala Game Reserve (henceforth Ithala; 27°45'S, 31°37'E), South Africa (Fig. 1). Ithala generally experiences wet summers (October to March) and dry winters (April to September; Fig. 2A). However, the onset and duration of each season during the study period (1999 to 2019) varied immensely between years (Fig. 2B). The mean annual rainfall during the study was 681 mm (range 394 to 1,125 mm), with a mean dry season rainfall of 81 mm (range 3 to 200 mm), and wet season rainfall of 560 mm (range 230 to 1,027 mm). Surface water is available year-round throughout the reserve in small springs, perennial streams, pans, and the Pongola River, which forms the northern boundary of the reserve.

Ithala is characterized by a combination of plains, hills, scarps, plateaus, and valleys, with its elevation ranging from 320 to 1,446 m a.s.l. (Van Rooyen and Van Rooyen 2008). In total, there are 26 vegetation types in the reserve that differ in their composition of trees, shrubs, forbs, and grasses (Van Rooyen and Van Rooyen 2008). However, for this study, we combined these vegetation types into 6 broad habitat categories based on their structure and use by white rhinos (Supplementary Data SD1). This approach is similar to Owen-Smith (1988) and Shrader et al. (2006) who used broad habitat classifications in Hluhluwe-iMfolozi Park,



**Fig. 1.** Ithala Game Reserve is located in northern KwaZulu-Natal, South Africa.



**Fig. 2.** (A) The average rainfall ( $\bar{x} \pm SD$ ; black line) and number of white rhino calves that died (gray bars) during each month from 1999 to 2019. (B) The duration of the dry season each year (gray bars) and its preceding wet season (white bars).

South Africa. Woodlands (67% of the total area) and bunch grasslands (23% of the total area) were the most widespread habitat types. Grazing lawns were small (<0.5 ha), clustered within old field grasslands where former agriculture created nutrient hotspots, and only constituted 0.14% of the area in the reserve (Valls Fox et al. 2015). While Ithala hosts a diverse assemblage of large mammalian herbivores, e.g., Cape Buffalo (*Syncerus caffer*), African Savanna Elephant (*Loxodonta africana*), Northern Giraffe (*Giraffa camelopardalis*), Impala (*Aepyceros melampus*), and Nyala (*Tragelaphus angasii*), predators are limited to Leopard (*Panthera pardus*) and Spotted hyena (*Crocuta crocuta*; Van Rooyen and Van Rooyen 2008). Most of the reserve is fenced, except for the northern boundary, which runs along the Pongola River.

### Source data

All adult and subadult white rhinos in Ithala are ear-notched with unique patterns, which allows for individual identification. As staff patrol through the reserve, they record the identity and Global Positioning System (GPS) location of each rhino they see. Thus, the position of each rhino was recorded approximately every 2 weeks throughout the study period (1999 to 2019). For each sighting, the age, sex—and if possible—identity of individuals moving with each rhino was recorded. We used this information to determine the birth and death of calves. Births were recorded when calves were first seen with their mothers, while deaths were recorded when their carcasses were found. If a carcass was not found, we estimated the date of death using the first

time when the calf was recorded as missing. Due to the intervals between sightings, this gave an error of ca. 14 days (range 1 to 25 days). To determine the age at which a calf had died, we counted the months from when it was first seen to the day its carcass was found or it was noticed to be missing. We limited calf mortalities in the analysis to those presumed to be caused by natural causes. Thus, calves killed by anomalies such as lightning strikes ( $n = 5$  calves) were excluded.

White rhino calves generally remain with their mothers until they are 2 to 3.5 years of age (Owen-Smith 1988; Shrader and Owen-Smith 2002). Therefore, to determine the amount of woodland and bunch grassland (i.e., reserve and buffer resources, respectively) available to each calf, we calculated the percentage of the dry season home range comprising these habitats for each mother. We used dry season home ranges because this is when these habitats are primarily used (Owen-Smith 1988; Shrader and Perrin 2006). Using the GPS locations, we first generated home ranges for each breeding female ( $n = 23$  females). We limited sightings to those that were separated by at least 24 h to prevent autocorrelation of the positions (Swihart and Slade 1985; Noonan et al. 2019), giving a mean value of ca. 260 positions per home range (range 73 to 559 positions). We limited our analyses to females that had at least 100 GPS positions, as this is required for estimation biases and variation to asymptote (Girard et al. 2002). Therefore, all but 2 females ( $n = 73$  and 76 sightings) had enough sightings to ensure accurate home range estimations. These 2 females, however, only had 1 calf each, and therefore

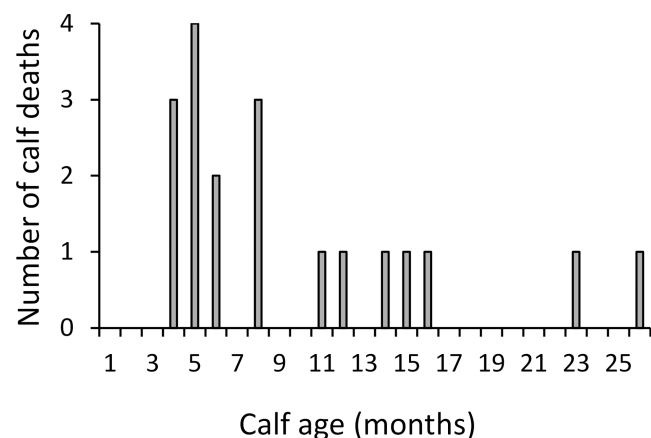
only represented 2 data points out of the entire data set ( $n = 78$  calves).

White rhinos tend to use the full extent of their home ranges during dry seasons (Owen-Smith 1988). We therefore generated the 95% boundary of each female home range using kernel density estimations (Standard Sextane Bi-weight kernel type; bandwidth = 0.017; cell size = 0.001). We then overlaid the 95% boundaries onto a habitat map of Ithala and calculated the percentage of each female home range that comprised woodlands and bunch grasslands. On average, woodlands made up 70% (range 42% to 88%) of the home ranges, while bunch grasslands made up 21% (range 7% to 36%). All home range analyses were done using the Home Range Analysis and Estimation toolbox (Steiniger and Hunter 2012) in OpenJUMP (version 1.7.1 release rev.4004), and QGIS (QGIS Development Team 2020).

Monthly rainfall between 1999 and 2019 was measured by reserve personnel. Due to the high variability in seasonal rainfall (Fig. 2B), we did not assign fixed dry or wet seasons. Instead, we defined these periods separately for each year based on breaks in the rainfall data. Dry season months received  $\leq 35$  mm of rain, transitional months received between 35 and 59 mm of rain, and wet season months received  $\geq 60$  mm of rain. Months that experienced unseasonal amounts of rainfall (e.g., high-rainfall months flanked by dry season months) were considered part of the same season as its adjacent months. This allowed each season to be defined as a continuous collection of months. For our study, dry season rainfall was a measurement of the total amount of rain that fell during the first dry season of a calf after the age of 4 months. Wet season rainfall measured the total amount of rain that fell during the preceding wet season. Dry and wet season duration comprised the number of months that each season lasted. Data collection and handling followed ASM guidelines (Sikes et al. 2016), and were consistent with the University of Pretoria and South African animal ethics protocols (clearance certificate NAS218/2020).

## Data analysis

Nearly all of the deceased calves died during their first dry season after the age of 4 months (Figs. 2A and 3). We therefore measured calf survival during this time, and only used rainfall measurements from this dry season and its preceding wet season for the analyses. Calves that died during their second



**Fig. 3.** The number and age of white rhino calves that died between 1999 and 2019.

and third dry seasons were not considered as mortalities during our analyses. As calf survival had a binary distribution (survival = 1; mortality = 0), we used a generalized linear mixed model with a binomial distribution and logit link function to determine which variables influenced the likelihood of calf survival. The variables that we considered included dry season rainfall, dry season duration, wet season rainfall, wet season duration, and their interactions with the availability of woodlands and bunch grasslands (i.e., percentage woodland and percentage bunch grassland) within the home range of a mother. Since the sex of a calf may have influenced its survival (White et al. 2007b; Foley et al. 2008), we included calf sex as a covariate. We also included mother ID as a random effect to control for violations of independence between calves belonging to the same mother. The availability of grazing lawns was not considered for the analyses, because its limited extent and poor spread across the reserve (Valls Fox et al. 2015) made it unlikely that the home ranges of mothers provided sufficient access to grazing lawns for it to affect calf survival. White rhinos that did not have access to grazing lawns likely fed on short grasses spread throughout other habitats during wet seasons. In addition, grazing lawns require at least 26 mm of rainfall per month for grass growth to be maintained (Bonnet et al. 2010). Only 15% of the dry season months during our study period received more rain than this, with 8 of the dry seasons not including any of these months. Therefore, even if a home range provided adequate access to grazing lawns, it was unlikely that grass growth would have been maintained long enough during dry seasons to support the calves.

Multicollinearity violates the assumptions of mixed models, thereby inflating standard errors and deflating power in significance tests (Disatnik and Sivan 2016). Thus, we tested for multicollinearity between the predictor variables using Spearman rank correlation tests. Wet season rainfall and duration had a very strong positive correlation ( $r_s = 0.903$ ;  $P < 0.001$ ). In addition, percentage woodland and bunch grassland were strongly negatively correlated ( $r_s = -0.906$ ;  $P < 0.001$ ; Supplementary Data SD2). We therefore removed wet season duration and percentage bunch grassland from the analysis. There was a moderate positive correlation between dry season rainfall and dry season duration ( $r_s = 0.642$ ;  $P < 0.001$ ). However, this was unproblematic for the analyses given that dry season rainfall and duration produced low Variance Inflation Factor values (2.62 and 2.74). The remaining variables and model met the model assumptions.

We used a manual likelihood ratio test-based backward selection process to determine which collection of variables best fit the data (Supplementary Data SD3). We then evaluated the model of best fit using a likelihood ratio test, a Hosmer-Lemeshow test, and by calculating its AUC statistic (i.e., the area under the receiver operating characteristic curve; Peng et al. 2002). To identify conditions under which calf survival would have been low enough to cause the observed mortalities, we used the model to predict calf survival at different combinations of each variable. To do this, we identified 3 representative categories for the availability of woodlands within the home ranges of mothers: low (1 SD below the mean = 57%); intermediate (mean = 70%); and high (1 SD above the mean = 83%). We then used these categories together with continuous dry season rainfall and duration measurements to calculate the probability of calf survival across a range of dry season conditions. We performed all data analyses using RStudio software (R Development Core Team 2012).

## Results

From 1999 to 2019, 23 adult females gave birth to 78 calves. Of these calves, 19 died from natural causes (calf mortality rate of 24.4%). Only 4 died outside of the dry season, 3 of which died 1 month after the dry season had ceased, and 1 that died 1 month before the dry season. No calves died during the peak wet season months (i.e., December, January, February; Fig. 2A). Calves generally died during their first full dry season, but never before the age of 4 months (Fig. 3). Only 3 calves died during their second or third dry seasons (16 months and older; Fig. 3), all of which occurred during 2002 which had an exceptionally long dry season (9 months; Fig. 2B). Calf mortality was highest between the ages of 4 and 8 months (12 out of the 19 deaths; Fig. 3).

The most parsimonious model included percentage woodland, dry season duration, and dry season rainfall (Table 1). Calf sex ( $P = 0.37$ ), wet season rainfall ( $P = 0.97$ ), and the interaction between wet season rainfall and percentage woodland ( $P = 0.44$ ) did not influence calf survival and were therefore removed from the model (Supplementary Data SD3). According to the likelihood ratio test ( $\chi^2_3 = 1.395$ ;  $P = 0.71$ ), and a comparison of the AIC values ( $AIC_{FullModel} = 80.5$ ,  $AIC_{FinalModel} = 75.9$ ; Supplementary Data SD3), the final model performed significantly better than the full model. The Hosmer–Lemeshow test revealed that the final model was a good fit to the data ( $\chi^2_8 = 4.64$ ;  $P = 0.80$ ). The model also rendered an AUC value of 0.83, indicating that there was an 83% chance that a pair of subjects (a true mortality and a true survival) would be correctly ordered by the test (Peng et al. 2002).

The model revealed a significant 2-way interaction between dry season rainfall and percentage woodland ( $z_1 = 3.907$ ;  $P < 0.001$ ; Table 1). Moreover, the 2-way interaction between dry season duration and percentage woodland was also significant ( $z_1 = -3.671$ ;  $P < 0.001$ ; Table 1). Therefore, the effects of dry season rainfall and duration on the likelihood of calf survival depended on the availability of woodlands within the home range of the mother.

### Effects of dry season rainfall and duration

We found that dry season rainfall positively influenced the likelihood of a calf surviving (Fig. 4A). This effect was enhanced as percentage woodland within the home range of the mother increased (Fig. 4A). Thus, if dry season duration was kept constant, the likelihood of a calf surviving was greatest during high-rainfall dry seasons in home ranges that had a high availability of woodlands (Supplementary Data SD4). However, as

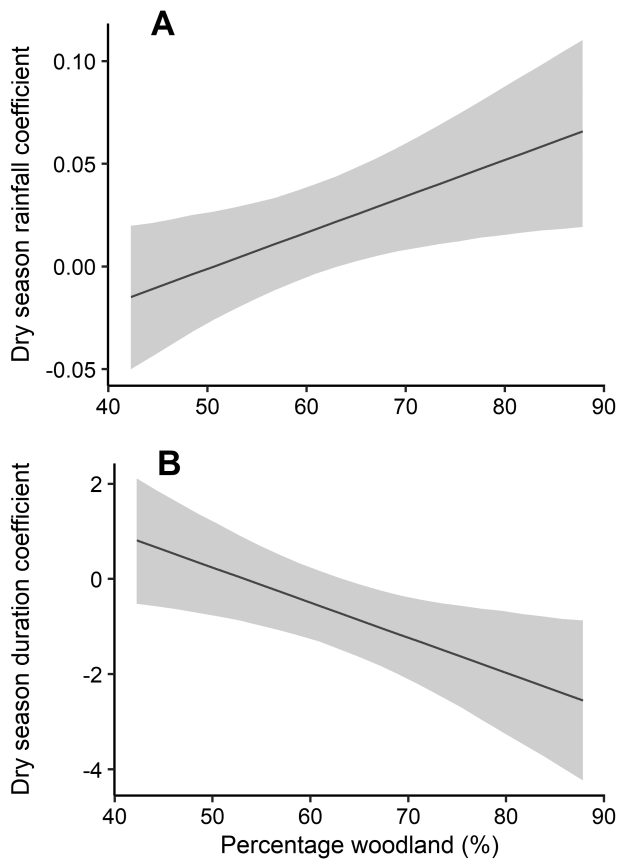
predicted, the likelihood of a calf surviving was also negatively affected by dry season duration (Fig. 4B). This adverse effect was exacerbated as percentage woodland within the home range of the mother increased (Fig. 4B). This meant that, given a fixed amount of dry season rainfall, the likelihood of a calf surviving was lowest during long dry seasons in home ranges that had a high availability of woodlands (Supplementary Data SD4) and thus a low availability of bunch grasslands (Supplementary Data SD2). The change in direction of dry season rainfall and duration effects at low woodland percentages fell within regions of nonsignificance, and likely arose due to interpolation of the assumption of linear interaction effects in the model (Fig. 4A and B; Hainmueller et al. 2019).

### Estimated likelihood of calf survival

To identify conditions under which calf survival would have been low enough to cause the observed mortalities, we predicted the probability of a calf surviving in home ranges with a low, intermediate, and high availability of woodlands across a range of dry season conditions. Unsurprisingly, these predictions revealed that calf survival declined across all home ranges as dry season rainfall decreased and dry season duration increased (Fig. 5). However, this decline was more pronounced in home ranges with an intermediate or high availability of woodlands (Fig. 5B and C) compared to home ranges with a low availability of woodlands (Fig. 5A), specifically during dry seasons with above-average durations and/or below-average rainfall. As a result, the minimum likelihood of calf survival was lower and spread across a larger range of dry season conditions for these calves. For instance, the lowest probability of survival in home ranges with a low availability of woodlands was between 0.3 and 0.4, and only occurred during dry seasons that lasted  $\geq 8$  months and received  $\leq 25$  mm of rain (Fig. 5A). By contrast, the lowest survival probability dropped to between 0 and 0.1 in home ranges with intermediate or high woodland availability (Fig. 5B and C). In home ranges with an intermediate amount of woodland, this was predicted to happen during dry seasons that lasted  $\geq 7$  months and received  $\leq 75$  mm of rain (Fig. 5B), while in home ranges with a high amount of woodland this was predicted to happen during dry seasons that lasted  $\geq 6$  months and received  $\leq 120$  mm of rain (Fig. 5C). Ultimately, it is clear that the calves were most vulnerable during dry seasons with above-average durations and/or below-average rainfall. In addition, their chances of surviving these conditions decreased as the availability of woodlands within the home ranges of mothers increased. Having a higher availability of woodlands was only beneficial during dry seasons with below-average durations and/or above-average rainfall.

**Table 1.** Variables and interactions that were related to white rhino calf survival between 1999 and 2019. Variables included percentage woodland (percentage of the mother's home range comprising woodlands), dry season duration (the number of months spanning the calf's first dry season after the age of 4 months), and dry season rainfall (total amount of rainfall [mm] during the calf's first dry season after the age of 4 months). Asterisks indicate a significant effect ( $P \leq 0.05$ ).

Predictor variables	Coefficient	Standard error	Degrees of freedom	z-value	P-value
Intercept	-17.772	7.453		-2.385	0.017*
Percentage woodland	0.345	0.112	1	3.076	0.002*
Dry season duration	3.907	1.364	1	2.865	0.004*
Dry season rainfall	-0.09	0.032	1	-2.817	0.005*
Percentage woodland $\times$ dry season duration	-0.074	0.02	1	-3.671	<0.001*
Percentage woodland $\times$ dry season rainfall	0.002	0.001	1	3.907	<0.001*

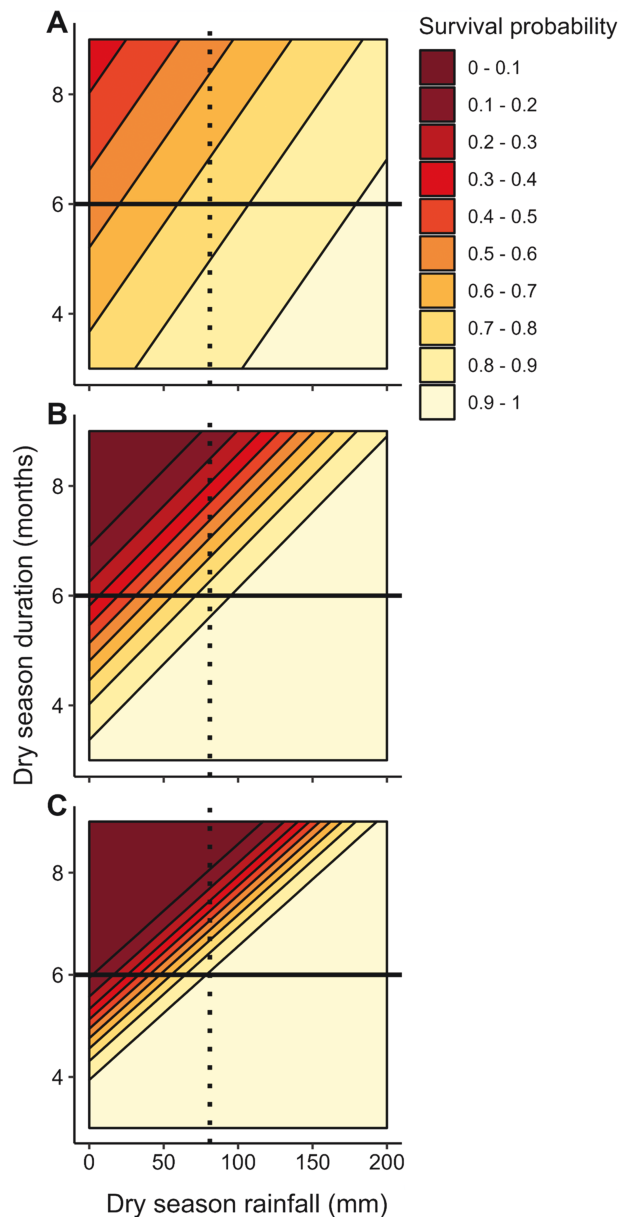


**Fig. 4.** The effects of (A) dry season rainfall and (B) dry season duration on the likelihood of white rhino calf survival (represented by coefficient values) throughout the observed range of percentage woodland within the mothers' ranges (42% to 88%). Gray area represents the 95% confidence interval.

These predictions indicate that calf mortalities were most likely to occur if the first dry season of a calf after the age of 4 months was unusually long and dry, and the home ranges of their mothers contained an intermediate to high availability of woodlands. In line with this, all of the deceased calves within our study experienced dry seasons with above-average durations and/or below-average rainfall at the time of their deaths (Supplementary Data SD4). In addition, 70% (11 out of the 16) calves had intermediate to high availabilities of woodlands in their home ranges (Supplementary Data SD4). Consequently, their estimated probability survival was reduced to an average of 0.59 (range 0.07 to 0.92), suggesting that this combination of factors likely caused their deaths.

## Discussion

From 1999 to 2019, 19 of the 78 (24%) white rhino calves born in Ithala died. Yet the cause of these deaths remained unknown. Upon investigation, we found that nearly all the calves that died did so during their first dry season, but never while they were still predominantly nursing (i.e., younger than 4 months; Owen-Smith 1988). This suggests that lactating females met the dietary demands of new-born calves during dry seasons, likely by utilizing stored body reserves (Oftedal 2000). Most of the calves died between the ages of 4 and 8 months, when calves supplement most of their milk intake with grass (Owen-Smith 1988) but are still too small to cope with declines in grass quality (Munn



**Fig. 5.** The likelihood that a white rhino calf with a (A) low (57%), (B) intermediate (70%), or (C) high (83%) availability of woodlands within the home range of its mother would have survived at different combinations of dry season rainfall and duration. The horizontal solid line represents the average dry season duration (6 months). The vertical dotted line depicts Ithala's average dry season rainfall (81 mm).

and Dawson 2006). As expected, the likelihood of a calf surviving this period was determined by dry season rainfall and duration. However, the extent of these effects varied depending on the availability of woodlands within the home range of a mother.

## Dry season rainfall and duration

A number of studies have highlighted the importance of dry season rainfall in determining the survival of large herbivores (Mduma et al. 1999; Dunham et al. 2004; Owen-Smith et al. 2005). In Kruger National Park, for instance, a reduction in dry season rainfall was responsible for rapid population declines in several large-bodied ungulates, including Waterbuck (*Kobus ellipsiprymnus*) and Tsessebe (*Damaliscus lunatus*; Ogotu and Owen-Smith 2003; Dunham et al. 2004). Within our study, the

likelihood of a white rhino calf surviving was positively influenced by the amount of rain that fell during its first dry season. However, contrary to our prediction, this effect was enhanced as the availability of woodlands within the home range of the mother increased. This finding suggests that dry season rainfall did not benefit the calves by maintaining the availability of nutritious short grasses throughout the dry season, but instead by maintaining the availability of woodland reserve resources. An increase in woodland availability therefore amplified this benefit by increasing the overall amount of reserve resources that were being maintained.

The likelihood of a calf surviving was also negatively influenced by the duration of its first dry season. This was likely because the duration determined the time that calves had to endure a shortage of high-quality food, and hence the risk of dying from malnourishment or starvation (Fryxell 1987; Shrader et al. 2006; Hempson et al. 2015). In contrast to the effect of dry season rainfall, an increase in the availability of woodlands within the home range of a mother did not reduce the negative effects of dry season duration. Instead, more woodlands exacerbated the adverse effects of dry season duration. This was likely due to the collinearity between the proportions of a home range comprising woodlands and bunch grasslands, with an increase in one resulting in a decrease in the other. Thus, as the availability of woodlands increased, the availability of bunch grasslands decreased. This meant that calves in home ranges incorporating large amounts of woodlands had fewer buffer resources to alleviate starvation, further reducing their chances of survival.

### Home range choice and calf survival

Dry season rainfall and duration fluctuated considerably within Ithala. However, the impact of this on the calves depended on the home range choices of their mothers, which ultimately determined their access to woodlands and bunch grasslands. Given that offspring survival is often a crucial component of the fitness of a female (Wolf and Wade 2001), one would expect that the mothers established home ranges in areas maximizing the survival of their calves despite the variability in dry season conditions (i.e., “mother knows best” hypothesis; Jaenike 1978).

Within our study, however, females established home ranges in a wide variety of areas, each differing in its composition of woodlands and bunch grasslands (e.g., woodlands comprised between 42% and 88% of the home ranges). Calves born to mothers that selected areas with a relatively low availability of woodlands had access to enough bunch grasslands, and hence buffer resources, to alleviate starvation despite dry spells and droughts during their first dry season. However, they did not have access to enough reserve resources to fully benefit if this period was short or received an abundance of rainfall. Regardless, their overall likelihood of surviving remained high under such conditions. In contrast, calves born to mothers that selected areas with an intermediate to high availability of woodlands lacked sufficient buffer resources, and were thus extremely sensitive to dry spells and droughts during their first dry season. This closely resembles the vulnerability of other juvenile megaherbivores, e.g., African elephants (Moss 2001; Foley et al. 2008; Shrader et al. 2010), and large mammalian herbivores, e.g., Kudu (*Tragelaphus strepsiceros*; Owen-Smith 1990), to harsh dry season conditions. These home ranges were only beneficial to calves when access to buffer resources was not crucial. This included years that had short dry seasons, or when dry season rainfall was abundant enough to maintain

reserve resources throughout critical periods. Due to our small sample size ( $n = 78$  calves), we acknowledge that some of the predictions may be a construct of where data were available and could therefore be a limitation of our study. However, the data were well-spread across the prediction range (Supplementary Data SD4), thereby reducing inaccuracies that may have occurred due to interpolation.

Nearly all of the deceased calves in Ithala belonged to mothers that had an intermediate to high availability of woodlands, and experienced dry spells or droughts during their first dry seasons. Given that calf survival was predicted to be considerably low under such conditions, we can conclude that this combination of factors likely caused their deaths. Dry season droughts were also the only time when older calves experiencing their second and third dry seasons died during our study. In addition, these calves resided in home ranges with very different availabilities of woodlands and bunch grasslands (i.e., woodlands comprised 82%, 72%, and 43% of their home ranges). This suggests that severe food limitations during prolonged dry season droughts are likely to impact all white rhino calves, irrespective of differences in age, body size, and access to reserve and buffer resources.

Annual dry season burns by reserve management might also have played an important role in determining calf survival during the study. This is because postfire regrowth provides a source of high-quality grass during this time (Shrader et al. 2006; Yoganand and Owen-Smith 2014). However, only an average of 25% (range 6% to 43%) of Ithala was burnt every year, with many sections only being burnt every 2 to 3 years. Therefore, only a portion of the calves would have benefited from burns during some years. In addition, a landscape requires sufficient soil moisture or rainfall after a burn to trigger and maintain grass regrowth (Parrini and Owen-Smith 2010). Thus, burning would have further reduced food availability during dry seasons with long durations or little rainfall, negatively impacting calf survival (Parrini and Owen-Smith 2010).

There are 4 possible reasons why some females established home ranges with a suboptimal availability of bunch grasslands. The first incorporates white rhino density and competition for buffer resources. It is possible that the mothers traded-off optimal home range locations for suboptimal areas that had lower white rhino densities, and thus less competition for resources (Ideal Free Distribution; Fretwell and Lucas 1970). However, the home ranges of mothers clustered together and overlapped extensively in Ithala—see Pienaar et al. (1993), Rachlow et al. (1999), and White et al. (2007a) for examples from other reserves. Therefore, it is unlikely that competition for buffer resources deterred females from establishing home ranges in areas offering a high availability of bunch grasslands. On the other hand, density does affect the size of female home ranges, with higher densities rendering smaller home ranges (Rachlow et al. 1999; White et al. 2007a). It is therefore possible that competition influenced the availability of bunch grasslands within the home ranges of mothers, not by causing mothers to select suboptimal areas, but by limiting the size of their home ranges. Yet, Ithala has a fairly low density of white rhinos (0.14 rhinos/km<sup>2</sup>), and therefore the females had relatively large home ranges ( $34 \pm 18$  km<sup>2</sup>; Hebbelmann 2013)—see Owen-Smith (1975), Pienaar et al. (1993), Rachlow et al. (1999), and White et al. (2007a) for comparisons. It is thus unlikely that white rhino density in Ithala impacted the availability of bunch grasslands within the home ranges of mothers by limiting home range sizes.

Another possibility is that the mothers simply established home ranges near their natal home ranges without considering habitat composition. If this was the case, then the availability of buffer resources would have been determined by the decisions made by female ancestors and not by the mothers. However, there is no evidence indicating that subadult females establish home ranges close to their natal home ranges. Instead, by forming temporary associations with other subadults or adult females without calves (i.e., the buddy system), subadult white rhinos can disperse large distances before establishing a home range (Owen-Smith 1988; Shrader and Owen-Smith 2002). Moreover, Owen-Smith (1973) observed subadults dispersing away from their natal home ranges without settling nearby. Thus, this suggestion is unlikely.

The third possible explanation is that mothers selected areas where the combined availability of reserve and buffer resources was optimal given the dry season conditions at the time of dispersal. Then, due to the variability in dry season conditions, these areas were suboptimal during other years. For instance, areas with a high availability of woodlands and low availability of bunch grasslands may have been selected by females if they established their home ranges during years with short dry seasons and/or high dry season rainfall. However, these areas would have rendered low calf survival during subsequent years when dry season dry spells or droughts occurred. The last possible explanation is that females were not considering the availability of bunch grasslands when deciding where to establish their home ranges, but rather considered the availability of males (White et al. 2007a). If males were not distributed across the landscape based on the availability of buffer resources, then neither would the females.

Our results revealed that the likelihood of a calf surviving its first dry season after weaning had commenced increased with dry season rainfall and decreased with its duration. However, these effects were most pronounced in home ranges rendering a low availability of bunch grasslands. Consequently, a combination of low dry season rainfall, long dry seasons, and selection of home ranges lacking buffer resources by some mothers likely caused the white rhino calf loss in Ithala. Unfortunately, large parts of Southern Africa are expected to experience increasing dry season durations and a reduction in dry season rainfall due to climate change (Dunning et al. 2018; Wainwright et al. 2021). As such, harsh dry season conditions will become more frequent (Abiodun et al. 2019) and could lead to increased white rhino calf mortality throughout Southern Africa. Mothers may be able to temper these impacts by adjusting the location of their home ranges. However, it was evident from our data that white rhino mothers seldom move after they have established a home range, which may also be true for other large mammalian herbivores. Thus, these adjustments are unlikely to happen, or would at least be a very slow process. Reduced calf survival due to harsher dry seasons may have devastating impacts on the demographic rates of white rhino populations (Gaillard et al. 1998, 2000; Trimble et al. 2009).

Ultimately, our study highlights a link between changes in environmental conditions, the home range choice of a mother, and the ability of a mother to adjust her home range in response to environmental change. The survival of many other juvenile mammalian herbivores within African savannahs, e.g., African savannah elephants and wildebeest (*Connochaetes taurinus*; Mduma et al. 1999; Shrader et al. 2010), and other systems (e.g., eastern grey kangaroos *Macropus giganteus*; Plaisir et al. 2022) is influenced by changes in dry season conditions. While white rhino mothers seem unable to make the required home range adjustments, it

remains unclear how other herbivores may respond. Hence, our results signal a warning about the potential future impacts that climate change may have not only on white rhinos but also on other large mammalian herbivores in different parts of the world.

## Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—The 26 vegetation types in Ithala Game Reserve, and their respective areas (ha), as described by Van Rooyen and Van Rooyen (2008).

**Supplementary Data SD2.**—Negative correlation between percentage woodland and percentage bunch grassland within each mothers' home range.

**Supplementary Data SD3.**—Outcomes of the manual likelihood ratio test-based backward selection process used to determine the model of best fit.

**Supplementary Data SD4.**—The combined effects of (A) dry season rainfall and percentage woodland, and (B) dry season duration and percentage woodland on the probability of calf survival.

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## Author contributions

CJdL obtained and analyzed the data, interpreted the results, and wrote the paper. OB conceptualized the study and obtained the data. AMS conceptualized the study, interpreted the results, and edited the paper.

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## Conflict of interest

None declared.

## Data availability

Data available from authors upon request.

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