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Running header: Drivers of white rhino calf survival

Effect of rainfall on white rhino calf survival depends on a mother's home range choice

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Teaser Text

How is white rhino calf survival influenced by seasonal rainfall and a mother's home range choice? In our study, calf survival was positively affected by dry season rainfall and negatively affected by dry season duration. However, these effects were amplified if a mother selected a home range with an abundance of woodlands.

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 an individual's home range. From 1999-2019, 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 calves' 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 the dry season's rainfall and negatively influenced by its duration. However, these effects were more pronounced when the availability of woodlands within the mother's home range was high. Ultimately, the 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's 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 resources (i.e., forage with little nutritious value that herbivores can utilise when all other food sources have been exhausted) within an animal's home range (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 a grazer's vulnerability 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 two months, the calves nurse exclusively. However, weaning commences shortly after this, with calves dramatically increasing their reliance on grass when they are four months old (Owen-Smith 1988). Due to the timing of births, this stage of weaning often coincides with a calf's first dry season. Unfortunately, calves are still small (200-250 kg; Wagner and Edwards 2002) at this age compared to adults (1600-2300 kg; Owen-Smith 1988) and are therefore less capable of tolerating food limitations (Munn and Dawson 2006). Interactions between a mother's home range choice and seasonal rainfall are thus likely to be critical determinants of a calf's 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 the preceding wet season's rainfall and duration) on white rhino calf survival, and whether these relationships were modified by the availability of woodlands and bunch grasslands within the mother's chosen home range. 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 mother's home range 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^2 Ithala Game Reserve (henceforth Ithala) (27°45'S 31°37'E), South Africa (Fig. 1). Ithala generally experiences wet summers (October-March) and dry winters (April-September; Fig. 2A). However, the onset and duration of each season during the study period (1999-2019) varied immensely between years (Fig. 2B). The mean annual rainfall during the study was 681 mm (range 394-1125 mm), with a mean dry season rainfall of 81 mm (range 3-200 mm), and wet season rainfall of 560 mm (range 230-1027 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 characterised by a combination of plains, hills, scarps, plateaus, and valleys, with its elevation ranging from 320 m to 1446 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 six broad habitat categories based on their structure and use by white rhinos (see 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, 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 reserve's area (Valls Fox et al. 2015). While Ithala hosts a diverse assemblage of large mammalian herbivores (e.g., buffalo *Syncerus caffer*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus*, nyala *Tragelaphus angasii*), predators are limited to leopards (*Panthera pardus*) and spotted hyenas (*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 two weeks throughout the study period (1999-2019). For each sighting, the age, sex, and if possible, the 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 1-25 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 were excluded.

White rhino calves generally remain with their mothers until they are 2-3.5 years of age (Owen-Smith 1988; Shrader and Owen-Smith 2002). Therefore, to determine the availability of woodlands and bunch grasslands (i.e., reserve and buffer resources respectively) available to each calf, we calculated the percentage of each mother's dry season home range comprising these habitats. 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 hours to prevent autocorrelation of the positions (Swihart and Slade 1985; Noonan et al. 2019). This gave a mean value of c.a. 260 positions per home range (range 73-559 positions). We limited our analyses to females that had at least 100-300 GPS positions, as this is required for estimation biases and variation to asymptote (Girard et al. 2002). Therefore, all but two females (n = 73 and 76 sightings) had enough sightings to ensure accurate home range estimations. These two females, however, only had one calf each, and therefore only represented two data points out of the whole dataset (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's 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's home range that comprised woodlands and bunch grasslands. On average, woodlands made up 70% (range 42-88%) of the home ranges, while bunch grasslands made up 21% (range 7-36%). All the home range analyses were done using the Home Range Analysis and Estimation (HoRAE) toolbox (Steiniger and Hunter 2012) in OpenJUMP (version 1.7.1 release rev.4004), and QGIS (QGIS development team 2020).

Monthly rainfall between 1999-2019 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 ≤35 mm of rain, transitional months received between 35-59 mm of rain, and wet season months received ≥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 a calf's first dry season after the age of four 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 four months (Fig. 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 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 generalised 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 mother's home range. Since a calf's sex may have influenced its survival (White et al. 2007b; Foley et al. 2008), we included calf sex as a covariate. We also included the mother's 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. This was because its limited extent and poor spread across the reserve (Valls Fox et al. 2015) made it unlikely that the mothers' home ranges 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 eight 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 ($r_{76} = 0.903$; $P < 0.001$). In addition, percentage woodland and bunch grassland were strongly negatively correlated ($r_{76} = -0.906$; $P < 0.001$; see Supplementary Data SD2). We therefore removed wet season duration and percentage bunch grassland from the analysis. 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 (see 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 (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 three representative categories for the availability of woodlands within the mothers' home ranges: low (one standard deviation below the mean = 57%), intermediate (mean = 70%), and high (one standard the deviation above 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 Core Team 2019).

RESULTS

From 1999-2019, 23 adult females gave birth to 78 calves. Of these calves, 19 died from natural causes (calf mortality rate of 24.4 %). Only four died outside of the dry season, three of which died one month after the dry season had ceased, and one which died one 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 four months (Fig. 3). Only three 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 (nine months; Fig. 2B). Calf mortality was highest between the ages of four and eight 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 (see Supplementary Data SD3).

According to the likelihood ratio test (X^2_3 = 1.395; P = 0.71), and a comparison of the AIC values ($AIC_{FullModel}$ = 80.5, $AIC_{FinalModel}$ = 75.9; see 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 (X^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 two-way interaction between dry season rainfall and percentage woodland (z_1 = 3.907; P <0.001; Table 1). Moreover, the two-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 mother's home range.

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 mother's home range 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 (see 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 mother's home range 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 (see Supplementary Data SD4) and thus a low availability of bunch grasslands (see Supplementary Data SD2). The change in direction of dry season rainfall and duration's effects at low woodland percentages fell within regions of nonsignificance, and likely arose due to interpolation of the model's assumption of linear interaction effects (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 ≥8 months and received ≤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 ≥7 months and received ≤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 ≥6 months and received ≤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 their mothers' home ranges increased. Having a higher availability of woodlands was only beneficial during dry seasons with below average durations and/or above average rainfall.

These predictions indicate that calf mortalities were most likely to occur if the calves' first dry season after the age of four months was unusually long and dry, and their mothers' home ranges 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 0.07-0.92), 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 four months; Owen-Smith 1988). This suggests that lactating females met the dietary demands of new-born calves during dry seasons, likely by utilising stored body reserves (Oftedal 2000). Most of the calves died between the ages of four and eight 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 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 a calf's mother's home range.

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 (*Ogutu 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 its mother's home range 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 dry season rainfall's effect, an increase in the availability of woodlands within a mother's home range 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 mother's 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 their mother's home range choices, which ultimately determined their access to woodlands and bunch grasslands. Given that the survival of a female's offspring is often a crucial component of her own fitness (Wolf and Wade 2001), one would expect that the mothers established home ranges in areas maximising 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 42-88% 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 was well spread across the prediction range (see 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 post-fire 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 6-43%) of Ithala was burnt every year, with many sections only being burnt every two to three 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 three 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 mothers' home ranges 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 mothers' home ranges, not by causing mothers to select sub-optimal areas, but by limiting the size of their home ranges. Yet, Ithala has a fairly low density of white rhinos (0.14 rhinos/km^2), and therefore the females had relatively large home ranges (34 ± 18 km^2; Hebbelmann 2013) (see Owen-Smith 1975, Pienaar et al. 1993, Rachlow et al. 1999, and White et al. 2007a for comparisons). It is therefore unlikely that Ithala's white rhino density impacted the availability of bunch grasslands within the mothers' home ranges by limiting their home range sizes.

The second possible explanation is that the mothers selected areas where the combined availability of reserve and buffer resources was optimal given the dry season conditions at the time of dispersal. However, 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 the 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 the dry season's 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 the selection of home ranges lacking buffer resources by some mothers likely caused Ithala's white rhino calf loss. 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, a mother's home range choice, and the ability of a mother to adjust her home range in response to the 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.

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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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FIGURE LEGENDS

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

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

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

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 (42–88%). Grey area represents the 95% confidence interval.

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 its mother's home range would have survived at different combinations of dry season rainfall and duration. The horizontal solid line represents the average dry season duration (six months). The vertical dotted line depicts Ithala's average dry season rainfall (81 mm).

TABLES

Table 1. —Variables and interactions that were related to white rhino calf survival between 1999-2019. 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 four months), and dry season rainfall (total amount of rainfall (mm) during the calf's first dry season after the age of four 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* dry season duration	-0.074	0.02	1	-3.671	<0.001 *
Percentage woodland* dry season rainfall	0.002	0.001	1	3.907	<0.001 *

Fig 1

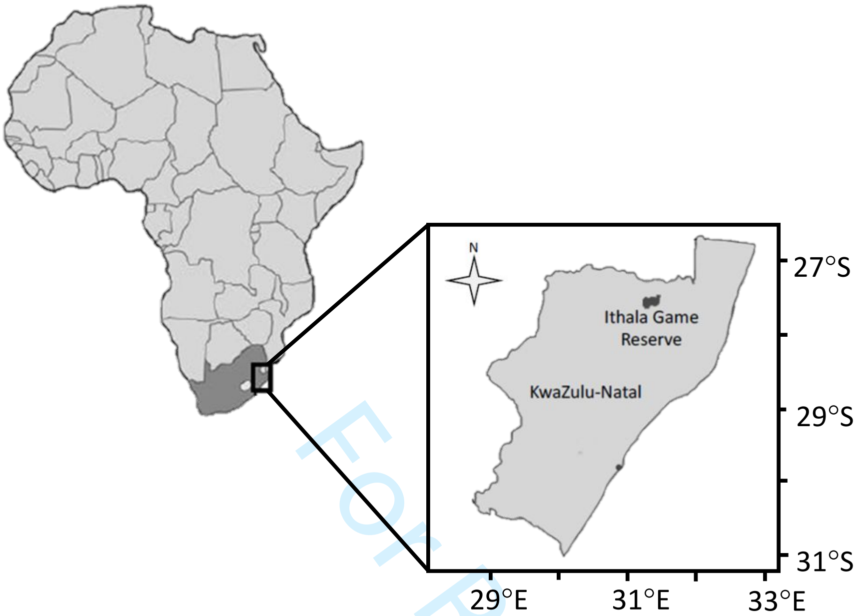


Fig 2.

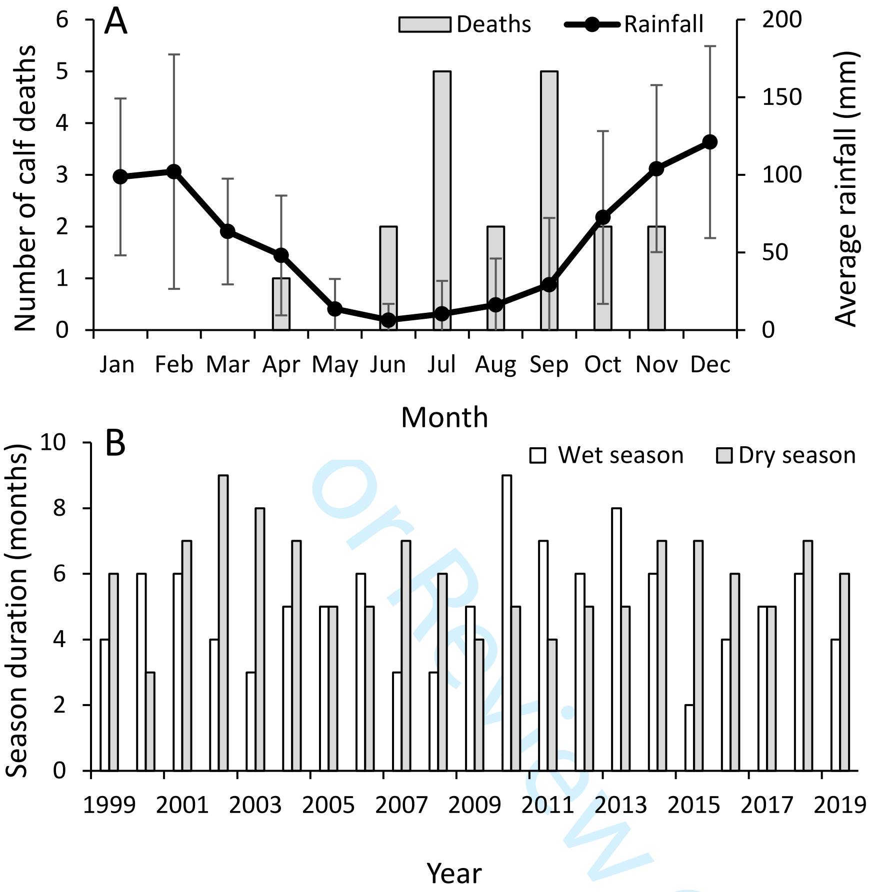

A
Deaths
Rainfall
Number of calf deaths
Average rainfall (mm)
0
1
2
3
4
5
6
0
50
100
150
200
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month
B
Wet season
Dry season
Season duration (months)
0
2
4
6
8
10
1999
2001
2003
2005
2007
2009
2011
2013
2015
2017
2019
Year

Fig. 3

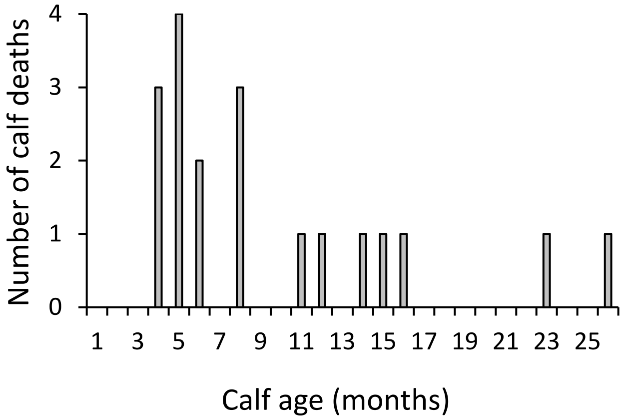

Number of calf deaths
4
3
2
1
0
1 3 5 7 9 11 13 15 17 19 21 23 25
Calf age (months)

Fig 4.

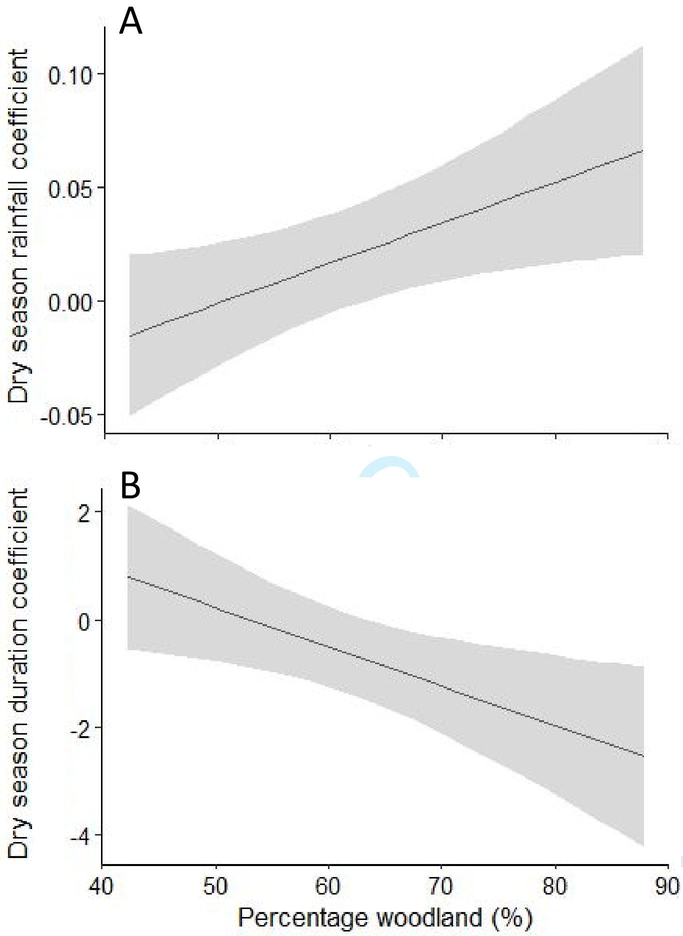
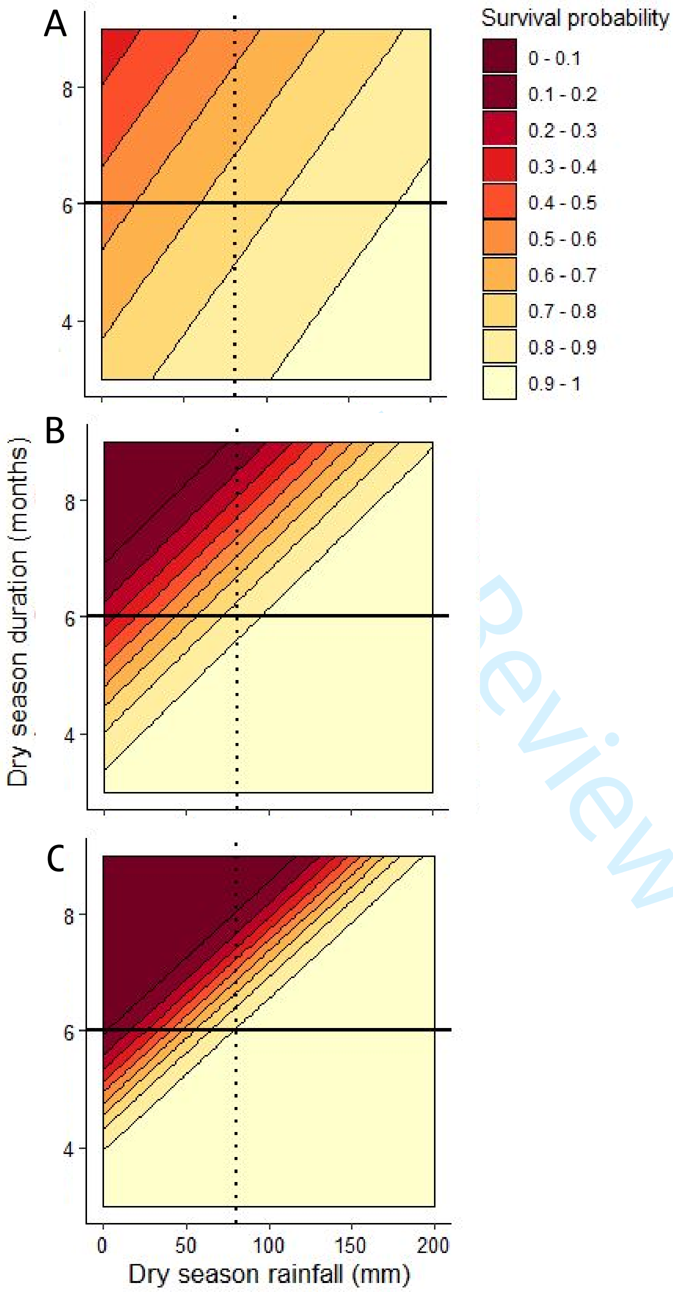

A
Dry season rainfall coefficient
0.10
0.05
0.00
-0.05
B
Dry season duration coefficient
2
0
-2
-4
40
50
60
70
80
90
Percentage woodland (%)

Fig. 5


A
B
C
Survival probability
0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1
Dry season duration (months)
Dry season rainfall (mm)
0
50
100
150
200
4
6
8

Effect of rainfall on white rhino calf survival depends on a mother's home range choice

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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). No* refers to the number assigned to each vegetation type by Van Rooyen and Van Rooyen (2008). We grouped these vegetation types into six broad habitat categories, namely woodlands, montane habitats, rocky wooded grasslands, bunch grasslands, wetlands, and disturbed areas.

No*	**Vegetation types included into "woodlands"**	**Area (ha)**
6	*Faurea saligna – Searsia harveyi – Cymbopogon excavates* wooded grassland to open woodland	1520.4
8	*Ficus glumosa - Euphorbia cooperi* open bushveld on rocky outcrops	1001.6
9.1	*Combretum apiculatum – Euclea schimperi* rocky Bushveld	4698.8
9.2	*Combretum apiculatum – Diospyro slycioides* subsp. *nitens* rocky Bushveld	3139.1
9.3	*Acacia nigrescens – Combretum apiculatum* rocky Bushveld and woodland	2239.2
9.4	*Combretum apiculatum - Bauhinia galpinii* open to dense Bushveld	968
10.1	*Olea europaea* subsp. *africana – Euclea schimperi* dense Bushveld	889.2
10.2	*Acacia nilotica - Acacia ataxacantha* dense Bushveld	2426.9
12	*Ficussur – Trimeria grandifolia* forests	670.5
13.2	*Breonadia salicina – Ficus sycomorus* riparian vegetation	2305.1
No*	**Vegetation types included into "montane habitats"**	**Area (ha)**
1.1 & 1.2	*Cliffortia nitidula* rocky montane grasslands	324.8
2.1	*Leucosidea sericea* thickets and Bushveld of dolerite cliffs and scarps	106
2.2	*Greyia sutherlandii* wooded grasslands of sandstone cliffs and scarps	232.4
No*	**Vegetation types included into "rocky wooded grasslands"**	**Area (ha)**

3.1	*Englerophytum magalismontanum – Loudetia simplex* rocky wooded grassland and open Bushveld	489.8
3.2	*Pterocarpus angolensis – Tetraselago* natalensis rocky wooded grassland and open Bushveld	468.2
5.1	*Trachypogon spicatus – Themeda triandra – Euclea crispa rocky* wooded grassland	993.3
No*	**Vegetation types included into "bunch grasslands"**	**Area (ha)**
4.1	*Hyparrhenia hirta - Acacia tortilis* old field grassland	660.4
4.2.1	*Hyparrhenia hirta – Acacia karroo* old field grassland	174.4
4.2.2	*Hyparrhenia hirta – Dichrostachys cinerea* old field grassland	485.2
4.2.3	*Hyparrhenia hirta – Sporobolus africanus* old field grassland	1152.7
5.2	*Trachypogon spicatus – Tristachya leucothrix* rocky wooded grassland	4197.9
7	*Senecio microglossus – Bewsia biflora* grassland	121.4
No*	**Vegetation types included into "wetlands"**	**Area (ha)**
13.1	*Imperata cylindrica* wetlands	195
No*	**Vegetation types included into "disturbed areas"**	**Area (ha)**
11	*Dichrostachys cinerea – Solanum incanum* shrubland of open disturbed patches	9.2
14	Built-up areas	45

Effect of rainfall on white rhino calf survival depends on a mother's home range choice

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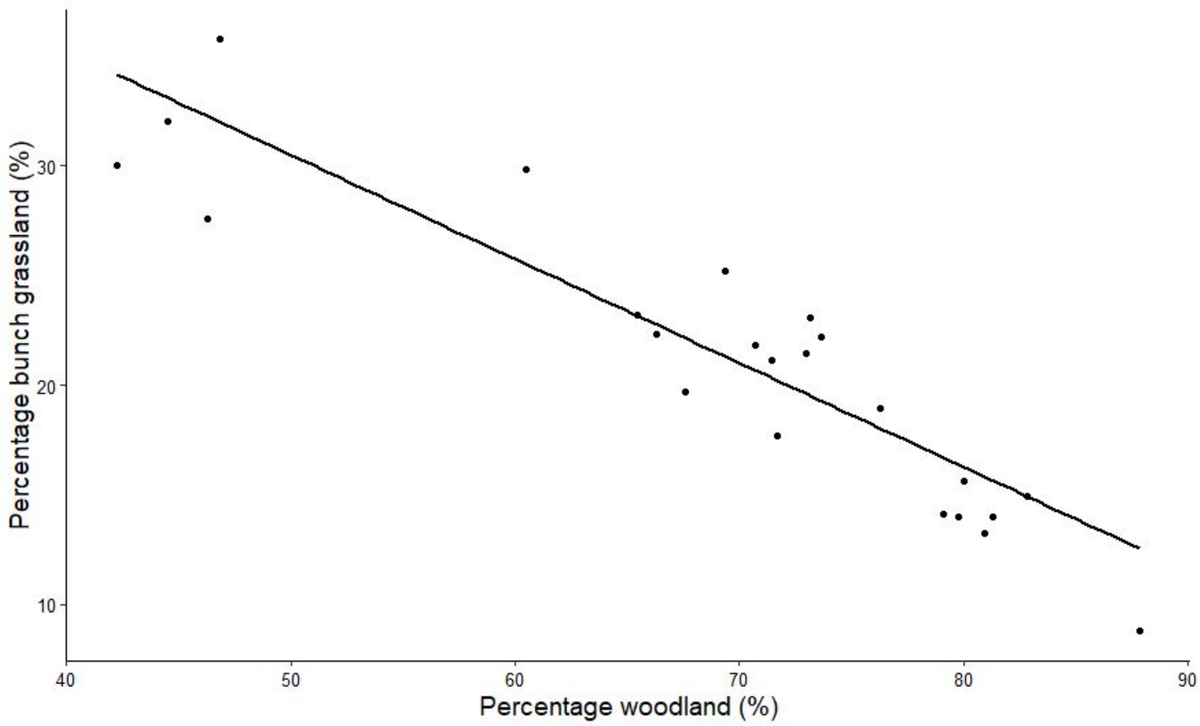

Supplementary Data SD2. —Negative correlation between percentage woodland and percentage bunch grassland within the mothers' home ranges.

Effect of rainfall on white rhino calf survival depends on a mother's home range choice

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Supplementary Data SD3. —Outcomes of the manual likelihood-ratio-test based backward selection process used to determine the model of best fit. The bold variable represents the variable that was removed during the subsequent step. Asterisks indicates a significant effect (P ≤ 0.05).

Step	Variables to be removed	*d.f.*	AIC	LRT	*P*-value
1 (Full model)	None		80.459		
	Calf sex	1	79.163	0.704	0.401
	Wet season rainfall*Percentage woodland	**1**	**79.045**	**0.586**	**0.444**
	Dry season duration*Percentage woodland	1	86.516	8.056	0.005 *
	Dry season rainfall*Percentage woodland	1	84.196	5.737	0.017 *
2	None		79.045		
	Calf sex	1	77.833	0.788	0.374
	Wet season rainfall	**1**	**77.047**	**0.001**	**0.968**
	Dry season duration*percentage woodland	1	84.516	7.470	0.006 *
	Dry season rainfall*percentage woodland	1	83.260	6.214	0.012 *
3	None		77.047		
	Calf sex	**1**	**75.855**	**0.808**	**0.368**
	Dry season duration*percentage woodland	1	82.527	7.480	0.006 *
	Dry season rainfall*percentage woodland	1	81.296	6.249	0.012 *

4 (Final model)	**None**		**75.855**		
	Dry season duration*percentage woodland	1	81.717	7.862	0.005 *
	Dry season rainfall*percentage woodland	1	80.216	6.360	0.012 *

Effect of rainfall on white rhino calf survival depends on a mother's home range choice

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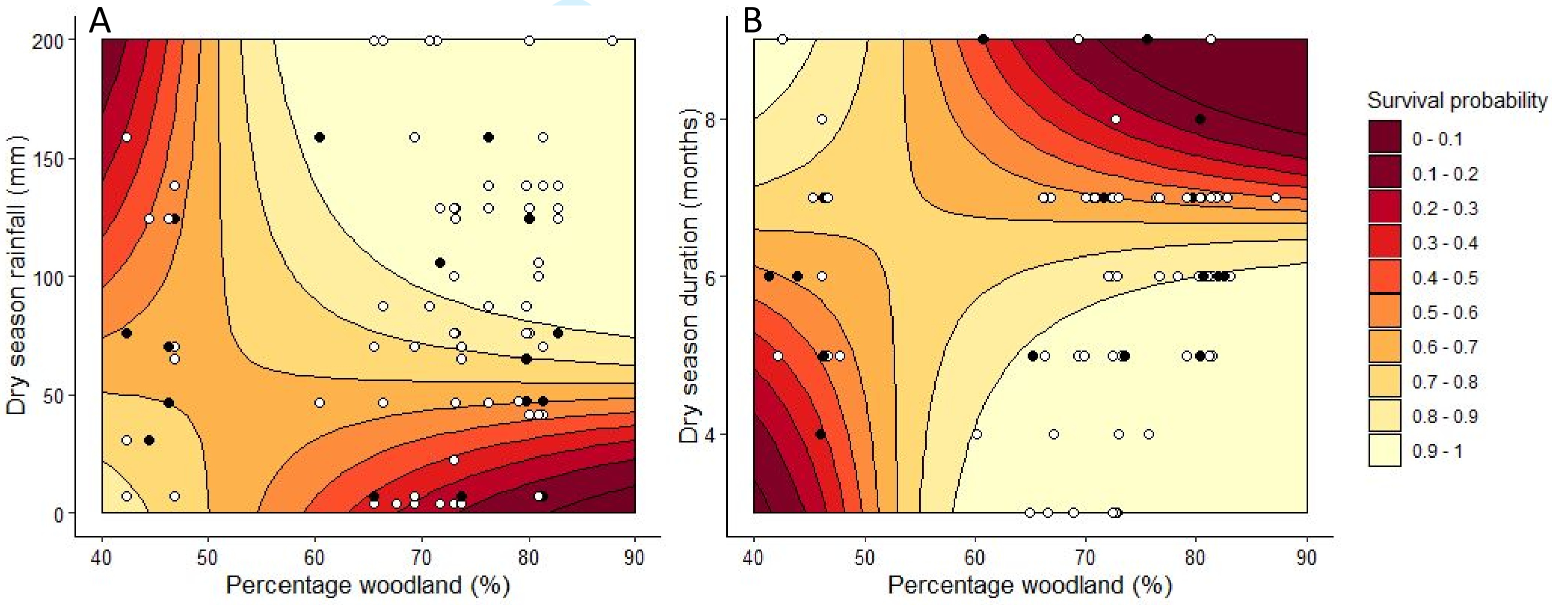
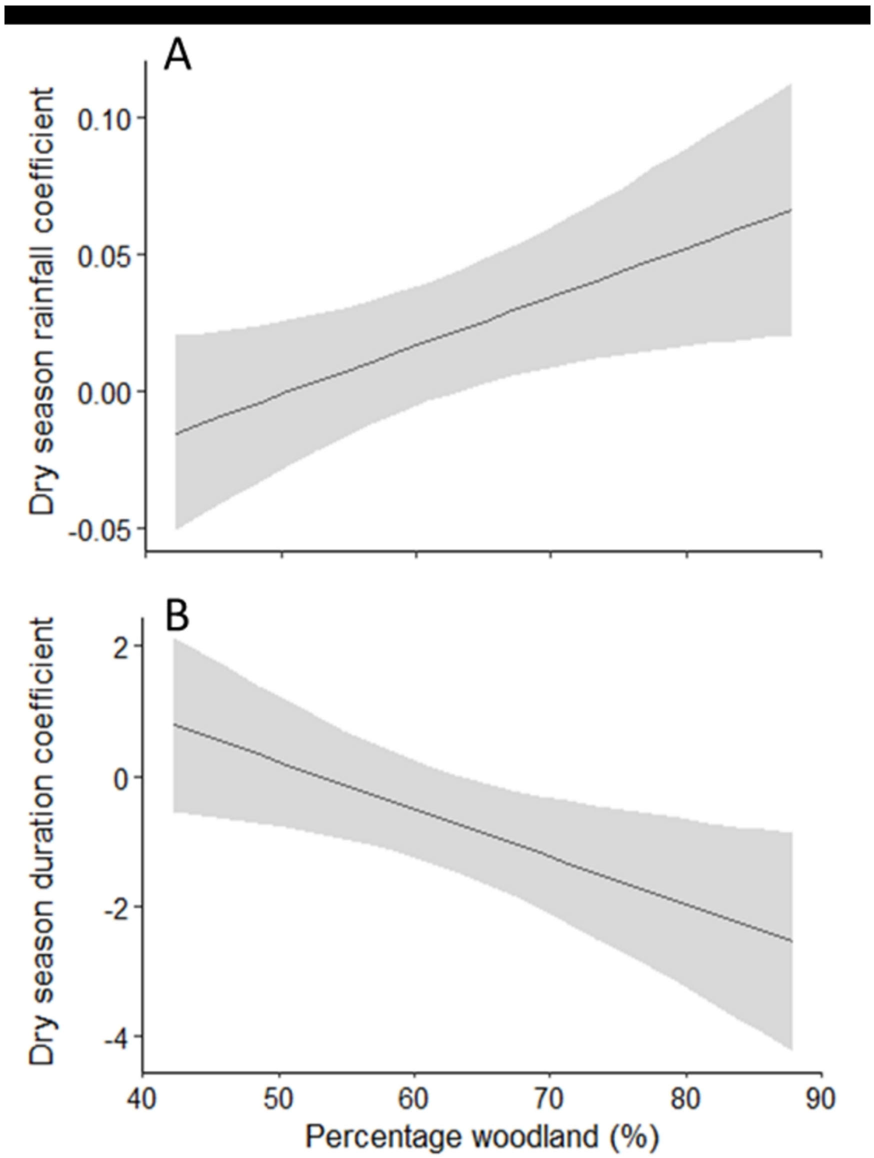


Supplementary Data SD4. —The combined effects of (A) dry season rainfall and percentage woodland and (B) dry season duration and percentage woodland on the probability of calf survival. The colour scale represents the different intervals of predicted survival probability. The black data points represent calves that died, while the white data points represent calves that survived. (A) Dry season duration was kept constant at the average duration experienced by calves (i.e., 6 months), and (B) dry season rainfall was kept constant at the average amount that the calves received (i.e., 81 mm).



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