Influence of environmental conditions on sex allocation in the black rhinoceros population of Mkhuze Game Reserve, South Africa

Robert B. Weladji* and Karine Laflamme-Mayer

Department of Biology, Concordia University, 7141 Sherbrooke St. West, Montreal, QC H4B 1R6, Canada

Abstract

According to the Trivers–Willard and local resource competition (LRC) hypotheses, for species where reproductive success is more variable in one sex, natural selection may lead to a bias in sex allocation of a female's offspring according to her body condition. The extrinsic modification hypothesis (EMH) suggests that offspring sex can also be influenced by environmental conditions experienced by mothers. We investigated the influence of rainfall, El Niño-Southern Oscillation (ENSO), population size and burning, in the year before conception and during pregnancy, on sex allocation in the black rhinoceros population of Mkhuze Game Reserve, South Africa, during 1970–2007. Females were more likely to have a male calf as rainfall during pregnancy increased, supporting the Trivers–Willard hypothesis. Also, the probability of having a male calf increased with population size, supporting the LRC hypothesis. Calf sex allocation was not influenced by ENSO. In conclusion, local environmental conditions may influence sex allocation in black rhinoceros, thereby supporting the EMH. Burning and population size may influence sex allocation in black rhinoceros, and yet can be manipulated by managers. Thus, this knowledge can be applied to improve population structure assessments and management regimes, especially in enclosed reserves, which is essential to maintain endangered species' productivity.

Key words: conservation, *Diceros bicornis*, endangered species, extrinsic modification hypothesis, population management, sex ratio

Resume

Selon l'hypothèse de Trivers-Willard et celle de la compétition pour les ressources locales (LRC), pour des espèces où le succès reproducteur est plus variable chez un des sexes, la sélection naturelle peut entraîner un biais dans la détermination du sexe de la descendance d'une femelle selon sa condition physique. L'hypothèse de modification extrinsèque (EMH) suggère que le sexe de la progéniture peut aussi être influencé par les conditions environnementales rencontrées par les mères. Nous avons étudié l'influence de la pluviométrie, du phénomène d'oscillation australe d'El Nino(ENSO), de la taille de la population et des feux contrôlés, dans l'année qui précède la conception et au cours de la gestation, sur la détermination du sexe dans la population de rhinos noirs de la Réserve de chasse de Mkhuze, en Afrique du Sud, entre 1970 et 2007. Les femelles étaient plus susceptibles de donner naissance à des mâles lorsque la pluviométrie durant la gestation augmentaient, ce qui conforte l'hypothèse de Trivers-Willard. La probabilité de donner naissance à un mâle augmentait aussi avec la taille de la population, ce qui conforte l'hypothèse de LRC. L'allocation du sexe du jeune n'était pas influencée par l'ENSO. En conclusion, les conditions environnementales locales peuvent influencer la détermination du sexe du jeune chez le rhinocéros noir, supportant ainsi l'EMH. Les feux contrôlés et la taille de la population influencent l'allocation du sexe chez le rhinocéros noir, et peuvent être manipulés par les gestionnaires. Donc cette information peut être utilisée pour améliorer les évaluations de structure de population et les régimes de gestion, particuliérement dans les réserves clôturées, ce qui est essentiel pour préserver la productivité des espéces menacées.

Correspondence: E-mail: rweladji@alcor.concordia.ca

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 offspring sex ratio in relation to the costs and benefits of producing sons and daughters (Clutton-Brock & Iason, 1986). For polygynous mammals, most of the suggested mechanisms are based on the assumption that sons are the more costly sex to produce (Clutton-Brock, Albon & Guinness, 1981). Generally, two adaptive modifications of maternal investment have been proposed to explain the variation in offspring sex ratios among ungulates, the Trivers & Willard (1973) model (TWM) and the local resource competition (LRC) (Clark, 1978; Silk, 1983) hypothesis. These models assume that a female's investment in her offspring can influence its reproductive success and fitness. The TWM (1973) hypothesizes 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. Accordingly, we would expect females in good body condition to be more likely to produce male calves, whereas females in poorer body condition would be more likely to produce female calves (Trivers & Willard, 1973) when the son's reproductive success is differentially affected by advantages in condition. The LRC hypothesis (Clark, 1978; Silk, 1983), however, predicts that females in poor condition will produce more of the sex that disperses. Under female phylopatry, the LRC hypothesis predicts that females in poor condition will produce males, because sons will emigrate and therefore are less likely than daughters to compete for resources in the mother's home range. Although there is strong empirical support for conditional sex allocation in some taxa (Hewison & Gaillard, 1999; West, Shuker & Sheldon, 2005), the extent to which the TWM can be applied to mammals, particularly ungulates, has been more controversial (but see Sheldon & West, 2004). There are indeed several discrepancies in the application of this model in various ungulate species, such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), moose (*Alces alces*) and 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 (reviewed by Hewison & Gaillard, 1999).

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 states that environmental forces affecting the condition of the mother affect 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 previous studies on species such as the red deer (Kruuk *et al.*, 1999; Post *et al.*, 1999; Mysterud *et al.*, 2000), reindeer (Weladji & Holand, 2003) and the black rhinoceros (*Diceros bicornis*) (Hrabar & Du Toit, 2005; Berkeley & Linklater, 2010), the effect being often mediated through female condition.

Sex ratio, age structure and reproductive status are important population and demographic parameters to be considered in management and conservation of wildlife (Mysterud & Ostbye, 2006) as they can affect productivity (Caughley, 1977). For polygynous species, as long as there are enough males to mate with the available females, it is the female component of the population that determines growth rate (Caughley, 1977); the pattern may, however, be influenced by the number of males as well as their age structure (Ginsberg & Milner-Gulland, 1994; Milner, Nilsen & Andreassen, 2007). 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.*, 2010).

The black rhinoceros is a Critically Endangered Species on the IUCN Red list of Threatened Species and has been a CITES Appendix 1 species since 1977 (Emslie & Brooks, 1999; Amin *et al.*, 2006; IUCN, 2010). As a result of large-scale poaching, this species has suffered a drastic population decline of over 90% in the last 60 years, reaching its lowest population size of 2410 in 1995 (IUCN, 2010). Since 1995, populations have begun to steadily recover as a result of increased conservation and anti-poaching efforts (Amin *et al.*, 2006, IUCN, 2010), but remain at a critical level and have become isolated into smaller subpopulations (Hrabar & Du Toit, 2005). The black rhinoceros population of Mkhuze Game Reserve (MGR), South Africa, is a founder population of the *Diceros bicornis minor* subspecies that exhibits a male-biased sex ratio (1.3 : 1 for calves between 1970 and 2007 from identifiable females), similar to what has been observed in other wild and captive populations (Hrabar & Du Toit, 2005; Dennis *et al.*, 2007; Linklater, 2007). 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. Black rhinoceros show some level of sexual dimorphism (Skinner & Smithers, 1990), are polygynous, are territorial (Adcock, 1994; Hrabar & Du Toit, 2005), show a high variance in reproductive success (Garnier, Bruford & Goossens, 2001) and may therefore be a good model species in which to test the TWM and the EMH. Moreover, given that males are the sex that disperses for black rhinoceros, we are also able to test the LRC hypothesis.

In subtropical savanna, rainfall has often been used as a proxy for changes in the vegetation productivity (Rasmussen, Wittemyer & Douglas-Hamilton, 2006). 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 & Owen-Smith, 2003). On the other hand, density dependence is known to influence black rhinoceros population dynamics. Increases in population size reduce resource availability, which affects mortality, fecundity and age at maturity (Hrabar & Du Toit, 2005).

In this study, we 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. Indeed, factors such as rainfall would be predicted by the EMH to affect female condition and hence the sex ratio. 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. Given the widespread influence of the El Niño-Southern Oscillation (ENSO) on many large ungulates (Ogutu & Owen-Smith, 2003), we also assessed its influence on black rhino's calf sex allocation. These factors are expected to influence the body condition and reproductive capacity of black rhino females thereby affecting the sex of their calf, if TWM and EMH hold. Accordingly, we predicted that the probability of mothers to have a male calf would (i) increase with increasing rainfall and with the ENSO and decrease with increasing population size, if TWM holds, and (ii) decrease with increasing rainfall and with the ENSO and increase with increasing population size if the LRC hypothesis is supported. We also predicted that the probability of mothers to have a male calf would (iii) be affected by variations in the burning history in the areas used by mother rhinos.

Material and methods

Study area

The MGR is an enclosed reserve of about 370 km^2 located in the KwaZulu-Natal Province of South Africa. The climate is semi-arid with a mean annual rainfall of 664 mm 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. Large mammals here include the black rhino, white rhino (*Ceratotherium simum*), cape buffalo (*Syncerus caffer*), leopard (*Panthera pardus*), elephant (*Loxodonta africana*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*), giraffe (*Giraffa camelopardalis*) and many antelope species. No lions (*Panthera leo*) have been seen in the reserve since the early 70s. The vegetation is categorized into seven types of habitat: forest and closed woodland, mixed bushland, mixed woodland, mixed thicket and scrub, wooded grassland, grassland and wetland (Goodman, 1990). As an important management tool, burning has been used extensively in the reserve (Mulqueeny, 2005). The burning is patchy and can occur throughout the reserve with the locations varying from year to year.

Black rhino and burning history data

Long-term black rhinoceros monitoring data collected by Ezemvelo KwaZulu-Natal Wildlife (EKZN Wildlife) were made available by the conservation manager and section rangers of the reserve. These data include field records, female calving records and population reports in the form of population growth rates from 1997 to present and population size estimates starting from 1990. The monthly rainfall records from 1960 to 2008 were made available by the reserve ecologist. The digital burning history maps from 1963 to 2007 were provided by EKZN Wildlife.

Black rhinoceros monitoring data included sighting records with the location of the individuals in formats of different levels of precision, from global positioning system coordinate points to simple area names. Overall, between 1983 and 2008, 2444 sightings were recorded, corresponding to about 98 sightings per year. Despite the discrepancy in the precision, we included all location data in the analyses as less precise data accounted for about half of the records. The sighting records provided specific distribution points for each identified female. A distribution map for each female was created using ArcGIS 9.3 Geographic Information System (Environmental Systems Research

Institute, Inc. (ESRI), CA, U.S.A.) and overlapped with the burning maps. For each precise location point, an area of 500 m in radius was created around the centre point. This was used to determine the burning history at the area of sighting. For each less precise location points (i.e. only area names), the burning history of the whole area was extracted. The burning history at each sighting location provided information on the proportion of the area burned the same year of the sighting (T_0), the proportion of the area burned the year previous to the sighting (T_{-1}) and the elapsed time (number of days) since the last burn in the area of sighting.

Field records also allowed us to monitor calving of females and provided information on the estimated age of the calf and its sex. We compiled calving records of identifiable females including the estimated date of birth of her calves and their sex. In the field, the age of the calf was determined by judging how big the calf was i.e. by comparing how high he was relative to his mother and then assigning an age class [there are six age classes from new born (A) up to sexually mature adult (F)]. Sex was determined by visualization of external genitalia. The data from the field later go through a 'quality control' process when the section ranger reviews them within a temporal resolution framework. For example, given that all known animals are on the reserve files, if the sex of a known calf is 'changed', this would trigger a reliable observer (ideally the section ranger) confirming the sex in the field. Likewise, if a calf is reported as a D 1 month and a C the next, this should trigger a reaction to confirm (or if it is reported as a certain age category for longer than the duration of the category). Once a new calf is sighted, a concerted effort is made to reliably sex it and try to estimate a date, or at least month of birth. Every time an identified calf was resighted, it would be checked for sex and age again. Despite increasing evidence of black rhinoceros calf predation, especially by lions (e.g. Plotz & Linklater, 2009), there are no data suggesting that neo-natal mortality is sex biased (see also Berkeley & Linklater, 2010).

From the estimated date of birth, we estimated the date of conception, given that gestation length in black rhinoceros is about 15 months (Skinner & Smithers, 1990). Using the information available for individual mothers, females were classified into two time intervals, pregnancy (i.e. 15 month from the estimated date of birth) and preconception (i.e. 12 month from the estimated conception month), depending on whether the sighting occurred while the female was pregnant or while she was within

1 year preceding conception. Individual females could be seen multiple times in a given year. The total rainfall and the mean population size were then calculated for each time interval associated with each calf. To assess the influence of ENSO on calf sex allocation, we used mean annual of the standardized monthly anomalies of the Southern Oscillation Index (SOI) as a measure of ENSO. The SOI values are standardized differences in sea level pressures at Tahiti, French Polynesia and Darwin, Australia and were calculated as departures from a base period of 1951–1980. Standardized monthly anomalies of SOI, measuring the strength and phase of large-scale fluctuations in air pressure in the Southern Hemisphere, were obtained from the website of the Climate and Global Dynamics (http://www.cgd.ucar.edu/cas/catalog/climind/SOI.signal.ascii).

The data included 101 calves, 44 female calves and 57 male calves, from 41 mother rhinos from 1970 to 2007. There are a total of 314 sightings of females while pregnant and 231 sightings of females in the preconception period as defined above.

Statistical analyses

We used the generalized linear mixed model (GLIMMIX procedure in SAS version 9.2; SAS, 2008) with a logit-link function, because our response variable, calf sex, was binomial (male calf; female calf), to analyse the respective influence of rainfall, ENSO, population size and burning on the probability of producing a 'male' calf, with 'mother rhino identity' as a random term. We ran separate models for different sets of predictors for at least two reasons: first the various set of predictors were available for a different time frame (e.g. 1960–2008 for rainfall and SOI, and 1990–2008 for population size) and second, most of the predictor variables were correlated increasing the risk of multicollinearity (e.g. the correlation between rainfall and population size was 0.56 during pregnancy and 0.54 during preconception; the correlation between population size and elapsed time since last burn was −0.48 during pregnancy and −0.47 during preconception; and the correlation between total rainfall and the SOI during pregnancy was 0.45).

The data from identified mother rhinos with identified calves were 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. Two models were also performed to assess the influence of ENSO on calf sex during pregnancy (SOI the year before the estimated year of birth; SOI_{t-1}) and during preconception (SOI 2 years before the estimated year of birth; SOI_{t-2}). Similarly, two models were performed to determine the influence of burning history on calf sex during preconception and pregnancy. The burning history variables were the proportion of burnt area at T_0 (year of sighting), the proportion of burnt area at T_{-1} (year prior to sighting) and the elapsed time since last burn. When none of the predictor variables 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 0.017 as we had three burning variables separately
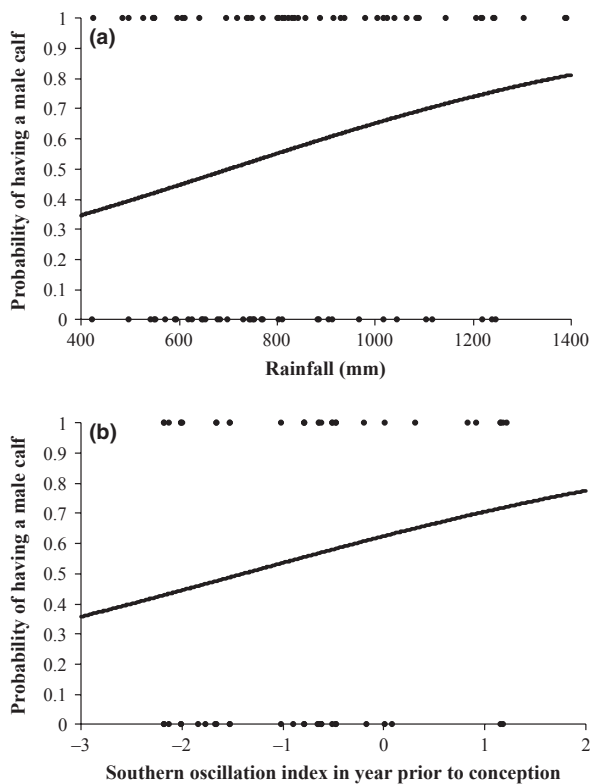
(Sokal & Rohlf, 2000) for the pregnancy and the preconception periods. The denominator degrees of freedom for the GLIMMIX models were calculated using the Kenward–Rogers approximation (Littell *et al.*, 2006). All estimates are presented ±SE. We used binomial test to assess whether the overall sex ratio differed significantly from a 50 : 50 ratio.

Results

Effect of rainfall, ENSO and population size on sex allocation

Overall, the sex ratio in the population was male biased (57 : 44) but did not differ significantly from a 50 : 50 ratio ($P = 0.232$). The probability that a mother rhino gave birth to a male calf was positively influenced by the amount of rainfall during pregnancy (0.0021 ± 0.0009, $F_{1,99} = 5.06$, $P = 0.027$; Fig. 1a) but not during preconception ($P = 0.36$). Calf sex allocation was not affected by the ENSO during pregnancy ($P = 0.46$) or the year prior to conception ($P = 0.07$). However, there was a tendency for the probability that a mother rhino gave birth to a male calf to increase with the SOI_{t-2} (0.3650 ± 0.2010, $F_{1,99} = 3.3$, $P = 0.07$; Fig. 1b). Sex allocation was also significantly influenced by population size during both pregnancy ($F_{1,74} = 6.93$, $P = 0.01$) and preconception ($F_{1,73} = 4.90$, $P = 0.03$) periods. There was a clear tendency for females to produce more male offspring as the population size increased, during both pregnancy (0.0712 ± 0.0270; Fig. 2a) and preconception (0.0616 ± 0.0278; Fig. 2b) periods.

Effect of burning on sex allocation

When taken together (i.e. including proportion of burnt at T_0, proportion of burn at T_{-1} and elapsed time since last burn), there was no evidence that burning influenced calf sex allocation both during the pregnancy and during the preconception periods (all $P > 0.05$). When taken individually, there was still no significant effect for any of the burning variables on calf sex allocation (all $P > 0.017$; Table 1). There was, however, a tendency for a negative relationship between the elapsed time since last burn of the area used by mother rhinos and the probability that they will produce a male calf, both during pregnancy (-0.0007 ± 0.0004, $F_{1,54} = 3.49$, $P = 0.07$; Fig. 3a; Table 1) and during preconception (-0.0009 ± 0.0005, $F_{1,52} = 3.26$, $P = 0.08$; Fig. 3b; Table 1).

Fig 1 Logistic regression curve representing the effect of (a) rainfall (mm) during pregnancy and (b) Southern Oscillation Index the year prior to conception (i.e. SOI_{t-2}) on the probability of having a male calf. The points represent the observed values
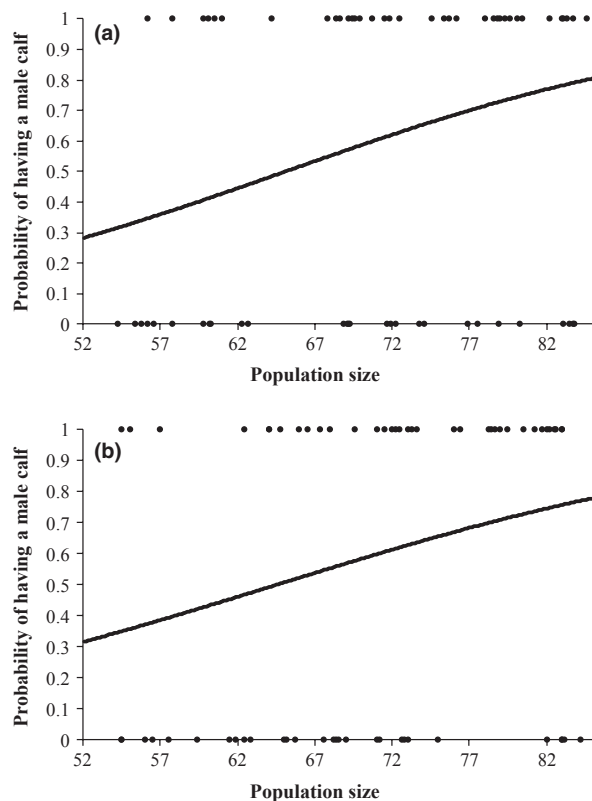
Fig 2 Logistic regression curve representing the effect of population size during (a) pregnancy and (b) preconception on the probability of having a male calf. The points represent the observed values

Discussion

Overall, we found that environmental conditions during preconception and/or during pregnancy influenced calf sex allocation, thereby supporting the EMH. Indeed, variation in rainfall and population size influenced sex allocation in this population of black rhinoceros. In support of the TWM, we found that females were more likely to have a male calf as rainfall increased. There were indications that the ENSO also had the potential to positively influence the probability that a female would produce a male calf. This was not surprising given the positive relationship between SOI and total rainfall in our study area ($r = 0.47$, $P < 0.001$). We also found that females were more likely to produce a male calf as population size increased, in support of the LRC hypothesis. Several studies have shown environmental conditions to influence sex allocation in large mammals through nutritional stress brought on by extrinsic factors [red deer (Kruuk *et al.*, 1999; Post *et al.*,

1999; Mysterud *et al.*, 2000); reindeer (Weladji & Holand, 2003); and black and white rhino (Hrabar & Du Toit, 2005; Linklater, 2007; Berkeley & Linklater, 2010)]. Indeed, nutritional stress experienced by the mother prior to conception or during mid-to-late gestation could lead to higher male embryo death (Kruuk *et al.*, 1999; Forsyth *et al.*, 2004; Cameron & Linklater, 2007; Linklater, 2007) and lead to a biased sex ratio at birth.

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 black rhinos, which can lead to changes in the body condition of females, ultimately affecting calf sex. Our results correspond to previous findings that rainfall influences population dynamics and the body condition of individuals [e.g. African ungulates (Owen-Smith, 1990; Ogutu & Owen-Smith, 2003, 2005), including black rhinoceros (Hrabar & Du Toit, 2005; Berkeley & Linklater, 2010) and Asian elephants *Elaphas maximus* (Slade, Schulte & Rasmussen, 2003)]. Similar to our results, Hrabar & Du Toit (2005) found in the black rhino population of Pilanesberg National Park in South Africa that the percentage of male calves increased with increasing rainfall and the inter-calving interval decreased with increasing rainfall. Likewise, Berkeley & Linklater (2010) found that female black rhinos were more likely to raise male calves if they conceived during wet years than during dry years in Hluhluwe-iMfolozi National Park, South Africa. The distribution of rainfall in South Africa's is erratic and highly variable between years. Because of global warming, an increase in temperatures in South Africa and changes in rainfall patterns are predicted, with an increase in winter rainfall regions and a reduction in summer rainfall regions of the country. With these predictions, and despite the positive correlation between SOI and rainfall, or the marked effect of ENSO and rainfall on the dynamics of African savanna ungulates (Ogutu & Owen-Smith, 2003), it is difficult to make firm predictions on how future climate will affect the sex ratio of black rhinoceros based on our results.

In black rhinos, population density is known to influence habitat and forage selection (Morgan, Mackey & Slotow, 2009) as well as population dynamics (Rachlow & Berger, 1998; Patton, Campbell & Parfet, 2008). Contrary to our TWM-based prediction, we found in this MGR population that the probability of producing a male calf was positively related to population size during both preconception and pregnancy. This may be due to the fact

Table 1 Parameter estimates, standard errors (SE) of the parameter estimate and *P*-values from the generalised linear mixed models describing the individual effect the burning (proportion that has burned the same year of the sighting (T_0), proportion that has burned the year previous to the sighting (T_{-1}) and elapsed time since last burn) of the area used by the mother rhinos during preconception and pregnancy on calf sex. The analyses are modelling the probability that the calf sex is 'male'

Burning history	Parameter estimates	SE	*P* value
Preconception			
Intercept	0.1908	0.3562	0.5955
Proportion of burn at T_0	1.2294	2.0607	0.5546
Intercept	−0.0134	0.3165	0.9664
Proportion of burn at T_{-1}	1.8164	1.3124	0.1723
Intercept	1.0317	0.5278	0.0560
Elapsed time since last burn	−0.0009	0.0005	0.0769
Pregnancy			
Intercept	0.2595	0.3220	0.4228
Proportion of burn at T_0	−0.6828	2.1547	0.7564
Intercept	−0.0645	0.3369	0.8489
Proportion of burn at T_{-1}	2.5338	1.5827	0.1156
Intercept	1.0467	0.5183	0.0484
Elapsed time since last burn	−0.0007	0.0004	0.0672

Fig 3 Logistic regression curve representing the effect of the elapsed time (no. of days) since the last burn of the area used by the mother rhino during (a) pregnancy and (b) during preconception on the probability of having a male calf. The points represent the observed values

that even at its highest population size, the population density of the reserve reaches 0.22 rhinoceros per km², which is potentially below the carrying capacity in this type of environment (Conway & Goodman, 1989; Hrabar & Du Toit, 2005). On the other hand, removals and translocations may disrupt the social structure of a population, leading to shifts in home ranges, creating conflicts between individuals and ultimately decreasing population productivity (Reid *et al.*, 2007; Patton, Campbell & Parfet, 2008). Thus, our results may not necessarily represent a positive relationship between population size and the probability of having a male calf, but could rather represent a period of greater social stability caused by the absence of removals which resulted in a tendency of female rhinos to produce male calves. Alternatively, our results may provide support to the LRC hypothesis (Clark 1978, Silk, 1983), whereby an increase in population size would mean increased competition for individual mother (i.e. reduced condition), and therefore mothers would be advantaged by producing mostly sons, the dispersers. Similar supports to the LRC have been reported in a number of mammal species [e.g. roe deer (Hewison & Gaillard, 1996; Silk 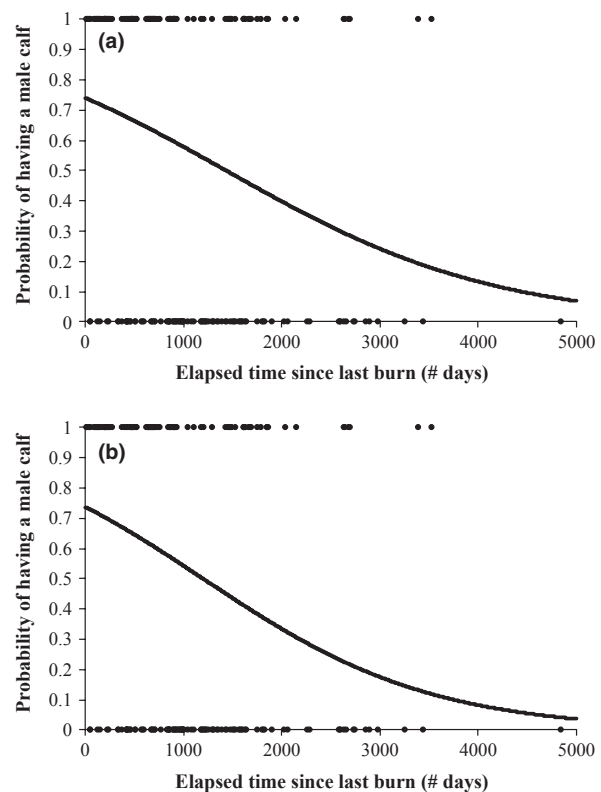& Brown, 2008), primates (Johnson, 1988; Silk & Brown, 2008; White, 2009) and brushtail possum *Trichosurus vulpecula* (Johnson *et al.*, 2001)].

Many factors can affect black rhino habitat selection including the distribution of highly preferred food resources, such as *Acacias* and *Euphorbias* (Emslie & Adcock, 1994; Heilmann *et al.*, 2006), the location of water and cover (Tatman, Stevens-Wood & Smith, 2000; Mukinya, 2005) and burning history (Emslie & Adcock, 1994). The location of the home range of a female black rhino can influence her access to food resources (Skinner & Smithers, 1990) which in turn affects her fecundity (Bronson, 1985). Burning is an effective tool in habitat management and is widely used in game reserves in South Africa, including MGR (Tainton, 1999; Mulqueeny, 2005). It 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). Our results indicate that in MGR, areas that have burned more recently may promote black rhinoceros habitat probably leading to females with a greater body condition and a tendency of having a male calf. It is hypothesized that black rhinoceros prefer browsing on burned trees because fire may alter the smell and taste of twigs, denature chemical composition and decrease the physical defence of plants (Emslie & Adcock, 1994). From our burning data, we were not able to differentiate between habitat categories, so that we are here talking about all habitats lumped together. Indeed, there may be some variations in the manner in which burning affects forage quality and quantity depending on the type of habitat. In MGR, burning as a management tool has been used extensively for many decades, which may have impacts on the resources and habitat quality. We therefore conclude that management regime also has the potential to influence sex allocation and hence the population structure, and this should be taken into account when setting future management plans (Okita-Ouma *et al.*, 2010). On the other hand, burning may force females to leave established home ranges, thereby causing social disruptions that may also influence sex allocation.

Our results supported both the TWM (e.g. effect of rainfall) and the LRC hypothesis (e.g. effect of population size), emphasizing the fact that the two predictions are not mutually exclusive. The influences of rainfall and population size are mediated through their effect on female condition, and as such, our results support the EMH. In an enclosed reserve, effective management is crucial to maintaining the productivity of endangered or vulnerable populations. In MGR, the black rhino is considered a priority species, and sound management is of utmost importance. This study provides insights into the influence of rainfall, population size and burning history on sex allocation that can benefit both the short- and long-term management of the MGR black rhinoceros 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. Burning regime depends on many considerations and involves several other species. Population size can, however, be controlled by managers according to their influence on calf sex, even though our data suggest that sex ratio may even out over time. Indeed, sex- and age-specific removal can be scheduled (Berkeley & Linklater, 2010), subsequently achieving maximum productivity and optimal genetic diversity. Depending on the objectives of a given reserve, these factors could provide a complement or alternative to translocation and hunting of black rhinoceros. Thus, increased knowledge on sex allocation improves population and meta-population management of the black rhinoceros.

Acknowledgements

References

Adcock, K. (1994) The relevance of 'territorial' behaviour in black rhino to their population management. In: *Proceedings of a Symposium on Rhinos as Game Ranch Animals* (Eds B. Penzorn and N. Kriek). Onderstepoort, Republic of South Africa, 9–10 September 1994.

Amin, R., Okita-Ouma, B., Adcock, K., Emslie, R.H., Mulama, M. & Pearce-Kelly, P. (2006) An integrated management strategy for the conservation of Eastern black rhinoceros *Diceros bicornis michaeli* in Kenya. *Int. Zoo Yearbook* **40**, 118–129.

Berkeley, E.V. & Linklater, W.L. (2010) Annual and seasonal rainfall may influence progeny sex ratio in the black rhinoceros. *S. Afr. J. Wildl. Res.* **40**, 53–57.

Bronson, F.H. (1985) Mammalian reproduction – an ecological perspective. *Biol. Reprod.* **32**, 1–26.

Cameron, E.Z. & Linklater, W.L. (2007) Extreme sex ratio variation in relation to change in condition around conception. *Biol. Lett.* **3**, 395–397.

Caughley, G. (1977) *Analysis of Vertebrate Populations*. John Wiley and Sons, New York, NY, U.S.A.

Clark, A.B. (1978) Sex-ratio and local resource competition in a prosimian primate. *Science* **201**, 163–165.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1981) Parental investment in male and female offspring in polygynous mammals. *Nature* **289**, 487–489.

Clutton-Brock, T.H. & Iason, G.R. (1986) Sex-ratio variation in mammals. *Q. Rev. Biol.* **61**, 339–374.

Conway, A.J. & Goodman, P.S. (1989) Population characteristics and management of black rhinoceros *Diceros bicornis minor* and white rhinoceros *Ceratotherium simum simum* in ndumu-game-reserve, South-Africa. *Biol. Conserv.* **47**, 109–122.

DENNIS, P.M., RAJALA-SCHULTZ, P.J., FUNK, J.A., BLUMER, E.S., MILLER, R.E., WITTUM, T.E. & WILLIAM, J.A. (2007) Risk factors associated with a skewed natal sex ratio in captive black rhinoceroses (*Diceros bicornis*) in the United States. *J. Zoo Wildl. Med.* **38**, 533–539.

EMSLIE, R.H. & ADCOCK, K. (1994) Feeding ecology of black rhinos. In: *Proceedings of a Symposium on Rhinos as Game Ranch Animals* (Eds B.L. PENZHORN and N.P.J. KRIEK). Onderstepoort, Republic of South Africa, 9–10 September 1994.

EMSLIE, R.H. & BROOKS, P.M. (1999) *African Rhino. Status Survey and Action Plan.* IUCN/SSC, Gland, Switzerland and Cambridge, U.K.

FORSYTH, D.M., TUSTIN, K.G., GAILLARD, J.M. & LOISON, A. (2004) Fetal sex ratio variation in the highly polygynous Himalayan tahr: evidence for differential male mortality. *Behav. Ecol.* **15**, 572–578.

GARNIER, J.N., BRUFORD, M.W. & GOOSSENS, B. (2001) Mating system and reproductive skew in the black rhinoceros. *Mol. Ecol.* **10**, 2031–2041.

GINSBERG, J.R. & MILNER-GULLAND, E.J. (1994) Sex-biased harvesting and population-dynamics in ungulates – implications for conservation and sustainable use. *Conserv. Biol.* **8**, 157–166.

GOODMAN, P.S. (1990) *Soil, Vegetation and Large Herbivore Relations in Mkuzi Game Reserve, Natal.* University of Witwatersrand, Johannesburg, South Africa.

HEILMANN, L.C., DE JONG, K., LENT, P.C. & DE BOER, W.F. (2006) Will tree euphorbias (*Euphorbia tetragona* and *Euphorbia triangularis*) survive under the impact of black rhinoceros (*Bicornis diceros minor*) browsing in the Great Fish River Reserve, South Africa? *Afr. J. Ecol.* **44**, 87–94.

HEWISON, A.J.M. & GAILLARD, J.M. (1996) Birth-sex ratios and local resource competition in roe deer, *Capreolus capreolus*. *Behav. Ecol.* **7**, 461–464.

HEWISON, A.J.M. & GAILLARD, J.M. (1999) Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. *Trends Ecol. Evol.* **14**, 229–234.

HRABAR, H. & DU TOIT, J.T. (2005) Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Anim. Conserv.* **8**, 259–267.

IUCN (2010) *IUCN Red List of Threatened Species Version 2010.* IUCN, Gland, Switzerland. http://www.iucnredlist.org (accessed on 9 June 2010).

JOHNSON, C.N. (1988) Dispersal and the sex-ratio at birth in primates. *Nature* **332**, 726–728.

JOHNSON, C.N., CLINCHY, M., TAYLOR, A.C., KREBS, C.J., JARMAN, P.J., PAYNE, A. & RITCHIE, E.G. (2001) Adjustment of offspring sex ratios in relation to the availability of resources for philopatric offspring in the common brushtail possum. *Proc. Biol. Sci.* **268**, 2001–2005.

KRUUK, L.E.B., CLUTTON-BROCK, T.H., ALBON, S.D., PEMBERTON, J.M. & GUINNESS, F.E. (1999) Population density affects sex ratio variation in red deer. *Nature* **399**, 459–461.

LINKLATER, W.L. (2007) Translocation reverses birth sex ratio bias depending on its timing during gestation: evidence for the

action of two sex-allocation mechanisms. *Reprod. Fertil. Dev.* **19**, 831–839.

LITTELL, R.C., MILIKEN, G.A., STROUP, W.W., WOLFINGER, R.D. & SCHABENBERGER, O. (2006) *SAS for Mixed Models*, 2nd edn. SAS Institute Inc, Cary, NC, U.S.A.

MILNER, J.M., NILSEN, E.B. & ANDREASSEN, H.P. (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conserv. Biol.* **21**, 36–47.

MORGAN, S., MACKEY, R.L. & SLOTOW, R. (2009) A priori valuation of land use for the conservation of black rhinoceros (*Diceros bicornis*). *Biol. Conserv.* **142**, 384–393.

MUKINYA, J.G. (2005) Density, distribution, population structure and social organization of the black rhinoceros in Masai Mara Game Reserve. *E. Afr. Wildl. J.* **11**, 385–400.

MULQUEENY, C.M. (2005) *Spatial and Temporal Variation of the Fire Regime in Mkuzi Game Reserve*. University of Witwatersrand, Johannesbourg, South Africa.

MYSTERUD, A. & OSTBYE, E. (2006) Effect of climate and density on individual and population growth of roe deer *Capreolus capreolus* at northern latitudes: the Lier valley, Norway. *Wildl. Biol.* **12**, 321–329.

MYSTERUD, A., YOCCOZ, N.G., STENSETH, N.C. & LANGVATN, R. (2000) Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *J. Anim. Ecol.* **69**, 959–974.

OGUTU, J.O. & OWEN-SMITH, N. (2003) ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecol. Lett.* **6**, 412–419.

OGUTU, J.O. & OWEN-SMITH, N. (2005) Oscillations in large mammal populations: are they related to predation or rainfall? *Afr. J. Ecol.* **43**, 332–339.

OKITA-OUMA, B., AMIN, R., VAN LANGEVELDE, F. & LEADER-WILLIAMS, N. (2010) Density dependence and population dynamics of black rhinos (*Diceros bicornis michaeli*) in Kenya's rhino sanctuaries. *Afr. J. Ecol.* **48**, 791–799.

OWEN-SMITH, N. (1990) Demography of a large herbivore, the greater kudu tragelaphus-strepsiceros, in relation to rainfall. *J. Anim. Ecol.* **59**, 893–913.

PATTON, F., CAMPBELL, P. & PARFET, E. (2008) Biological management of the high density black rhino population in Solio Game Reserve, central Kenya. *Pachyderm* **44**, 72–79.

PLOTZ, R.D. & LINKLATER, W.L. (2009) Black rhinoceros (*Diceros bicornis*) calf succumbs after lion predation attempt: implications for conservation management. *Afr. Zool.* **44**, 283–287.

POST, E., FORCHHAMMER, M.C., STENSETH, N.C. & LANGVATN, R. (1999) Extrinsic modification of vertebrate sex ratios by climatic variation. *Am. Nat.* **154**, 194–204.

RACHLOW, J.L. & BERGER, J. (1998) Reproduction and population density: trade-offs for the conservation of rhinos in situ. *Anim. Conserv.* **1**, 101–106.

RASMUSSEN, H.B., WITTEMYER, G. & DOUGLAS-HAMILTON, I. (2006) Predicting time-specific changes in demographic processes using remote-sensing data. *J. Appl. Ecol.* **43**, 366–376.

REID, C., SLOTOW, R., HOWISON, O. & BALFOUR, D. (2007) Habitat changes reduce the carrying capacity of Hluhluwe-Umfolozi

Park, South Africa, for critically endangered black rhinoceros *Diceros bicornis. Oryx* **41**, 247–254.

SAS (2008) *SAS/STAT Guide for Personal Computers, Version 9.2.* SAS Institute Inc., Cary, NC, U.S.A.

SHELDON, B.C. & WEST, S.A. (2004) Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *Am. Nat.* **163**, 40–54.

SILK, J.B. (1983) Local resource competition and facultative adjustment of sex-ratios in relation to competitive abilities. *Am. Nat.* **121**, 56–66.

SILK, J.B. & BROWN, G.R. (2008) Local resource competition and local resource enhancement shape primate birth sex ratios. *Proc. Biol. Sci.* **275**, 1761–1765.

SKINNER, J.D. & SMITHERS, R.H.N. (1990) *The Mammals of the Southern African Subregion.* University of Pretoria, Pretoria, South Africa.

SLADE, B.E., SCHULTE, B.A. & RASMUSSEN, L.E.L. (2003) Oestrous state dynamics in chemical communication by captive female Asian elephants. *Anim. Behav.* **65**, 813–819.

SOKAL, R.R. & ROHLF, F.J. (2000) *Biometry.* Freeman, San Francisco, CA, U.S.A.

TAINTON, N.M. (1999) *Veld Burning. Veld Management in South Africa.* University of Natal Press, Pietermaritzburg, South Africa.

TATMAN, S.C., STEVENS-WOOD, B. & SMITH, V.B.T. (2000) Ranging behaviour and habitat usage in black rhinoceros, *Diceros bicornis*, in a Kenyan sanctuary. *Afr. J. Ecol.* **38**, 163–172.

TRIVERS, R.L. & WILLARD, D.E. (1973) Natural-selection of parental ability to vary sex-ratio of offspring. *Science* **179**, 90–92.

WELADJI, R.B. & HOLAND, Ø. (2003) Sex ratio variation in reindeer *Rangifer tarandus*: a test of the extrinsic modification hypothesis. *Wildl. Biol.* **9**, 29–36.

WEST, S.A., SHUKER, D.M. & SHELDON, B.C. (2005) Sex-ratio adjustment when relatives interact: a test of constraints on adaptation. *Evolution* **59**, 1211–1228.

WHITE, F.J. (2009) Sex ratio at birth and age-reversed dominance among female *Varecia. Folia Primatol.* **80**, 341–352.