Influence of environmental conditions on sex allocation in the black rhinoceros (*Diceros bicornis minor*) population of Mkhuze Game Reserve, South Africa

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Abstract

Influence of environmental conditions on sex allocation in the black rhinoceros (*Diceros bicornis minor*) population of Mkhuze Game Reserve, South Africa

Karine Laflamme-Mayer

The Trivers and Willard hypothesis (1973) states that in a species where reproductive success is more variable in one sex, natural selection could lead to females having the ability to bias the sex allocation of her offspring according to her body condition. The extrinsic modification hypothesis (EMH) recently suggested that offspring sex can also be influenced by environmental conditions experienced by mothers. I investigated the influence of rainfall, population size, vegetation type and burning history, in the year prior to conception and during pregnancy, on sex allocation in the black rhinoceros (*Diceros bicornis minor*) population of Mkhuze Game Reserve, South Africa. I found that increases in rainfall and population size during preconception and pregnancy decrease the probability of having a female calf. The results also show that the frequency of burn and the elapsed time since the last burn of the area used prior to conception have a positive influence on the probability of having a female calf. Vegetation type in the area used by mother rhinos during preconception and pregnancy did not influence sex allocation. In conclusion, I found that environmental conditions may influence sex allocation in the black rhinoceros, thereby supporting the EMH. This knowledge can be applied to improve population structure assessments and management, especially in enclosed reserves, which is essential to maintain the productivity of endangered species.

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Introduction

In mammalian species, several mechanisms have been suggested to influence birth sex ratio according to the hypothesis that parents will increase their fitness by varying the sex ratio of their offspring in relation to the costs and benefits of producing sons and daughters (Clutton-Brock and Iason, 1986), most of them based on the assumption that sons are more costly to produce than daughters (Clutton-Brock *et al.*, 1981). In many polygynous species, parental investment can more strongly affect the fitness of a male offspring compared to a female offspring, since males compete more intensely for access to mates and have a more variable reproductive success (Clutton-Brock and Iason, 1986).

One of the most influential models of sex allocation in mammals is that of Trivers and Willard (1973). The Trivers and Willard (1973) model (TWM) hypothesises that in a species where reproductive success is more variable in one sex, natural selection could lead to females having the ability to bias the sex allocation of her offspring according to her body condition. This model assumes that a female's investment in her offspring can influence its reproductive success and fitness. Accordingly, we would expect that females in good body condition would be more likely to produce male calves where as females in poorer body condition would be more likely to produce female calves (Trivers and Willard, 1973). Although there is strong empirical support for conditional sex allocation in some taxa (e.g. invertebrates; West *et al.*, 2005), the extent to which the TWM can be applied to mammals, particularly ungulates, has been more controversial (Sheldon and West, 2004). There is several discrepancies in the application of this model in various species, such as the roe deer (*Capreolus capreolus*), the red deer (*Cervus elaphus*), the

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moose (*Alces alces*) and the reindeer (*Rangifer tarandus*), in respect to male-biased maternal costs, male-biased maternal care and male-biased offspring phenotypic quality as well as the tendency of high ranking and good condition mothers to have sons (Hewison and Gaillard, 1999). In a species like the black rhinoceros (*Diceros bicornis*) that shows some level of sexual dimorphism (Skinner and Smithers, 1990), where males are polygynous, have a territorial dominance (Adcock, 1994; Hrabar and du Toit, 2005) and show a high variance in reproductive success (Garnier *et al.*, 2001), one would infer that the TWM could apply.

Recently, factors beyond the control of the mother, such as density and climate, were reported to affect offspring sex ratio, leading to the extrinsic modification hypothesis (EMH) (Post *et al.*, 1999). This hypothesis, contrary to the TWM, states that environmental forces affecting the condition of the mother affects sex ratio independently of maternal sex allocation strategies (Post *et al.*, 1999). The relationship between offspring sex ratio and extrinsic factors has been established by multiple previous studies on species such as the black rhino (Hrabar and du Toit, 2005; Berkeley and Linklater, 2010), the red deer (Kruuk *et al.*, 1999; Post *et al.*, 1999; Mysterud *et al.*, 2000) and the reindeer (Weladji and Holand, 2003).

The black rhino has been categorized as a Critically Endangered Species on the IUCN Red list of Threatened Species since 1996 and has been listed on the CITES Appendix 1 since 1977 (Emslie and Brooks, 1999; Amin *et al.*, 2006; IUCN, 2010). As a result of large-scale poaching, the black rhino has suffered a drastic decline of over 90% of its population in the last 60 years to reach its lowest in 1995 with a population size of

2,410 (IUCN, 2010). Since then, with increasing conservation and anti-poaching efforts, populations are steadily recuperating (Amin *et al.*, 2006; IUCN, 2010).

Despite these efforts and the improvement in population numbers, the species remains at a critical level and has become isolated into smaller subpopulations (Hrabar and du Toit, 2005). To alleviate the deleterious impacts of small populations and to optimise their productivity (Foose, 1993), the Rhino Management Group recommends the meta-population management of each rhino subspecies (Foose, 1993; Hrabar and du Toit, 2005; Amin *et al.*, 2006). Translocations between subpopulations are also recommended to minimise negative genetic and demographic effects (Hrabar and du Toit, 2005).

Management and conservation of wild animals require knowledge on demographic and population parameters, including sex ratio, age structure and reproductive status (Mysterud and Ostbye, 2006). The age and sex structure of a population are likely to affect productivity (Caughley, 1977). For polygynous species, as long as there are enough males to mate available females, it is the female component of the population that determines growth rate (Caughley, 1977). Sex ratio is thus an essential factor influencing growth rates and population dynamics of many large mammal populations through its effect on reproductive potential (Okita-Ouma *et al.*, 2009). In the black rhino, skews towards males in calf sex ratios have been observed in both wild and captive populations (Hrabar and du Toit, 2005; Dennis *et al.*, 2007; Linklater, 2007).

The black rhino population of Mkhuze Game Reserve (MGR), South Africa, is a founder population of the *Diceros bicornis minor* subspecies that exhibits a skew in calf sex ratio with a greater proportion of male calves than female calves (1.3:1) born between 1970 and 2007 from identifiable females (Table 1). However, according to the reserve

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management, this population has a positive growth rate that has allowed for multiple removals of individuals for translocations into other subpopulations (unpublished MGR management report). Determining and understanding the factors influencing sex allocation could provide crucial information for the sex ratio management, an essential element for the continued optimal management and productivity of this population.

In subtropical savanna, rainfall has often been used as a proxy for changes in the green biomass (Rasmussen *et al.*, 2006). In this ecosystem, rainfall is known to affect ungulate population dynamics through its influence on the availability of drinking water and its effect on vegetation productivity and heterogeneity (Hrabar and du Toit, 2005; Redfern *et al.*, 2005; Rasmussen *et al.*, 2006; Chamaillé-Jammes and Fritz, 2009; Young *et al.*, 2009). Its effect is particularly significant in arid and semi-arid areas where the availability of water is a major limiting resource subject to large seasonal variations (Guttal and Jayaprakash, 2007). Wet season rainfall controls vegetation growth and the production of food that will be available to herbivores, while dry season rainfall determines the duration of the availability of forage during the period of resource scarcity (Ogutu and Owen-Smith, 2003).

In mammals, population density is also a key factor in regulating population dynamics (Okita-Ouma *et al.*, 2009). In ungulates, density-dependence can lower fecundity, delay puberty and increase mortality (Rachlow and Berger, 1998). Density dependence is known to impact black rhino population performance. Increases in population size reduce resource availability which affects mortality, fecundity and age at maturity (Hrabar and du Toit, 2005). Changes in population size not only affect the intensity at which habitats are used but may also influence which type of habitats are

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used (Young *et al.*, 2009). Furthermore, the impact of population density may be exacerbated in the black rhino because of the unequal access to resources between individuals. The territorial dominance in the black rhino may lead some individuals to restrict access to certain resources (Morgan *et al.*, 2009).

Resource availability is an important factor in mammalian reproduction (Bronson, 1985). The black rhino selects for resources according to the availability and quality of browse (Muya and Oguge, 2000; Morgan *et al.*, 2009) as well as habitat heterogeneity, slope, rockiness and distance to water, roads and fences (Morgan *et al.*, 2009). Black rhinos have a greatly diversified diet (Muya and Oguge, 2000) and are highly selective for both plant species and size class (Emslie and Adcock, 1994). They also have marked preferences for certain resources from burned vegetation (Emslie and Adcock, 1994). Their diet and the chemical composition of their food are also known to vary with rainfall, herbage quality and season (Hall-Martin *et al.*, 1982; Oloo *et al.*, 1994). Individual black rhino variations in habitat use are likely and may lead to differential body condition between females.

In this study, I use the long-term black rhino monitoring data (1970-2007) from MGR to investigate the influence of environmental conditions on sex allocation; thereby testing the EMH. Four factors, rainfall, population size, vegetation type and burning history, have been selected for this study due to their ecological importance in this ecosystem and to the availability of long-term data. The objectives of this study were to assess the influence of rainfall, population size, vegetation type and burning history both prior to conception and during pregnancy, on black rhino sex allocation. These factors are expected to influence the body condition and reproductive capacity of black rhino

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females thereby affecting the sex of their calf, if TWM holds. I predict that increases in rainfall should increase the probability of mothers to have a male calf and decrease the probability of having a female calf. I also predict that increases in population size should decrease the probability of mothers to have a male calf and increase the probability of having a female calf. Finally, I explored the possible impacts of variations in the vegetation types and the burning history in the area used by mother rhinos on sex allocation.

Methods

Study area

Mkhuze Game Reserve (Figure 1) is an enclosed reserve of about 370km^2 located in the KwaZulu-Natal Province of South Africa. The climate is semi-arid with a mean annual rainfall of 664mm and a mean annual temperature of 23.2°C. The rainy season is from October to March and the dry season from April to September. Mkhuze includes black rhino, white rhino (*Ceratotherium simum*), cape buffalo (*Syncerus caffer*), leopard (*Panthera pardus*), elephant (*Loxodonta africana*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), giraffe (*Giraffa camelopardalis*) and many species of antelopes but excludes lion (*Panthera leo*). There are 12 vegetation types in the reserve (Appendix 1), of which the main eight were selected for this study: *Acacia nilotica* low closed woodland, *Acacia* tall open woodland, *Acacia tortillis* low open woodland, dry closed woodland, low thicket, open woodland, river floodplains and seasonal streams and *Terminalia sericea* savanna. The remaining four vegetation types are freshwater lakes and pans, Lebombo wooded grassland, palm savanna and riverine forest. Being an

important management tool, burning has been used extensively in the reserve (Mulqueeny, 2005). The burning is patchy and can occur throughout the reserve and its distribution varies from year to year.

Black rhino data

Long-term black rhino monitoring data performed by Ezemvelo KwaZulu-Natal Wildlife (EKZN Wildlife), including field records, calving records and population performance reports, such as population growth rates from 1997 to present and population size estimates starting from 1990, were made available by the conservation manager and section rangers of the reserve. The monthly rainfall (mm) records from 1960 to 2008 were made available by the reserve ecologist. The digital vegetation map of the reserve has been provided by iSimangaliso Wetland Park Authority. The digital burning history maps from 1963 to 2007 were provided by EKZN Wildlife.

The black rhino monitoring has allowed for the compilation of sighting records of identified animals providing the location of individuals in various formats of different levels of precision, from GPS points to area names. Despite the discrepancy in the precision, it was decided to include all location data in the analyses since less precise data accounted for about half of the records. The sighting records provided specific distribution points for each specific identified female. A distribution map for each female was created using ArcGIS 9.3 Geographic Information System (ESRI, California, USA) and overlapped with the vegetation and burning maps. For each precise location point, an area of 500m in radius was created around the center point. This was used to determine both the vegetation type and burning history at the area of sighting. For each less precise

area name type location points, the vegetation type and burning history of the whole area was extracted. Vegetation type was determined by recording the proportion for each type of vegetation present at the location of sighting. The burning history at each sighting location provided information on the proportion of the area that has burned the same year of the sighting (T_0), the proportion of the area that has burned the year previous to the sighting (T_{-1}), the frequency of burn of the area of sighting (number of times an area has burned since 1963) and elapsed time (number of days) since the last burn occurred at the area of sighting.

Field records have also allowed me to monitor the calving of females. When a female is seen with a calf, field records provide information on the estimated age of the calf and its sex. I was thus able to compile calving records of identifiable females including the estimated date of birth of her calves and their sex. The estimated date of birth of calves allowed me to estimate the date of conception, considering that gestation in black rhinos is of 15 months (Skinner and Smithers, 1990).

The sighting information of females has then been classified into two time intervals, pregnancy and preconception, depending whether the sighting occurred while the female was pregnant or while she was within one year preceding conception. The total rainfall and the mean population size were then calculated for each time interval associated with each calf.

Overall, the data includes 101 calves, 44 female calves and 57 male calves, from 41 mother rhinos with births from 1970 to 2007 (Table 1). There are a total of 314 sightings of females while pregnant and 231 sightings of females while in preconception.

Statistical analyses

I used the generalised linear mixed model (GLIMMIX procedure in SAS version 9.2; SAS 2008) with a logit link function, since our response variable was binomial (male calf; female calf), to analyse the respective influence of population size, rainfall, vegetation type and burning on the probability of producing a "female" calf, with "mother rhino identity" as a random term. The data from identified mother rhinos with identified calves was used to perform two separate sets of models, one during preconception and the other during pregnancy. More specifically, two GLIMMIX models were completed with rainfall as the predictor to determine its influence on calf sex during preconception and during pregnancy. Two models were also performed with population size as the predictor to determine its influence on calf sex during preconception and during pregnancy. Similarly, two models were performed for all four burn history variables to determine the influence of burning history on calf sex during preconception and pregnancy. The burning history variables were the proportion of burn at T_0 (year of sighting), the proportion of burn at T_{-1} (year prior to sighting), the elapsed time since last burn and the frequency of burn. When none of the predictor variable was significant, new analyses were performed using the burning history variables individually (i.e. one variable at a time) in which case a Bonferroni correction for multiple comparisons was applied with a significance level of 0.0125 since we had 4 burning variables separately (Sokal and Rohlf, 2000). Lastly, two sets of models were performed to determine the influence of the proportion of the vegetation type used by the mother rhino during preconception and during pregnancy on the sex of her calf. Similarly, when none of the predictor variable was significant, new analyses were performed using each vegetation

type data separately (i.e. one variable at a time), again applying a Bonferroni correction for multiple comparisons with a significance level of 0.00625 since we had 8 vegetation types (Sokal and Rohlf, 2000). The denominator degrees of freedom for the GLIMMIX models were calculated using the Kenward-Rogers approximation (Littell *et al.*, 2006). All estimates are presented ± SE. All the analyses were performed in SAS 9.2 (SAS 2008), and a significance level of 5% was adopted.

Results

Effect of rainfall and population size on sex allocation

Sex allocation was significantly influenced by the amount of rainfall during preconception ($F_{1,99} = 4.05$, $P = 0.047$) and during pregnancy ($F_{1,99} = 5.06$, $P = 0.027$). The probability that a mother rhino gave birth to a female calf was negatively influenced by the amount of rainfall during preconception (Table 2; Figure 2A) and pregnancy (Table 2; Figure 2B). The variance components of the random term "mother identity" were zero in both models, and the random term was therefore removed.

Sex allocation was also significantly influenced by population size both during the preconception ($F_{1,74} = 4.79$, $P = 0.032$) and during pregnancy ($F_{1,74} = 6.61$, $P = 0.012$). There was a clear tendency for females to produce more female offspring as the population size decreased both during preconception (Table 2; Figure 3A) and pregnancy (Table 2; Figure 3B). The variance components of the random terms "mother identity" were 0.2586 ± 0.6092 and 0.1986 ± 0.6200 for preconception and pregnancy time interval respectively.

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Effect of vegetation type on sex allocation

When taken together, there was no evidence that vegetation type influenced sex allocation. Indeed, the probability that a female produced a male or a female calf was not significantly influenced by the proportion of any of the eight main vegetation types used by the mother during both preconception and pregnancy (all $P > 0.05$; Table 3). Similarly, when taken individually (i.e. one vegetation type at a time), there was no relationship found between the proportion of vegetation type used by the mother rhino during preconception and pregnancy and the probability of producing a female calf (all $P > 0.00625$; Table 4 and Table 5).

Effect of burning history on sex allocation

When taken together, there was no evidence that burning history influenced calf sex allocation (all $P > 0.05$; Table 6). However, when taken individually, two effects of the burning history were found to influence calf sex allocation during preconception but no effect was found during pregnancy. The frequency of burn of the area used by mother rhinos during preconception showed a significant ($F_{1,220} = 8.55, P = 0.004$) influence on the sex of her calf. An increase in the frequency of burn of the area used by mother rhinos lead to an increase in the probability of the calf being female while a decrease in frequency of burn increases the probability of the calf being a male (Table 7; Figure 4). The elapsed time since last burn also had a near significant ($F_{1,220} = 5.83, P = 0.017$), and positive influence (Table 7; Figure 5) on the probability of having a female calf.

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Discussion

Overall, I found that calf sex allocation could be influenced by variations in environmental conditions during preconception and/or during pregnancy, thereby supporting the EMH. I predicted that if the TWM holds, the probability for a female black rhino to produce a male offspring will increase with increasing rainfall and increase with decreasing population size, as a result of the female being in a greater body condition. The results only support the first prediction i.e. increases in rainfall increased the probability of having a male calf. Similarly, because of the variation in vegetation type available to female rhinos, I expected the proportion of the different vegetation types used by female rhinos to affect sex allocation, but found no relationship. Lastly, because of the possible impacts of burning on black rhino resources, I expected that the probability of a female black rhino to produce a female calf would be affected by the burning history. I found that both the frequency of burn and the elapsed time since the last burn of the area used by mother rhinos during preconception have an effect on sex allocation.

In ungulates, several studies have identified many potential factors influencing sex allocation including intergenerational effects in white-tailed deer (*Odocoileus virginianus*) (Monteith *et al.*, 2009), social rank and maternal behavioural dominance in bighorn sheep (*Ovis canadensis*) (Blanchard *et al.*, 2005) and nutritional stress brought on by extrinsic effects in red deer (Kruuk *et al.*, 1999; Post *et al.*, 1999; Mysterud *et al.*, 2000), reindeer (Weladji and Holand, 2003) and black and white rhino (Hrabar and du Toit, 2005; Linklater, 2007; Berkeley and Linklater, 2010).

A study by Linklater (2007) on translocated female black and white rhinos suggests that at least two sex allocation mechanisms could influence birth sex ratio depending on the timing of the effect during pregnancy. Stress caused to a female black rhino could lead to both a male or female calf. Stress occurring shortly prior to conception would induce female-biased conceptions (Linklater, 2007). A female-biased birth sex ratio can also be induced by stress to the mother during mid to late gestation which could lead to higher male embryo death (Kruuk *et al.*, 1999; Forsyth *et al.*, 2004; Linklater, 2007).

Both changes in maternal condition and its timing relative to gestation are strong influences of calf sex (Rachlow and Berger, 1998; Linklater, 2007). However, maternal condition may not necessarily be easy to assess since it may not only encompass the female's total body size and body fat (Rachlow and Berger, 1998) but may also be better represented by a female's relative condition compared to the other females in the population (Schwanz *et al.*, 2010).

In the Mkhuze black rhino population, the amount of rainfall during preconception and pregnancy were found to influence calf sex. The positive relationship between rainfall and the probability of having a male calf suggests that rainfall can affect vegetation production and food resources available to the black rhinos which can lead to changes in the body condition of females, ultimately affecting calf sex. My results corresponds to previous findings that rainfall influences population dynamics and the body condition of individuals (Owen-Smith, 1990; Ogutu and Owen-Smith, 2003; Hrabar and du Toit, 2005; Ogutu and Owen-Smith, 2005; Rasmussen *et al.*, 2006; Berkeley and Linklater, 2010). For instance, the study of Hrabar and du Toit (2005) on a black rhino

population in Pilanesberg National Park in South Africa found similar results showing that the percentage of male calves born increased with increasing rainfall and the inter-calving interval decreased with an increasing rainfall. Rasmussen *et al.* (2006) have determined that rainfall and normalized differential vegetation index (NDVI) can effectively be used to measure vegetation productivity to predict conception rates in an elephant population of Kenya, clearly showing the potential impact of rainfall on the reproductive potential of females.

Population density, especially in an enclosed reserve, can influence resource availability and population growth (Rachlow and Berger, 1998; Morgan *et al.*, 2009; Young and van Aarde, 2010). In black rhinos, population density is known to influence habitat and forage selection (Morgan *et al.*, 2009) as well as population dynamics (Rachlow and Berger, 1998; Patton *et al.*, 2008). Many previous studies on the impacts of population density in black rhinos (Hitchins and Anderson, 1983; Rachlow and Berger, 1998; Birkett, 2002; Birkett and Stevens-Wood, 2005; Heilmann *et al.*, 2006) have lead to the prediction that an increase in population size would lead to an increase in the probability of having a female calf through its negative effect on food resources and maternal condition. However, I found the opposite in the black rhino population of MGR as the probability of producing a female calf was negatively related to population size during both preconception and pregnancy.

This result may be due to the fact that even at its highest population size, the population density of the reserve reaches 0.22 rhinos/km^2, which is not considered a particularly high density for black rhinos in this type of environment (Conway and Goodman, 1989; Hrabar and du Toit, 2005). Depending on the quality of the habitat,

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black rhino population density can range from 0.04 rhinos/km^2 to 1.6 rhinos/km^2 (Tatman et al., 2000). This suggests that the resources of MGR could sustain this increase in population size if there is a suitable amount of cover, food resources and water distribution (Conway and Goodman, 1989). Furthermore, despite incomplete information, the translocation history of the reserve seems to show that the period of higher population size from 1997 to 2000 coincides with an absence of removals, which subsequently occur yearly (unpublished MGR management report). Removals may disrupt the social structure of a population, lead to shifts in home ranges, create conflict between individuals and may ultimately decrease population productivity (Reid et al., 2007; Patton et al., 2008). Thus, my results may not necessarily represent a positive relationship between population size and the probability of having a male calf, but could rather represent the influence of a period of greater social stability caused by the absence of removals on the tendency of female rhinos to produce male calves.

Habitat use in black rhinos is highly dependent on the location of their home range which is heavily influenced by social interactions and varies according to the age and sex of individuals (Skinner and Smithers, 1990; Lent and Fike, 2003; Reid et al., 2007). Black rhinos are not strictly territorial but they tend to stay within an established home range (Skinner and Smithers, 1990). Female rhinos generally remain within their home range but they can be tolerated in the home range of other females and males (Adcock, 1994; Lent and Fike, 2003). The location of the home range of a female can influence her access to food resources (Skinner and Smithers, 1990) which in turn affects her productivity (Bronson, 1985). Black rhinos are highly selective in their food for both species and size class (Emslie and Adcock, 1994). They have a very complex diet which

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can be represented by the discrepancy in the results of studies which conclude that rhinos do not maximise nutrient intake or minimise fibre intake (van Lieverloo *et al.*, 2009) but can also select for quality and not quantity when feeding on *Euphorbias* (Heilmann *et al.*, 2006). They feed according to their preferences which shift with season, habitat, and burning history (Emslie and Adcock, 1994; Oloo *et al.*, 1994). In general, many factors can affect black rhino habitat selection such as the distribution of highly preferred food resources, such as *Acacias* and *Euphorbias* (Emslie and Adcock, 1994; Heilmann *et al.*, 2006), the location of water and cover (Mukinya, 1973; Tatman *et al.*, 2000) and burning history (Emslie and Adcock, 1994).

In MGR, the proportion of each vegetation type used by mother rhinos could represent individual resource preference. In this study, it was thus expected that the proportion of each vegetation type in the area used by females would vary, causing differential body condition, consequently affecting calf sex allocation. However, my results showed no significant relationship amongst the eight main vegetation types used by mother rhinos during preconception and pregnancy on the probability of having a female calf. Although the results on the influence of vegetation types on calf sex were inconclusive, they provide clues as to their possible impact and offer a direction for further research. Since resource use by black rhinos is highly diversified and selective (Muya and Oguge, 2000), this study might have used measures of vegetation types at a scale that may be too broad to effectively detect the more subtle differences between resource use by the females. As it has been suggested by Morgan *et al.* (2009), the scale at which we make the assessment of resource use by an individual should represent the scale of selection of the species. Thus, a more precise measurement of habitat use by

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females, including diet, a quantitative assessment of habitat quality and the home range structure of the population, may be needed to accurately determine its influence on sex allocation.

Burns are an effective tool in habitat management that is widely used in game reserves in South Africa (Tainton, 1999; Mulqueeny, 2005), including MGR. Burning is used to burn off unpalatable vegetation, control bush encroachment, stimulate growth, contribute to fire control by reducing fuel load and maintain grass cover for the conservation of soil and water (Tainton, 1999; Mulqueeny, 2005). My results indicate a positive relationship between the likelihood of having a female calf and both the frequency of burn and the elapsed time since the last burn in the area used by mother rhinos during preconception. This suggests that in MGR, areas that have burned less often and that have burned more recently may promote black rhino habitat which could lead to females having a greater body condition, thus a greater tendency of having a male calf. It is hypothesised that black rhinos show a preference for burned trees because fire may alter the smell and taste of twigs, denature chemical composition and decrease the physical defence of plants (Emslie and Adcock, 1994). In areas that are prone to frequent burns, light to medium severity of burns are more beneficial to the habitat of black rhinos compared to highly intense burns (Emslie and Adcock, 1994). Burning can have both positive and negative impacts on the habitat of black rhinos depending on the burning strategy, rainfall and grazing and browsing pressure (Goodman, 1990; Bond and Keeley, 2005; Mills and Fey, 2005; Mulqueeny, 2005). The burning history of an area can affect the size of the preferred black rhino food species, the level of grass interference in the habitat, the level of unpalatable and palatable food and the quantity and diversity of

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woody plants (Emslie and Adcock, 1994; Bond and Keeley, 2005; Mills and Fey, 2005; Mulqueeny, 2005). In MGR, burning has been used extensively for many decades. It was thus expected in this study that the burning history of the area used by female rhinos could affect sex allocation, via its wide range of possible impacts on black rhino resources.

In an enclosed reserve, effective management is crucial to maintain the productivity of endangered populations. In MGR, the black rhino is considered a priority species, making its sound management and planning utmost important. This study provides insights on the influence of rainfall, population size, vegetation use and burning history on sex allocation that can benefit both the short and long term management of this and other similar populations. Although rainfall is out of our control, being able to predict its effect on sex allocation can improve population structure assessments. Population size, vegetation and burning are all factors that can be controlled by managers according to their respective influence on calf sex. These factors could be used as management tools to modify the sex structure of populations to maximise productivity and optimise genetic diversity, and which could provide a complement or alternative to translocation and hunting, depending on the objective. Thus, increased knowledge on sex allocation improves population and meta-population management of the black rhino.
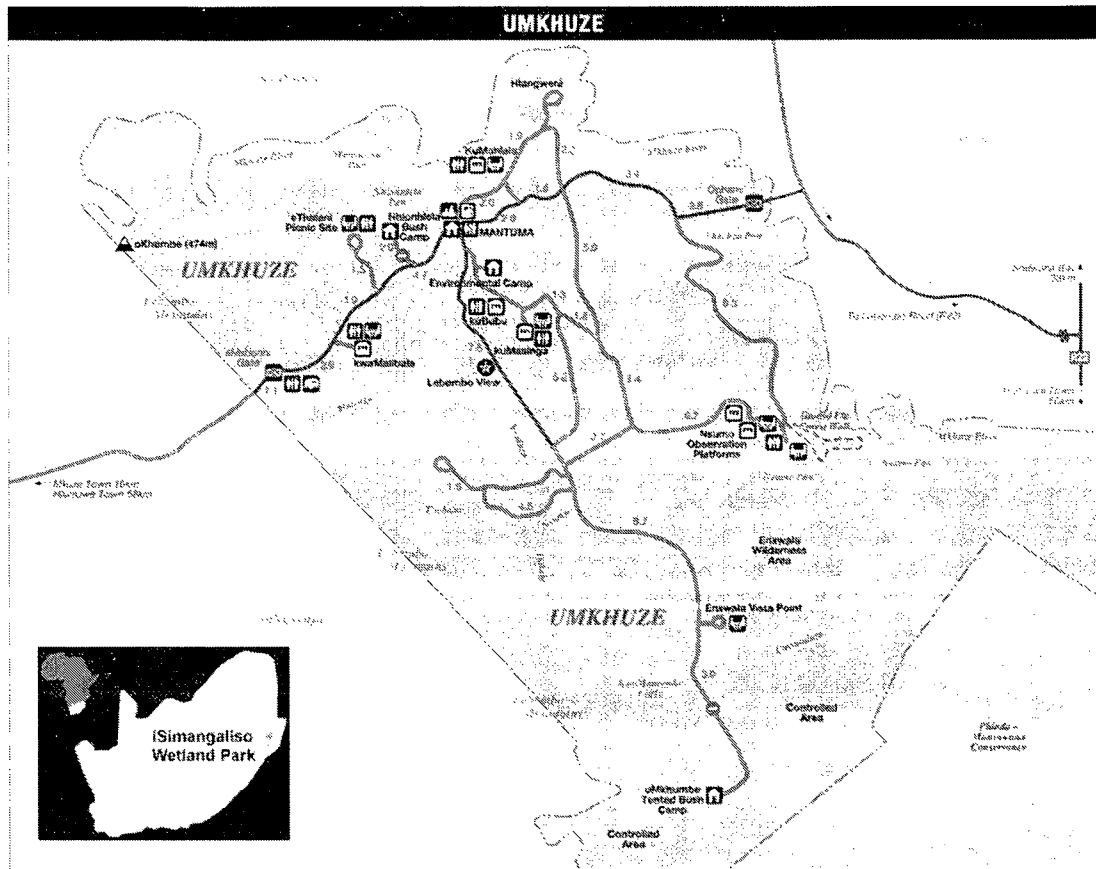
Figure 1. Map of Mkhuze Game Reserve and its location in South Africa (scale not available; www.isimangaliso.com/)
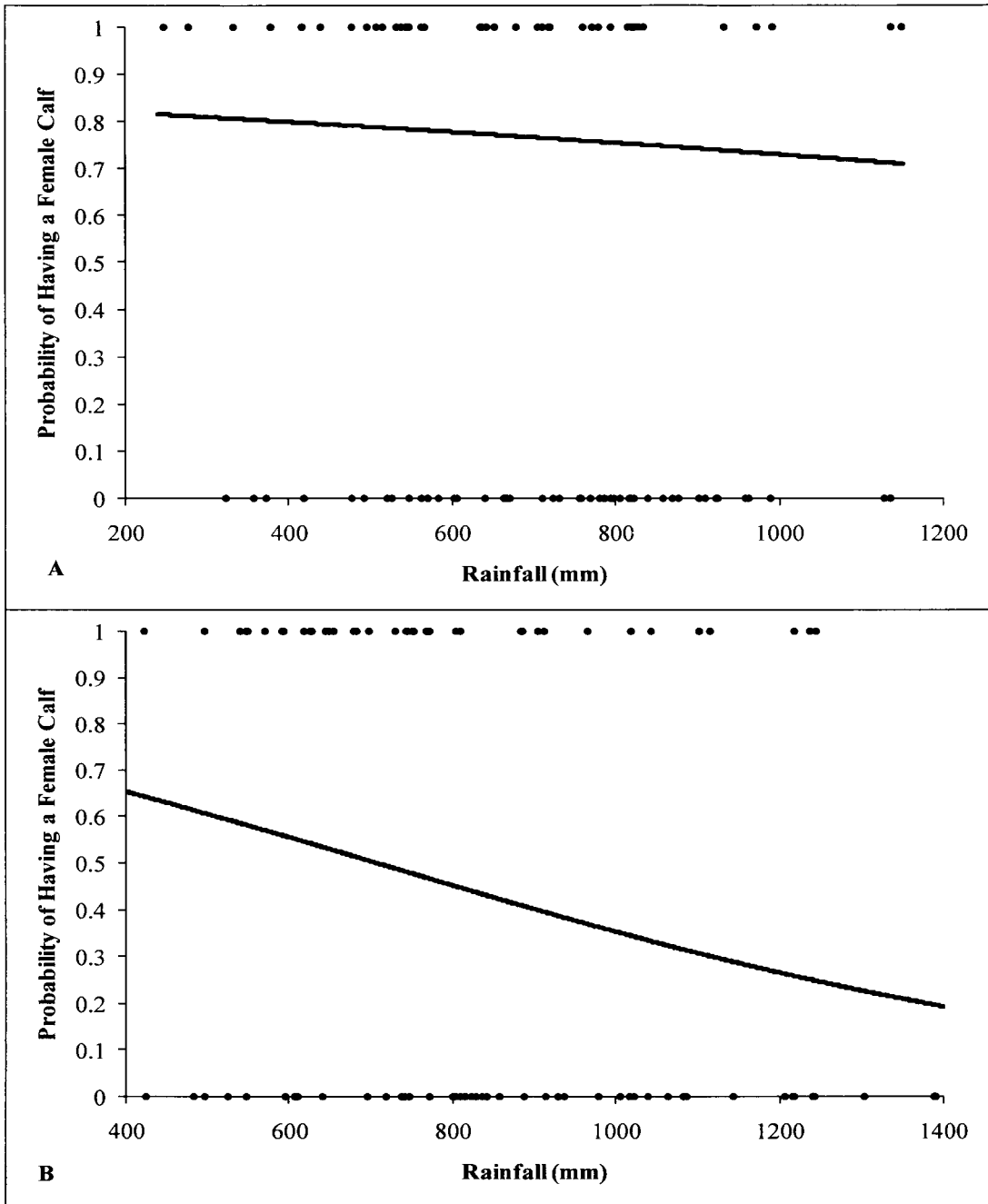
Figure 2. Logistic regression curve representing the effect of rainfall (mm) during A)

preconception (Estimate = -0.0007, P = 0.047) and B) pregnancy (Estimate = -0.0021, P

= 0.027), on the probability of having a female calf. The points represent the observed

values.
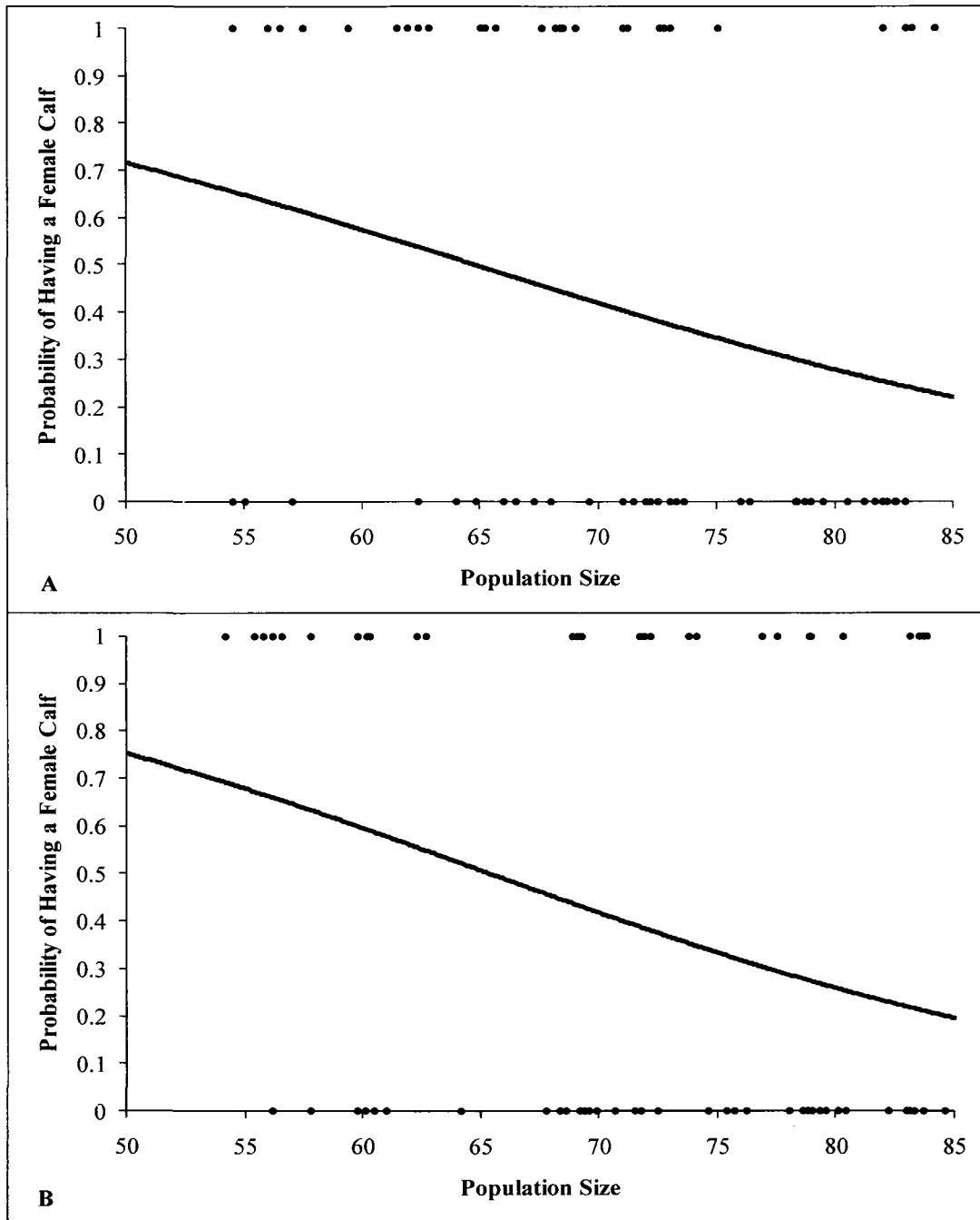
Figure 3. Logistic regression curve representing the effect of population size during A) preconception (Estimate = -0.063, P = 0.032) and B) pregnancy (Estimate = -0.072, P = 0.012) on the probability of having a female calf. The points represent the observed values.

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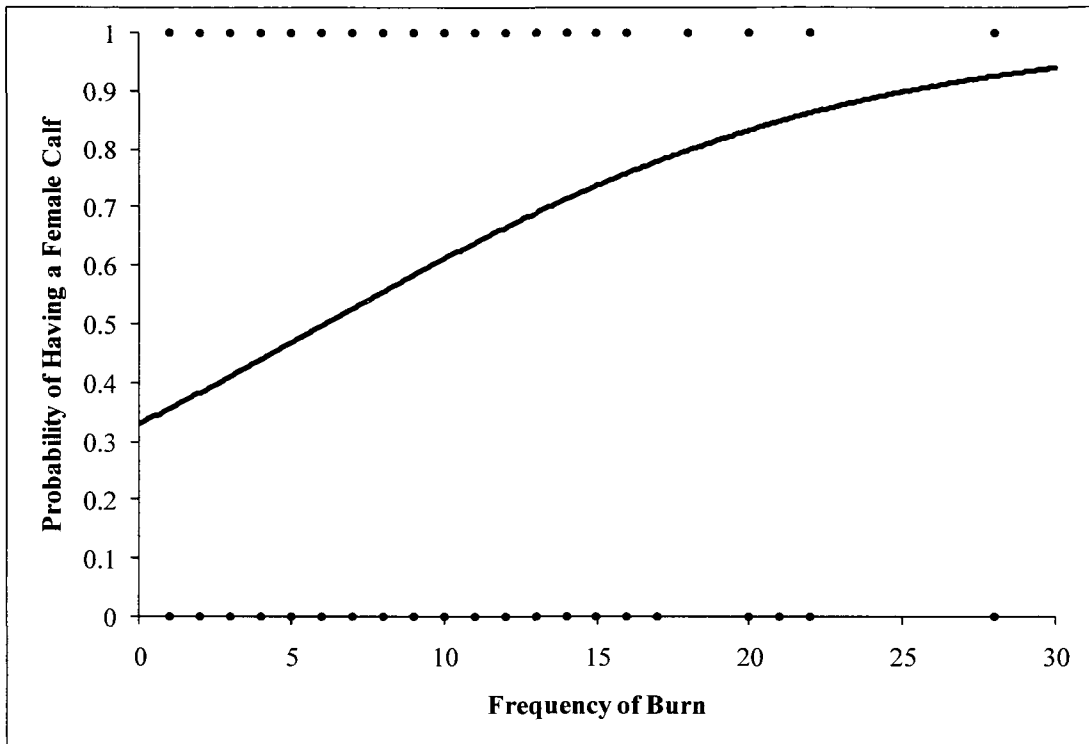
Figure 4. Logistic regression curve representing the effect of the frequency of burn

(number of times an area has burned since 1963) of the area used by the mother rhino

during preconception on the probability of having a female calf (Estimate = 0.1163, P =

0.004). The points represent the observed values.
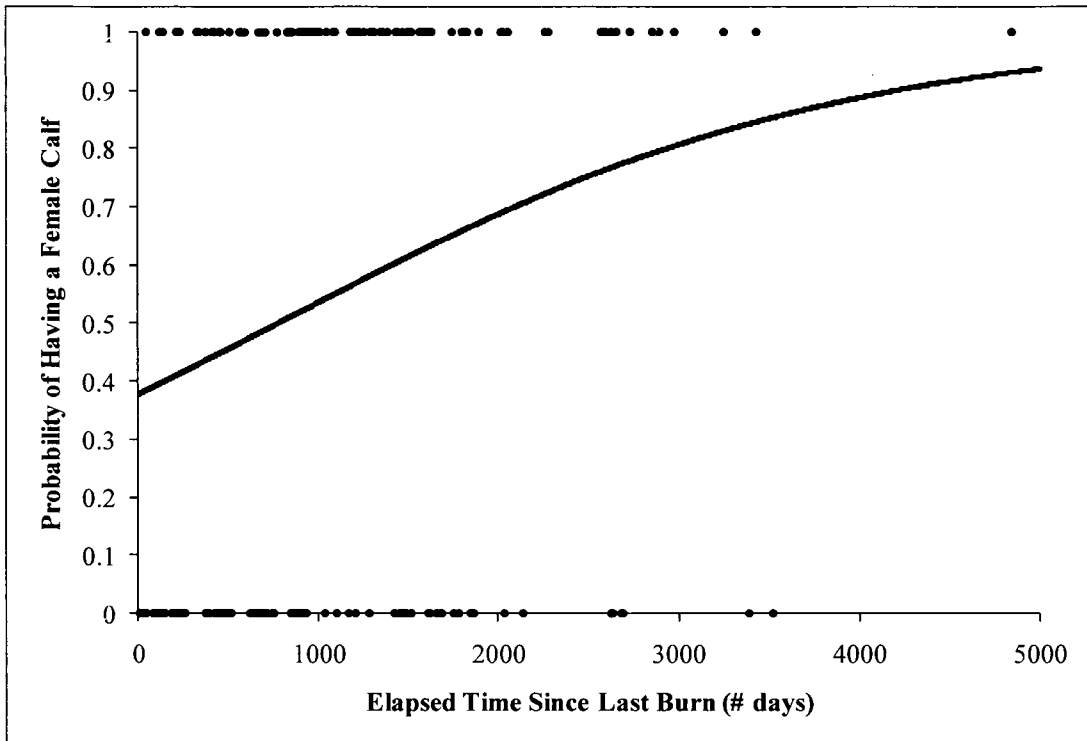
Figure 5. Logistic regression curve representing the effect of the elapsed time (# days) since the last burn of the area used by the mother rhino during preconception on the probability of having a female calf (Estimate = 0.0006, P = 0.017). The points represent the observed values.

Table 1. Number of known male and female calves born from identified mother rhinos per year

Year	Male Calves	Female Calves
1970	1	0
1979	0	1
1981	0	1
1982	0	1
1984	1	1
1985	0	1
1986	1	0
1987	0	2
1988	0	2
1989	3	3
1990	5	2
1991	1	0
1992	3	2
1993	4	3
1994	4	2
1995	4	2
1996	2	0
1997	4	4
1998	4	0
1999	0	1
2000	5	1
2001	3	0
2002	3	1
2003	2	1
2004	1	3
2005	2	4
2006	0	3
2007	4	3
Total	**57**	**44**

Table 2. Parameter estimates, standard errors (SE) and P-values from the generalised linear mixed models describing the effect of rainfall and population size during preconception and pregnancy on calf sex. The analyses are modeling the probability that the calf sex is "female". "Mother rhino identity" was entered as a random term in the models.

Effect	Estimates	SE	P-Value
Preconception			
Intercept	1.6440	0.9607	0.0902
Rainfall	-0.0007	0.0003	**0.0468**
Intercept	4.0715	2.0492	0.0507
Population size	-0.0628	0.0287	**0.0319**
Pregnancy			
Intercept	1.4718	0.7881	0.0648
Rainfall	-0.0021	0.0009	**0.0267**
Intercept	4.6877	1.9947	0.0214
Population size	-0.0717	0.0279	**0.0122**

Table 3. Parameter estimates, standard errors (SE) and P-values from the generalised linear mixed models describing the effect of the proportion of each vegetation type used by the mother rhino during preconception and pregnancy on calf sex. The analyses are modeling the probability that the calf sex is "female". "Mother rhino identity" was entered as a random term in the models.

Vegetation Type	Estimates	SE	P-Value
Preconception			
Intercept	0.5456	1.1032	0.6214
Acacia nilotica low closed woodland	1.9938	2.3606	0.3992
Acacia tall open woodland	-0.6729	1.0731	0.5313
Acacia tortillis low open woodland	-0.9869	1.5273	0.5188
Dry Closed Woodland	-0.5250	1.2028	0.6629
Low Thicket	-0.5229	1.3633	0.7017
Open woodland	0.0567	1.4033	0.9678
River floodplains and seasonal streams	1.9053	1.8699	0.3093
Terminalia sericea savanna	-2.0056	1.5164	0.1873
Pregnancy			
Intercept	-0.4292	1.0005	0.6688
Acacia nilotica low closed woodland	-1.6916	2.8533	0.5537
Acacia tall open woodland	0.1050	0.8312	0.8996
Acacia tortillis low open woodland	0.5433	1.1518	0.6375
Dry Closed Woodland	-0.1123	1.0698	0.9165
Low Thicket	1.2395	1.3061	0.3434
Open woodland	-1.6313	1.9244	0.3973
River floodplains and seasonal streams	-1.2549	1.5326	0.4135
Terminalia sericea savanna	1.2522	1.1294	0.2684

Table 4. Parameter estimates, standard errors (SE) and P-values from the generalised linear mixed models describing the individual effect of the proportion of each vegetation type used by the mother rhino during preconception on calf sex. The analyses are modeling the probability that the calf sex is "female". "Mother rhino identity" was entered as a random term in the models.

Vegetation Type	Estimates	SE	P-Value
Intercept	0.1295	0.5243	0.8075
Acacia nilotica low closed woodland	2.1350	2.1642	0.3249
Intercept	0.3452	0.5366	0.5266
Acacia tall open woodland	-0.4009	0.5312	0.4512
Intercept	0.2022	0.5103	0.6963
Acacia tortillis low open woodland	0.3446	1.0741	0.7486
Intercept	0.2712	0.5376	0.6188
Dry Closed Woodland	-0.2113	0.7157	0.7681
Intercept	0.2334	0.5156	0.6555
Low Thicket	-0.1194	0.9418	0.8992
Intercept	0.1786	0.5070	0.7285
Open woodland	0.9895	1.0204	0.3332
Intercept	0.0169	0.5376	0.9752
River floodplains and seasonal streams	2.7459	1.3799	0.0478
Intercept	0.3160	0.5106	0.5433
Terminalia sericea savanna	-1.6713	1.1013	0.1305

Table 5. Parameter estimates, standard errors (SE) and P-values from the generalised linear mixed models describing the individual effect of the proportion of each vegetation type used by the mother rhino during pregnancy on calf sex. The analyses are modeling the probability that the calf sex is "female". "Mother rhino identity" was entered as a random term in the models.

Vegetation Type	Estimates	SE	P-Value
Intercept	-0.2867	0.6154	0.6459
Acacia nilotica low closed woodland	-1.6969	2.6239	0.5183
Intercept	-0.3402	0.6076	0.5807
Acacia tall open woodland	-0.0596	0.4653	0.8981
Intercept	-0.3604	0.5928	0.5495
Acacia tortillis low open woodland	0.0507	0.8089	0.9500
Intercept	-0.3038	0.6380	0.6379
Dry Closed Woodland	-0.1858	0.7756	0.8108
Intercept	-0.4828	0.6169	0.4418
Low Thicket	1.0832	1.0605	0.3078
Intercept	-0.3068	0.5990	0.6137
Open woodland	-1.8776	1.7217	0.2763
Intercept	-0.2863	0.5994	0.6376
River floodplains and seasonal streams	-1.4172	1.2883	0.2722
Intercept	-0.4340	0.6057	0.4813
Terminalia sericea savanna	1.1974	0.8060	0.1384

Table 6. Parameter estimates, standard errors (SE) and P-values from the generalised

linear mixed models describing the effect the burning history (proportion that has burned

the same year of the sighting (T_0), proportion that has burned the year previous to the

sighting (T_{-1}), elapsed time since last burn and frequency of burn) of the area used by the

mother rhino during preconception and pregnancy on calf sex. The analyses are modeling

the probability that the calf sex is "female". "Mother rhino identity" was entered as a

random term in the models.

Burning History	Estimates	SE	P-Value
Preconception			
Intercept	-1.4798	1.2149	0.2283
Proportion of burn at T_0	0.0027	2.8654	0.9992
Proportion of burn at T_{-1}	1.3730	1.5591	0.3817
Elapsed time since last burn	0.0005	0.0005	0.3299
Frequency of burn	0.0424	0.0952	0.6576
Pregnancy			
Intercept	-1.3351	1.2219	0.2779
Proportion of burn at T_0	1.2795	1.7049	0.4545
Proportion of burn at T_{-1}	-2.6378	1.5671	0.0951
Elapsed time since last burn	0.0005	0.0006	0.3707
Frequency of burn	0.0911	0.1192	0.4463

Table 7. Parameter estimates, standard errors (SE) and P-values from the generalised

linear mixed models describing the individual effect the burning history (proportion that

has burned the same year of the sighting (T_0), proportion that has burned the year

previous to the sighting (T_{-1}), elapsed time since last burn and frequency of burn) of the

area used by the mother rhino during preconception and pregnancy on calf sex. The

analyses are modeling the probability that the calf sex is "female". "Mother rhino

identity" was entered as a random term in the models.

Burning History	Estimates	SE	P-Value
Preconception			
Intercept	-0.2188	0.5642	0.7024
Proportion of burn at T_0	-1.3796	2.5378	0.5883
Intercept	0.1163	0.4651	0.8052
Proportion of burn at T_{-1}	-1.2389	0.7396	0.0956
Intercept	-0.4914	0.5615	0.3880
Elapsed time since last burn	0.0006	0.0003	**0.0166**
Intercept	-0.7064	0.6128	0.2574
Frequency of burn	0.1163	0.0398	**0.0038**
Pregnancy			
Intercept	-0.5599	0.5020	0.2778
Proportion of burn at T_0	0.8919	1.1296	0.4312
Intercept	-0.3681	0.6443	0.5734
Proportion of burn at T_{-1}	-0.6407	0.7088	0.3670
Intercept	-0.7378	0.6093	0.2358
Elapsed time since last burn	0.0003	0.0002	0.1160
Intercept	-0.3219	0.6563	0.6269
Frequency of burn	-0.0066	0.0456	0.8844

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Appendix 1. Description of the vegetation types present in Mkhuze Game Reserve as provided by iSimangaliso Wetland Park Authority.

Acacia nilotica low closed woodland

This vegetation type is usually found on plains with sandy loam to clayey soils with impervious subsoils. It commonly includes *Acacia nilotica, Acacia grandicornuta, Acacia tortilis, Acacia nigrescens, Ziziphus mucronata, Sclerocarya birrea* and *Dichrostachys cinerea.*

Acacia tall open woodland

This vegetation type occurs on red loamy soils. It is dominated by *Acacia nigrescens* which reaches up to 12 meters in height. Other common species include *Sclerocarya birrea, Dichrostachys cinerea, Ozoroa paniculosa, Acacia tortilis, Dombeya rotundifolia* and *Gymnosporia buxifolia.*

Acacia tortillis low open woodland

This vegetation type is found on the plains east of the Lebombo Mountains. It is dominated by *Acacia tortillis* but it also includes the trees *Spirostachys africana, Schotia brachypetala* and *Acacia nilotica.*

Dry closed woodland

This vegetation type is commonly located in low areas along drainage lines and on soils with high clay content. The dominant tree species have an average height of 8 meters and consist of *Spirostachys africana, Berchemia zeyheri, Mystroxylon aethiopicum, Apodytes dimidiata, Ziziphus mucronata, Sideroxylon inerme, Schotia brachypetala, Acacia grandicornuta, Acacia luederitzii* and *Strychnos decussata.*

Freshwater lakes and pans

The Mkuze floodplain includes permanent, semi-permanent and seasonal pans. In summer, regular flooding and inundation regulate the pans. The salinity of the pans often increases in winter where as the summer floods flushes out the salt and provides nutrient rich silt.

Lebombo wooded grassland

This vegetation type is usually found on shallow and sandy rhyolitic soils on the Lebombo Mountains. It mostly includes sour grasses of low nutritional value and the tree species *Terminalia phanerophlebia, Combretum apiculatum, Acacia nigrescens* and *Lannea discolor.*

Low thicket

This vegetation type occurs on flat poorly drained lowland of clay soils. It consists of dense thickets including tall shrubs and short trees. The dominant species are *Euclea divinorum, Acacia luederitzii* and *Acacia grandicornuta.* The other common woody species found in low thickets include *Acacia nilotica, Spirostachys africana, Ziziphus mucronata, Acacia nigrescens* and *Euclea undulata.*

Open woodland

This vegetation type occurs on the rhyolitic rocky slopes of the Lebombo Mountains. It consists of a mixture of wooded grassland, woodland and patches of forest. It usually include trees of 6 to 7 meters in height of the species *Acacia nigrescens, Combretum apiculatum, Acacia burkei, Acacia caffra, Combretum molle, Combretum zeyheri, Lannea discolor* and *Pterocarpus rotundifolius.*

Palm savanna

This vegetation type is found on pallid sands. It includes a variety of tree species, it has a well-developed grass layer and it is dominated by two palm species, *Hyphaene coriacea* and *Phoenix reclinata.*

River floodplains and seasonal streams

The characteristics of this vegetation type vary according to the relative period of exposure to seasonal flooding. A riverine or fringing forest dominated by *Acacia xanthophloea* and *Ficus sycomorus* can be found in the protected areas of the Mkuze River and its tributaries. Floodplains experiencing frequent seasonal short-duration floods and the edges of pans are characterized by stands of *Acacia xanthophloea* and a dense cover of grasses. The more marshy areas that experience long summer floods and short dry winters are dominated by grass and sedge. Stands of reeds, mainly *Phragmites australis,* are found in the wettest areas of the reserve.

Riverine forest

This vegetation type is found along the Mkuze River and its tributaries. It is dominated by the trees *Ficus sycomorus* that can reach up to 25 meters in height. The other main species present are *Acacia xanthophloea, Rauvolfia caffra, Syzygium guineense, Cordyla africana, Trichilia emetica, Trichilia dregeana* and *Ekebergia capensis*.

***Terminalia sericea* savanna**

This vegetation type is an open to closed deciduous woodland that occurs on grey to reddish distric sandy soils. The canopy ranges from 5 to 12 meters in height. The main species are *Terminalia sericea, Sclerocarya birrea, Acacia burkei, Acacia robusta,*

Strychnos madagascariensis, Strychnos spinosa, Combretum molle, Combretum zeyheri,

Garcinia livingstonei, Peltophorum africanum, Afzelia quanzensis and *Albizia versicolor.*