Received: 19 February 2020 | Revised: 26 May 2020 | Accepted: 23 July 2020

DOI: 10.1111/aje.12779

ARTICLE

African Journal of Ecology WILEY

Relationships of reproductive performance indicators in black rhinoceros (*Diceros bicornis michaeli*) with plant available moisture, plant available nutrients and woody cover

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Funding information
World Wide Fund for Nature in Kenya; Wageningen University; Mohammed bin Zayed Species Conservation Fund; Zoological Society of London; Zoo D'Amneville in France; Leibniz Institute of Zoo Biology and Wildlife Research in Germany

Abstract

Plant available moisture and plant available nutrients in soils influence forage quality and availability and subsequently affect reproductive performance in herbivores. However, the relationship of soil moisture, soil nutrients and woody forage with reproductive performance indicators is not well understood in mega-browsers yet these three are important in selecting suitable areas for conservation of mega-browsers. Here, the eastern black rhinoceros (***Diceros bicornis michaeli***), a mega-browser, was studied in seven geographically distinct populations in Kenya to understand the relationships between its reproductive performance indicators and plant available moisture, plant available nutrients and woody cover. Reproductive parameters showed a complex relationship with plant available moisture and plant available nutrients. We found an increase in the predicted yearly percentage of females calving as plant available nutrients decreased in areas of high levels of plant available moisture but no relationship with plant available nutrients in areas of low plant available moisture. Age at first calving was earlier, inter-calving interval was longer and yearly percentage of females calving was higher at higher woody cover. Woody plant cover contributes positively to black rhino reproduction performance indicators, whereas plant available moisture and plant available nutrients add to the selection of conservation areas, in more subtle ways.

KEYWORDS

black rhinoceros, moisture, nutrients, reproductive performance, savannah, woody cover

Résumé

L'humidité et les nutriments assimilables par les plantes influencent la qualité et la disponibilité du fourrage pour affecter les performances de reproduction des herbivores. Cependant, la relation entre l'humidité du sol, les nutriments et le fourrage ligneux avec les indicateurs de performance de reproduction chez les grands brouteurs n'est pas encore bien comprise. Ces trois éléments sont importants dans la sélection des zones appropriées pour leur conservation. Le rhinocéros noir de l'Est (*Diceros bicornis michaeli*), un grand brouteur, a été ici étudié au sein de sept populations géographiquement distinctes au Kenya pour comprendre les relations entre ses indicateurs de performance de reproduction et l'humidité assimilable par les plantes, les nutriments assimilables les plantes et la couverture ligneuse. Les paramètres de reproduction ont montré une relation complexe avec l'humidité et les nutriments assimilables par les plantes. Nous avons constaté une augmentation du pourcentage annuel prévu de femelles vêlant alors que les nutriments assimilables par les plantes diminuait dans les zones où l'humidité assimilable par les plantes était élevée, mais aucune relation avec les nutriments assimilables par les plantes dans les zones où l'humidité assimilable par les plantes était faible. L'âge au premier vêlage était plus précoce, l'intervalle entre les vêlages était plus long et le pourcentage annuel de femelles vêlant était plus élevé avec une couverture ligneuse plus importante. La couverture végétale ligneuse contribue positivement aux indicateurs de performance de reproduction des rhinocéros noirs, tandis que l'humidité et les nutriments assimilables par les plantes s'ajoutent à la sélection des zones de conservation de manière plus subtile.

1 | INTRODUCTION

Mammalian herbivores exhibit better reproductive performance in habitats that provide sufficient quality and quantity of plants (Berryman, 2004; Jones et al., 2010; Lashley, Chitwood, Harper, Moorman, & DePerno, 2015; Sinclair, Dublin, & Borner, 1985; White, 2004), and this applies to mega-herbivores too (Atkinson, 1995; Birkett, 2002; Clauss et al., 2007; Danell, Bergstrom, Duncan, & Pastor, 2006; Lewis et al.., 2017; Owen-Smith, 1988). Quality and quantity of plants are functions of Plant Available Moisture (PAM), that is the potential water available in that can be absorbed by plants in every soil horizon and soil characteristics, particularly Plant Available Nutrients (PAN). Soil fertility is determined by a variety of factors (Sankaran et al., 2005; Walker & Langridge, 1997); however, PAN is the simplest index to represent soil fertility, because it is derived from the sum of exchangeable calcium, magnesium, sodium and potassium cations. The PAM/PAN concept has been used in comparing structure and functions of savannah habitats from a subcontinent scale to a global scale where the highest diversity of grazing mammalian herbivores is found to occur in areas with intermediate PAM and high PAN (Ahrestani et al.., 2011; Frost et al., 1986; Olff, Ritchie, & Prins, 2002; Ratnam, Sheth, & Sankaran, 2019; Solbrig, 1990; Walker & Menaut, 1988). PAM and PAN can influence forage quality and availability which would in turn affect nutritional and body condition status of females. Delays in the first age of reproduction and increases in inter-calving intervals are likely in black rhino population under nutritional stress (Hitchins & Anderson, 1983; Hrabar & du Toit, 2005). Females in good body condition for such mega-herbivores (adult body mass >1,000 kg: Owen-Smith, 1988) have better fecundity rates, allocate more resources to caring for offspring and reach reproductive maturity earlier than those in poor body condition (Bonenfant et al., 2009).

Woody plants provide nutritional and energy requirements for reproductive performance in browsers. The quality of browsing forage (woody twigs and leaves) increases with increase in PAM (Barbosa et al., 2014; Singh & Singh, 2004). Further, the strong negative correlation between woody cover and soil nitrogen (Sankaran, Ratnam, & Hanan, 2007) suggest an availability of large quantities of woody cover in areas of low PAN. Thus, areas of high PAM and low PAN should have high quality and quantity of woody browse. Therefore, the nutrient-dependent reproductive performance in mega-browsers—whose diet is dominated by woody plants—is expected to be good under such conditions. Shaw (2011) reported reproductive performance of female black rhinos in Tswalu Kalahari Reserve in South Africa to be dependent on adaptive use of the seasonally changing quality and quantity of forage resources. Similar observations were made for giraffe's (*Giraffa camelopardalis tippelskirchi*) reproductive success in Serengeti, Tanzania (Pellew, 1984), and for kudu (*Tragelaphus strepsiceros*) in Nylsvley Nature Reserve, South Africa (Owen-Smith & Cooper, 1989).

However, the concept of PAM and PAN has neither been used to explain reproductive performance in mega-herbivores nor in selecting suitable areas for re/introducing mega-herbivores because in doing so, one would assume an equilibrium or stability in the complex interplay between the deterministic density dependence feedbacks such as intra- and inter-competitive interaction and the stochastic environmental processes in a population, an assumption which our seven study sites provided. With this assumption, we focused on black rhinoceros, a mega-browser, to better understand its reproductive performance in relation to PAM and PAN through woody cover and explored the possibilities of using PAM and PAN to identify conservation areas for maximal reproductive performance.

Black rhinoceros comprising its three extant sub-species is critically endangered with continental numbers estimated at between 5,042 and 5,455 as of 2015 (Emslie, 2020). It still requires well informed biological management, including effective ways of selecting suitable areas to maximise its reproduction in recovery programs. The eastern black rhinoceros sub-species (*D. b. michaeli*), the focus of this study, is found only in the East Africa region except for a small out-of-range population on a private reserve in South Africa. Its current stronghold is Kenya with an increasing 745 animals which represented c. 75% of it in situ in 2017 (Emslie et al., 2019). They are conserved mostly within sanctuaries in both protected areas and on private land, and in three free-ranging areas in national parks and reserve with habitats ranging from dense forest to semi-arid scrubland. Tanzania had *c*. 155 eastern black rhinoceros in three populations in 2017 mostly in free-ranging populations in unfenced protected areas and a small population in one sanctuary (Emslie et al., 2019; Kohi & Lobora, 2019). Rwanda has recently re-established a population of 19 animals (RDB, 2016). These are considered remarkable turnarounds in rhino numbers since 1980s when the numbers drastically declined from c. 20,000 in the 1970s to less than 400 animals in Kenya alone due to culling to clear land for agriculture and exacerbated by intense poaching (Amin et al., 2006).

Three measures of reproductive performance namely, age at first calving, average inter-calving interval and yearly percentage of females calving in eastern black rhinoceros were used in this study, because they are directly linked to nutritional and the body condition status of the animal which are influenced by browse quality and quantity (du Toit, 2001). Sufficient food quality and quantity promotes attainment of approximately 80% of full adult body weight that a female requires for successful conception and parturition (Owen-Smith, 1988) with females' ages at first calving being about 7 years (du Toit, 2001). However, much earlier ages at first calving 5 years 10 months have been reported in East African (Goddard, 1970).

The shortest possible black rhinoceros' average inter-calving interval, that is the time from the birth of one calf to the next, can be between 1.4 and 1.5 years by factoring a gestation period of 1.2–1.3 years. The gestation includes a lactational anoestrus period of 8 months to 16 months observed in the wild (Garnier, Holt, & Watson, 2002) and in captivity (Gregory, Rowland, Thompson, & Kon, 1965) where the suckling of the calf suppresses reproductive cycle, and an oestrus cycle of about 30 days (Hildebrandt et al., 2007). Short inter-calving intervals of less than 2.1 years are very rare (Owen-Smith, 1988; du Toit, 2001); on average, an inter-calving interval of 2.5 years has been recorded for best performing black rhinoceros populations in situ (Adcock, 1999; Hrabar & du Toit, 2005). The period between one calf and the next requires quality nutrition for the lactation phase (Hildebrandt et al., 2007) and survival of the new born calf. Low-quality browse in this phase may lead to delays in conception or abortions. Neonate mortality may also increase when quality of browse is low (Emslie & Brooks, 1999). Hrabar and du Toit (2005) recorded longer inter-calving intervals in periods of lower rainfall (lower PAM) with low browse availability in Pilanesberg National Park in South Africa.

The yearly percentage of females calving is an equally important measure of population performance. This measure assumes that all females ≥7 years old are calving. This measure fluctuates a lot on a year to year basis because of the >1 year gestation period, and because most black rhinoceros populations are small (<100 animals) at present, thus giving rise to randomness in this parameter hence the need to average yearly percentage of females calving over ≥3 year periods. Overall, yearly percentage of females calving is considered excellent if >40%, good if ranging from 33% to 40% and below average if <33% (du Toit, 2001).

We hypothesised (a) early age at first calving (<7 years), (b) short average inter-calving interval (<2.5 years) and high yearly percentage of females calving (>40%) for black rhinoceros in areas with high PAM and low PAN. We first related these three measures of reproductive performance to woody cover that provides browse for black rhinoceros. We then tested whether the relationship with woody cover could be explained by PAM and PAN of seven populations in Kenyan savannah habitats between 1993 and 2010.

2 | MATERIAL AND METHODS

2.1 | Study areas

The study was carried out in seven geographically distinct areas (Figure 1). Characteristics of the study areas including size of the conservation area available to black rhinos, relative black rhino density (that is the ratio of absolute density to maximum stocking density), mean annual rainfall from January to December 2000 to 2010, brief vegetation descriptions and other factors likely to impact on populations performance between 1993 and 2010 are provided in Table 1.

2.2 | Reproductive performance

Reproductive performance measures were derived from demographic data stored in Kenya's rhinoceros information system (Okita-Ouma et al., 2011). All the field data underwent a process of quality control and entered into the information system by the dedicated field monitoring staff in each of the black rhinoceros population. Each site had dedicated personnel whose day–day work is to monitor individual animals that have been coded and assigned names for individual identification.

For each study area, age at first calving was calculated as the difference in years between the date of birth of a female and the date of birth of her first calf. The quality of birthdate accuracy is dependent on the quality of monitoring in different rhino sites and how easy a population is to monitor can be affected by the terrain and vegetation cover. Observations and recording of mating complimented these accuracies. New born calves were in most cases sighted within a year of birth. It is also easier to age calves of up to 2 years with a

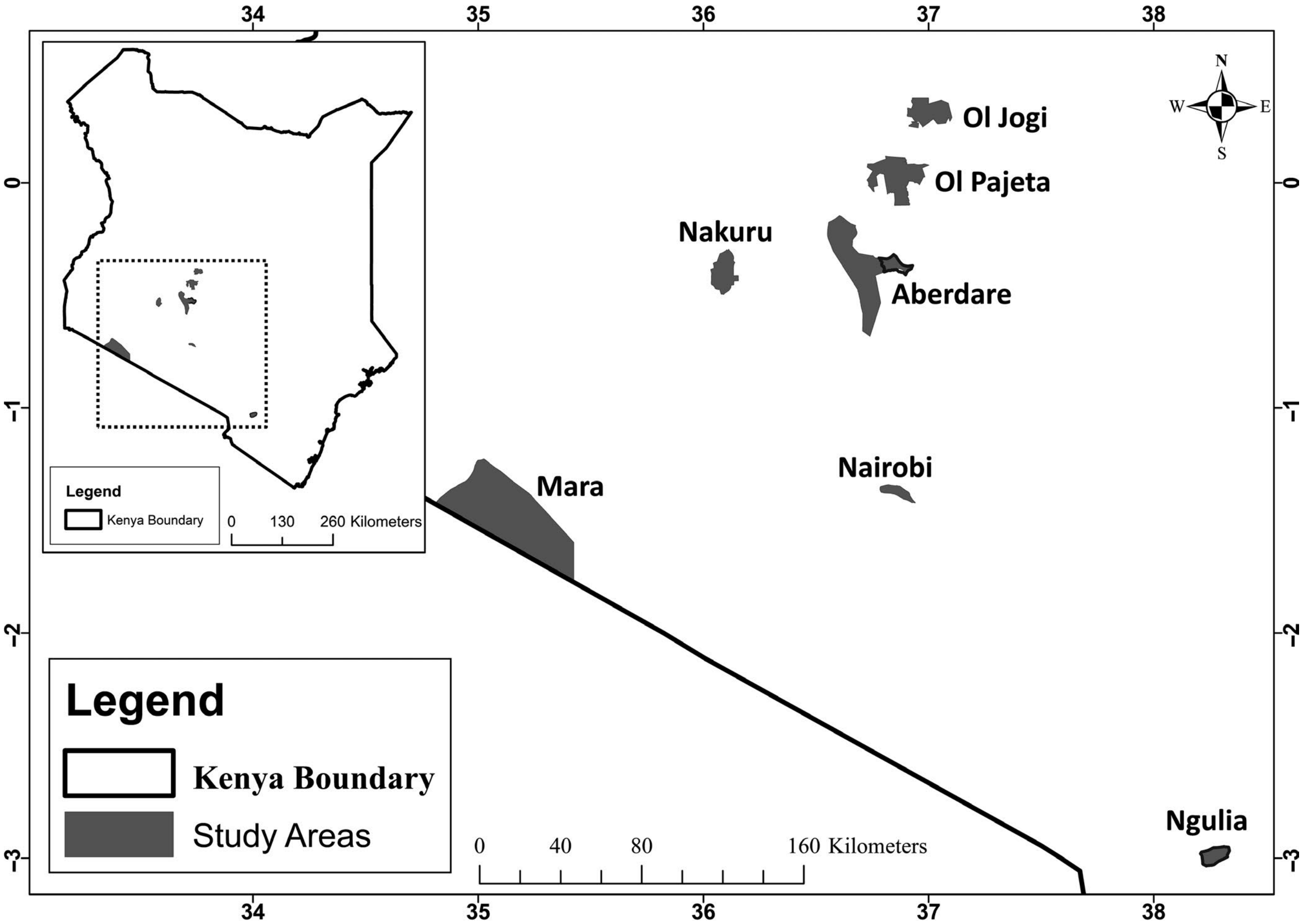

FIGURE 1 Locations of the seven study areas for black rhino reproduction in Kenya (East Africa)

birthdate accuracy of ±1 year by trained and accredited monitoring staff/observers (Adcock & Emslie, 2005). During the digitisation of rhino records in Kenya in 2001, the experienced long serving rhino monitoring personnel gave birthdate accuracies for animals whose birthdates were estimated. In this study, only females whose birthdate could not be ascertained to be of ±1 year of birthdate accuracy, all totalling 64 animals, were considered. The average inter-calving interval in years for a known female was derived by dividing the difference between the date of birth of first calf and date of birth of the last calf as at the end of 2010, by the female's total number of calves minus one. Yearly percentage of females calving was derived as the proportion of number of calves born in year '*t*' to the number of live adult females (≥7 years) in year '*t*.' The year to year variations in yearly percentage of females calving due to the long gestation period of about 1.3 years for black rhinoceros and the possibility of synchronised calving in small populations was solved by averaging yearly percentage of females calving over 3-year moving windows.

2.3 | Plant available moisture (PAM) index

PAM index for each study area was calculated by averaging the area's yearly PAM from January to December. Yearly PAM was derived as the monthly average of the Log_{10} of the ratio of actual rainfall (RAIN) and potential evapotranspiration (PET), that is Log_{10} RAIN/PET (Olff et al., 2002; Walker & Langridge, 1997). PAM ranged between −1.0 and +1.0 representing the lowest and highest Log_{10} RAIN/PET values in the study area. The Blaney–Criddle formula (Blaney & Criddle, 1962) was preferred over the detailed Penman-Monteith equation (Penman, 1948) due to the availability of data. PET was thus derived as follows:

$$\text{PET}_o = p \times (0.46\,T_{\text{mean}} + 8),$$

where PET_o is the reference Potential Evapotranspiration [mm/day] (monthly). T_{mean} is the mean daily temperature [°C] given as $T_{\text{mean}} = (T_{\text{max}} + T_{\text{min}})/2$. p is the mean daily percentage of daytime hours (assumed 50% for equatorial regions over the year).

Rainfall data collected from January to December of 2000–2011 included field measurements and decadal (10-day interval) estimates derived from rainfall raster images of 8 km resolution (http://www.cpc.ncep.noaa.gov/products/fews/AFR_CLIM/afr_clim.shtml). Hawth's Tools for ArcMap9.3.1© and ArcGIS™ software was used to extract specific rainfall estimates from raster images by overlaying GIS shape files of boundary for each study area on the raster images.

TABLE 1 Characteristics of the study areas including size, relative black rhino density, rainfall, vegetation descriptions and other factors likely to impact on populations performance between 1993 and 2010. The mean annual rainfall is reported from January to December of 2000 to 2011. The shortened names for the study areas as used in the main text are shown in brackets

Study area	Available area (km^2)	Relative[a] black rhino density Mean ± 95% CI	Rainfall (mm) Mean 2000 to 2011 ± *SD*	Vegetation	Other factors on population performance
Aberdare Nat. Park (Aberdare)	70	0.45 ± 0.15	607 ± 149	montane forest, undergrowth of mixed species of bushland, bamboo forests, grass tussocks on the moorlands.	Ring-fenced; significant poaching impact on population decline.
Lake Nakuru Nat. Park (Nakuru)	144	0.74 ± 0.11	755 ± 169	open grassland, *Acacia*, *Tarchonanthus* bush land, deciduous and *Euphorbia* forests and riverine bush land	Ring-fenced; 35 black rhinos in total translocated out during the period.
Masai Mara Nat. Reserve (Mara)	1,510	0.35 ± 0.02	911 ± 147	grassland with isolated scrublands and woodlands especially along drainage lines	Not fenced; Contiguous with Serengeti *N.P.* in Tanzania
Nairobi Nat. Park (Nairobi)	117	1.60 ± 0.08	540 ± 151	deciduous forest, riverine thorn forests, shrubs and grasslands	Ring-fenced except for a 20 km stretch for wildebeest migration; 67 black rhinos in total translocated out during the period.
Ngulia Rhino Sanctuary (Ngulia)	92	1.69 ± 0.25	385 ± 146	*Commiphora* and *Acacia* woodland with scattered baobab trees	Ring-fenced; Expanded from $63km^2$ to $92km^2$ in 2007; 255 elephants, 200 buffaloes and 12 black rhinos translocated out in 2008 to reduce competition (Okita-Ouma et al., 2008)
Ol Jogi Pyramid (Ol Jogi)	50	1.17 ± 0.19	459 ± 113	mosaic of grassland, *Acacia* woodland and shrubs	Ring-fenced; 30 black rhinos translocated out; 9 black rhinos died from disease (Ndeereh, Okita-Ouma, Gaymer, Mutinda, & Gakuya, 2011).
Ol Pejeta Conservancy (Ol Pejeta)	300	0.93 ± 0.15	557 ± 115	a mosaic of grassland, *Acacia* woodland, *Euclea* shrub and riverine woodland grassland	Ring-fence designed to allow migration of other species. Expanded from $93km^2$ to $300km^2$ and 27 black rhinos translocated in 2007; Vegetation damage and competition from giraffes and elephants (Birkett, 2002).

[a]The ratio of absolute density to the estimated maximum stocking density/ 'carrying capacity' (Adcock et al., 2007).

The same data source, analytical tools and procedures for extracting rainfall data were used in the derivation of minimum and maximum temperatures from raster files of 4 km resolution.

2.4 | Plant available nutrient (PAN) index

PAN was measured as the mean of the sums of soil exchangeable cations (Ca^{2+}, Mg^{2+}, Na^{+} and K^{+}) in milli-equivalent of hydrogen per 100 grams (mEq/100 g) (Ahrestani et al., 2011; Olff et al., 2002). Exchangeable cations were extracted from Kenya Soil Survey reports and data sets of scales 1:50,000 to 1:250,000 and World Soils Information (ISRIC) database (Batjes, 2006; Batjes & Gicheru, 2004; ISRIC, 2011). Specifically, for Aberdare NP (Batjes & Gicheru, 2004; Sombroek, Braun, & Van der Pouw, 1982), Lake Nakuru NP (Siderius & Muriuki, 1977; Van der Weg, Muriuki, & Kinyanjui, 1976; Wamicha, Gatahi, & Mungai, 1981), Masa Mara NR (Glover & Trump, 1970; Glover & Williams, 1966), Nairobi NP (Kinyanjui, 1996; Wamicha & Gachene, 1979; Waruru & Ita, 1986), Ol Jogi Pyramid and Ol Pejeta Conservancy (Ahn & Geiger, 1987; GTZ et al., 1987). To standardise comparisons, only exchangeable cations within 20 cm soil depth were used. Study areas that lacked estimates of exchangeable cations were represented by exchangeable cations estimates of neighbouring sites (Sombroek et al., 1982).

2.5 | Woody cover

Woody cover was used as broad-scale indicative measure of forage and assumed to be correlated with reproductive performance in black rhinoceros. This was derived from Moderate Resolution Imaging Spectroradiometer (MODIS) land cover maps comprising the vegetation continuous field layers. The layers included per cent bare ground, herbaceous and woody cover and, for woody cover, per cent evergreen, deciduous, needle-leaf and broad-leaf (Hansen et al., 2002; Kahiu & Hanan, 2018). We estimated woody cover of the seven study areas from these maps that were basically of 500 m sub-pixel. MODIS uses annual phenological metrics as the independent variables to predict woody cover. This methodology was developed based on a very large data set and has the potential to fairly estimate available forage of ≤2 m for black rhinoceros in savannah ecosystem (Adcock, Khayale, & Amin, 2007; Bucini & Hanan, 2007) because it combines vegetation classes including bushland and shrubland of ≤5 m. We are aware of the shortfalls of the precision of satellite-derived products such as MODIS (Gross, Achard, Dubois, Brink, & Prins, 2018) so to compare the different areas we only used the same product for all seven areas in the same year and month.

2.6 | Statistical analyses

Averages of PAM and PAN for each study area were used to distinguish the study areas in a PAM-PAN plane. IBM® SPSS® Statistics 19 was used for all statistical analyses. To test the relationship between reproductive performance and PAM, PAN and woody cover, we used curve estimation procedures to investigate the shape of relationships between the means of age at first calving and inter-calving interval for each study area and PAM, PAN and woody cover. We also related the standard deviations of the means of age at first calving and of inter-calving interval as dependent variables to PAM, PAN and woody cover as independent variables to investigate whether the variation between the individuals in each area could be explained by these independent variables. We tested for linear, logarithmic, inverse, power, S-shape and exponential relationships and used the highest R^2_{adj} values to measure goodness of fit. We used the Generalized Estimating Equation approach (GEE) (Diggle et al., 2002; McCullagh & Nelder, 1989; Zeger, Liang, & Albert, 1988) to investigate the relationship between yearly percentage of females calving as dependent variable and PAM, PAN (and the interaction between PAM and PAN) and woody cover as independent variables. GEEs can be used as extensions of generalised linear models for the analysis of longitudinal data such as yearly percentage of females calving. We applied 'Year' as within-subject variable and 'Area' as subject variable. The 3-year moving average of the yearly percentage of females calving was used as dependent variable, and we checked that the residuals were normally distributed.

3 | RESULTS

The seven black rhinoceros study areas were plotted on a PAM-PAN space (Figure 2).

The PAM (mm/day) and PAN (mEq/100g) values at 95% C.I. and n = 10 for all PAM indices and woody cover as a proportion to vegetation cover were as follows: Aberdare; PAM = 0.7 ± 0.2, PAN = 18.0 ± 7.9 (n = 23) and woody cover = 0.46. Nakuru; PAM = 0.7 ± 0.2, PAN = 13.2 ± 1.5 (n = 47) and woody cover = 0.18. Mara; PAM = 0.7 ± 0.1, PAN = 18.2 ± 1.9 (n = 43) and woody cover = 0.15. Ngulia; PAM = −0.2 ± 0.2, PAN = 19.3 ± 2.8 (n = 179) and woody cover = 0.15. Nairobi; PAM = 0.2 ± 0.2, PAN = 9.6 ± 2.9 (n = 28) and woody cover = 0.18. Oljogi; PAM = 0.2 ± 0.3, PAN = 8.2 ± 1.3 (n = 17) and woody cover = 0.03. Ol Pejeta; and PAM = 0.5 ± 0.1, PAN = 18.4 ± 3.8 (n = 19) and woody cover = 0.13.

3.1 | Reproductive performance measures as functions of PAM, PAN and woody cover

Age at first calving ranged between 4 and 12 years with a birthdate accuracy of ±1 year (Appendix Figure A1). Mean age at first calving was negatively related with woody cover (Figure 3a), with the linear model as the best model (R^2_{adj} = 0.84, n = 6, coefficient b_1 ± SE for woody cover = −16 ± 3.1, t = −5.2, p < 0.01). The curve estimation procedure showed no significant relationship between mean age at first calving or the standard deviation of the mean age at first calving and PAM, PAN or woody cover (all p > 0.05).

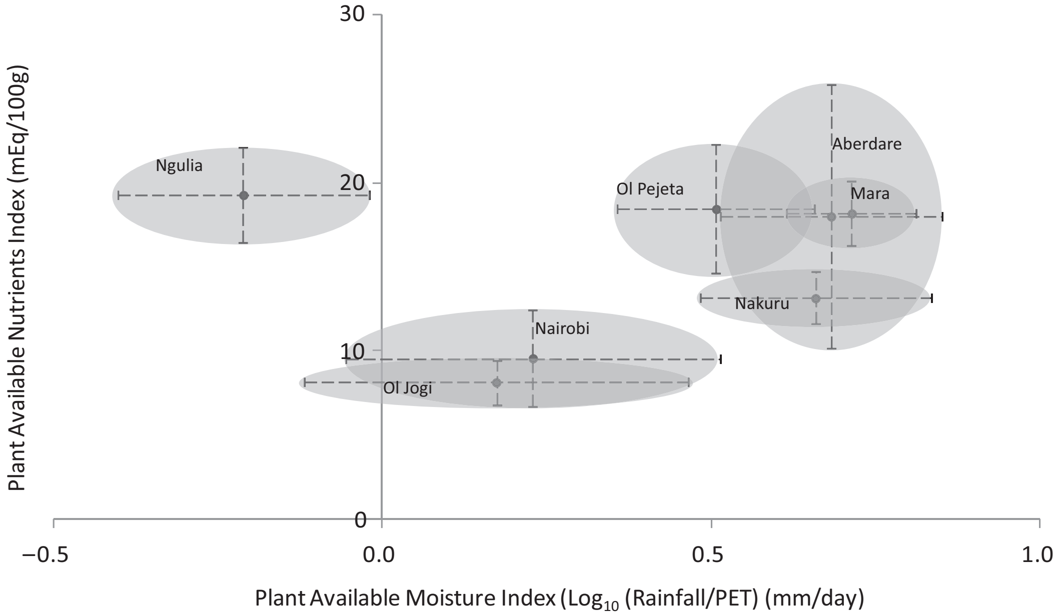

FIGURE 2 Seven black rhinoceros conservation areas plotted on a PAM-PAN plane. The x and y error bars are 95% confidence interval. The shading indicates the 95% CI of PAM and PAN for each of the rhinoceros conservation area. $n = 10$ for PAM in all areas. For PAN; $n = 179$ in Ngulia, $n = 17$ in Ol Jogi, $n = 28$ in Nairobi, $n = 19$ in Ol Pejeta, $n = 47$ in Nakuru, $n = 23$ in Aberdare and $n = 43$ in Mara. PAN-values are from the literature

Average inter-calving interval ranged between 1.5 and 6.0 years (Appendix Figure A2). The average inter-calving interval as related to PAN could be best described by an S-shaped curve ($\ln(Y) = b_0 + (b_1/X)$; PAN: $R^2_{adj} = 0.51$, $n = 7$, coefficient $b_1 \pm SE$ for 1/PAN = −3.0 ± 1.1, $t = -2.7$, $p < 0.05$) and a power function best described the relationship between the average inter-calving interval and woody cover ($\ln(Y) = \ln(b_0) + (b_1 * \ln(t))$; woody cover: $R^2_{adj} = 0.77$, $n = 6$, coefficient $b_1 \pm SE$ for ln(woody cover) = 0.1 ± 0.0, $t = 4.7$, $p < 0.01$). We found an increase in the mean inter-calving interval with increasing PAN (Figure 3b) and increasing woody cover (Figure 3c). There was no significant relationship between the mean inter-calving interval and the standard deviation of the mean inter-calving interval; and PAM, PAN or woody cover (all $p > 0.05$).

The yearly percentage of females calving averaged between 10% and 45% (Appendix Figure A3). There was a significant relationship between yearly percentage of females calving and PAM, and the interaction between PAM and PAN (Table 2). This model relationship is illustrated in Figure 4, which shows that there was a decrease in the predicted yearly percentage of females calving with increasing PAN at high levels of PAM, whereas PAN had no effect on the predicted yearly percentage of females calving at low levels of PAM. There was no significant correlation between yearly percentage of females calving and woody cover ($p > 0.05$).

4 | DISCUSSION

The observed early age at first calving in areas with high woody cover (Figure 3a) was consistent with the generally shorter inter-calving intervals in low PAN areas (Figure 3b) and in low woody cover (Figure 3c). Short inter-calving interval of ≤2.5 years was found in areas with PAN of less than 7.5 mEq/100 g, which supports the improved reproductive performance as PAN decreased. Our study supports the hypothesis that reproductive performance in mega-herbivores is influenced by the quantity and quality of forage that are functions of PAM and PAN. Our findings showed that a mega-browser reproduces better in areas of high PAM and low PAN reinforcing our knowledge of rainfall as the main driver of many large and mega-herbivores in the semi-arid tropics, through its effects on food resources (e.g. Illius & O'Connor, 2000). This is supported for black rhinoceros by historical evidence (Mitchell, 1953; Sidney, 1965) that showed black rhinoceros occur in abundance in areas such as coastal *nyika* (hinterlands) in Kenya, *Brachystegia* woodland of Malawi, and Rufiji delta in Selous Game Reserve in Tanzania where precipitation is high but soil fertility is low. However, mega-grazers follow a slightly different pattern (*e.g.* Frost et al., 1986, Walker & Menaut, 1988, Solbrig, 1990, Olff et al., 2002, Ahrestani et al., 2011) where they tend to be abundant in areas of intermediate PAM and high PAN. These findings contribute to our understanding that PAM and PAN determine the quantity and quality of different plant guilds differently and influence reproductive performance and spatial distribution of mega-browsers and mega-grazers. They also reinforce our knowledge on the nutritional requirements for different phases of the reproductive cycles for female black rhinoceros in captivity for maximal reproduction.

We suggest that PAN of ≤7.5 mEq/100 g allows for sufficient quantity of woody cover, leaves and twigs, such that above this threshold increases in PAN may have led to decreases in the quantity of woody cover as was observed elsewhere by Sankaran et al. (2007). However, inter-calving interval was longer (>2.5 years) in high woody

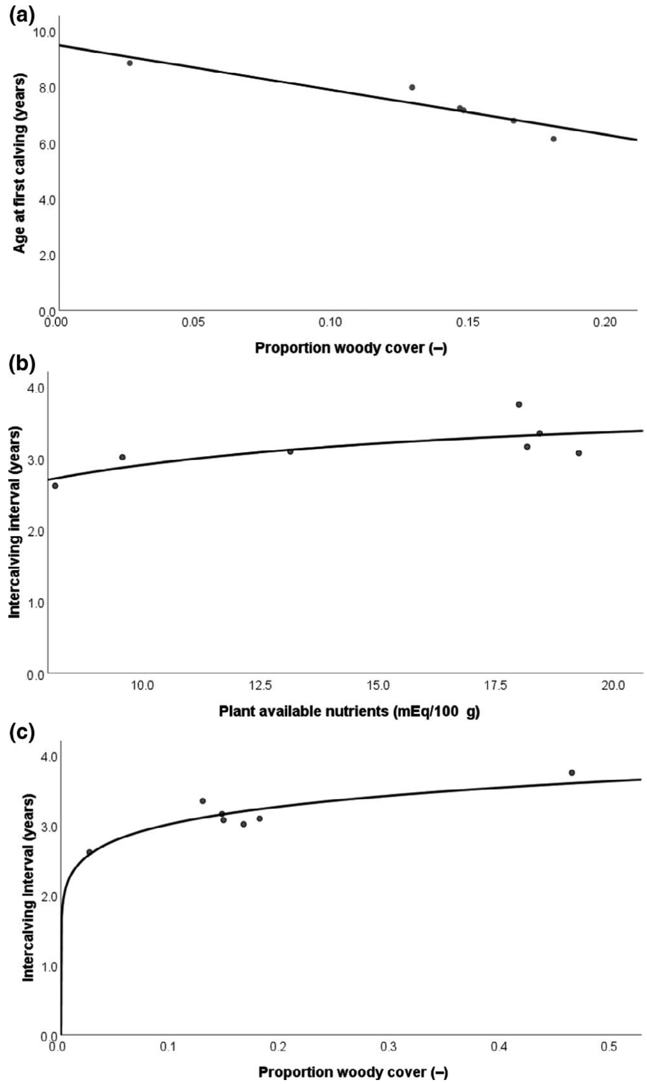

FIGURE 3 The relationships between (a) the age of first calving and woody cover (*linear model*); (b) the inter-calving interval and plant available nutrients (*S-shape curve*) and; (c) the inter-calving and woody cover (*power function*). The lines in the graph represent the best fitting regression models. (See text for statistics. Note the *Y*-axes do not start at 0)

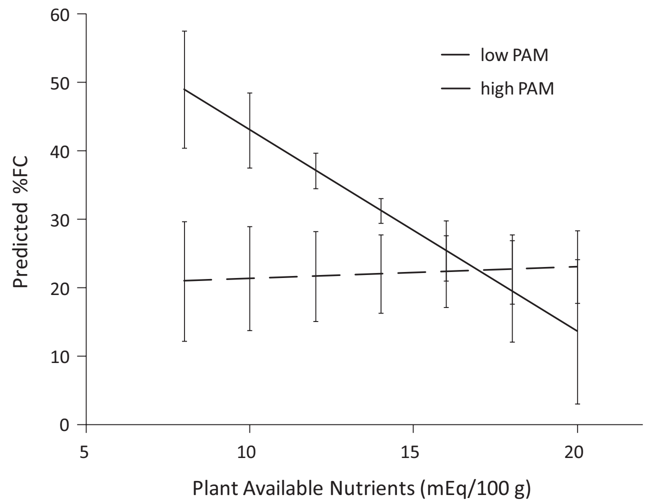

FIGURE 4 The predicted relationship between the yearly percentages of female black rhinoceros calving (%FC) and the interaction between Plant Available Moisture (PAM) and Plant Available Nutrients (PAN) in the seven study areas namely Aberdare, Nakuru, Mara, Ngulia, Nairobi, Ol Jogi and Ol Pejeta (see Table 2 for statistics). The error bars indicate the 95% confidence intervals of the predicted values. PAM index range from −0.1 to 0.6

cover (Figure 3c). These seemingly contradictory results are of interest, and we attribute them to the following two reasons:

Firstly, an early age at first calving of <7 years but longer inter-calving interval of >2.5 years in woody cover of >15% meant that early age at first calving is associated with vegetation characteristics of high woody cover, that is abundant leaves, twigs, forbs and shrubs, while short inter-calving interval is associated with vegetation characteristics of low woody cover of ≤15%, that is less abundant leaves, twigs, forbs and shrubs; and a characteristic of savannah ecosystems of high PAN (February, Higgins, Bond, & Swemmer, 2013; Sankaran et al., 2007; Walker & Langridge, 1997). Areas of low woody cover generally provide plants of high palatability (Prins & van-der-Jeugd, 1992; Russell & Ward, 2014) and high protein (Wright, Reich, & Westoby, 2001) with low lignin and low chemical compounds (Dierenfeld, Toit, & d., & Braselton, W. E., 1995; Wright et al., 2001). In our case, it could therefore be justifiably assumed that even though areas of low woody cover yielded less abundant leaves, twigs, forbs and shrubs, they were of high protein and of low chemical compounds.

Secondly, in horses (like rhinoceros also perissodactyls), age of puberty and first conception are affected by forage quality, but foaling at a young age often comes at the costs of a longer inter-foal period for the subsequent foal, though as compared to cattle this has been studied not much yet (Mantovani, Sartori, &

TABLE 2 Model relationship between the yearly percentage of female black rhinoceros calving and the interaction between Plant Available Moisture (PAM) and Plant Available Nutrients (PAN) in the seven study areas namely Aberdare, Nakuru, Mara, Ngulia, Nairobi, Ol Jogi and Ol Pejeta between 1993 and 2010 using Generalized Estimating Equations. The model shows a significant relationship between yearly percentage of females calving (n = 111) and PAM and interaction between PAM and PAN

Independent variable	Parameter estimate of GEE model (±*SE*)	Wald chi-square (χ^2)	*p*
Constant	27.1 (5.4)	24.99	<0.001
PAN (mEq/100 g)	−0.3 (0.3)	0.80	N.S.
PAM (mm/day)	76 (22)	11.49	<0.001
PAN × PAM	−4.5 (1.4)	10.26	<0.001

Pigozzi, 2013). Conception at too young an age in Grevy zebra's (*Equus grevyii*) may result in abortion (Asa et al., 2001) which may also point into a direction that young female perissodactyls may have difficulty foaling if the forage is not good enough. Indeed, in feral horses primiparous mares are less likely to foal the next year than multiparous mares (Roelle et al., 2010). Also in feral horses, there is density dependency too in fecundity of young mares (Grange, Duncan, & Gaillard, 2009), making a straightforward extrapolation to our study next to impossible. Since the gestation (more associated with age at first calving) and lactation (more associated with inter-calving interval) are energy and protein demanding phases, respectively, for mega-herbivores (Ahrestani, Langevelde, Heitkönig, & Prins, 2012; Geist, 1974; Prins, 1996), we would expect that the better the nutritional and energy requirements of (female) rhinos an area can meet, particularly in areas with high woody cover or areas with high PAM and low PAN, the earlier the age at first calving would be expected. Similar observations have been made in donkeys (Blench, 2004).

Energy has however been found to be the limiting black rhinoceros reproductive performance in the wild in South Africa (Shaw, 2011), in captivity in Zimbabwe (Atkinson, 1995) despite animals' intake of 25–35 kg daily. Lactation phase is more nutritional/protein than energy demanding for both female's body conditioning and survival of the calf. This is exhibited in herbivores that synchronise calving with seasons when forage is of high protein (Estes & Estes, 1979) and in female red deer in protein restrictions taking longer to recover body reserves before next parturition (Clutton-Brock & Coulson, 2002; Clutton-Brock, Guinness, & Albon, 1982). Areas of low woody cover are characterised by high-quality forage (Dierenfeld et al., 1995; Prins & van-der-Jeugd, 1993; Russell & Ward, 2014; Wright et al., 2001) and therefore likely to favour shorter inter-calving interval and subsequently higher yearly percentage of females calving. Black rhinoceros in Tswalu Kalahari Reserve in South Africa had an excellent inter-calving interval of 2.2 ± 0.1 (du Toit, 2001) in an energy limiting habitat but which offered sufficient protein from one wood plant species, *Acacia haematoxylon* in dry and wet seasons (Shaw, 2011). However, we can speculate that given lactation naturally downregulates the ovarian activity in black rhinoceros (T. Hildebrandt, 2011, *pers. comm*), as is in many mammalian species; and a possibility of the effects of interplay of intrinsic and extrinsic factors due to our small population sample size, the resultant inter-calving interval can be long in areas of high PAN favouring high protein forage.

The observed decrease in yearly percentage of females calving at high levels of PAM with increasing PAN and the lack of significant relationship between yearly percentage of females calving and PAN at low levels of PAM (Figure 4) can be explained by the influences of PAM and PAN on quantity and quality of woody cover (leaves, twigs, forbs and shrubs). Quantity of leaves, twigs, forbs and shrubs increases with increase in PAM (Barbosa et al., 2014; Owen-Smith, 1994, 2008; Singh & Singh, 2004), whereas quantity increases with decrease in PAN (Sankaran et al., 2007). Reproductive performance in the browsing black rhinoceros as influenced by quantity of forage would therefore be expected to be better in areas of high PAM with low PAN. This explains the good yearly percentage of females calving (33%–40%) (du Toit, 2001) recorded in this study in areas of high PAM particularly in Nakuru. Similar better reproductive and better stocking potentials for black rhinoceroses in Nakuru has been reported using a different approach of browse availability and suitability assessment (Adcock et al., 2007). The low yearly percentage of females calving of <29% and moderate inter-calving interval of slightly above 3 years in Ngulia despite its location in a moderate PAM and high PAN favourable for browse diet can be attributed to habitat degradation by intense inter-specific competition between 2000 and 2006 (Brett & Adcock, 2002; Okita-Ouma et al., 2008).

Yearly percentage of females calving was the reproductive performance measure that was best explained as a function of PAM and PAN. This is mainly because inherently yearly percentage of females calving compared to inter-calving interval or age at first calving has a large sample size that takes into account all females of breeding age. The average inter-calving interval excludes females that have calved once, whereas age at first calving excludes females whose birthdate accuracy is greater than ± 1 year.

In what may be viewed as a caveat of this study though not quite, is the PAM/PAN's assumption of the interplay between the deterministic density-dependent feedbacks such as intra- and inter-competitive interaction and the stochastic environmental processes in population regulation. Such an assumption is justifiable when studying a group of populations in heterogeneous environments rather than when studying a single population. The seven populations we studied had high variabilities in their deterministic and stochastic factors and even included human interventions such as translocations or expansion of available areas for black rhinoceros (Table 1),. thus provided a perfect opportunity to understand the relationships between PAM/PAN and woody cover and reproductive performance; and in exploring a new criterion for selecting suitable conservation areas for mega-browsers. This assumption was reinforced by the fact that all our study populations were 'stable.' In other words, over the many years of their existence, the deterministic and stochastic perturbations had led them to attaining points of 'equilibrium' and stability phase where their population over time (N_t) equalled 'carrying capacity' (K); and when fluctuations in N_t were within a constant range (e.g. Chamaillé-Jammes, Fritz, Valeix, Murindagomo, & Clobert, 2008; Gabriel, Saucy, & Bersier, 2005; Okita-Ouma, Amin, Van Langevelde, & Leader-Williams, 2009; Ross, 2009; Verhulst, 1838). More so mega-herbivores are not controlled top-down but bottom-up by food resources which are directly affected by PAM and PAN (Nicholson, 1933). Food limitation can result in lowered reproductive performance in mega-herbivores (see review in Li, Jiang, Tang, & Zeng, 2007). Therefore, our explainable results on the relationships between black rhinoceros reproductive performance indicators and PAM, PAN and woody cover are encouraging and a promising selection criterion for new conservation areas for (re)/introducing for maximal reproduction.

5 | CONCLUSION

Areas of high precipitation (PAM), low soil nutrients (PAN) and sparse woody cover yielded the best reproductive performance measures assuming a stability in the complex interplay between density dependence feedbacks and stochastic environmental processes in a population. The relationship between reproductive performance and woody cover showed that age at first calving was earlier, inter-calving interval was longer and yearly percentage of females calving was higher as woody cover increased. We found early age at first calving in areas with high PAM and low PAN, whereas inter-calving interval was not affected by PAM but was longer in areas of high PAN. The yearly percentage of females calving was high in areas with high PAM and low PAN, but it was not affected in areas with low PAM irrespective of the levels of PAN. We suggest that age at first calving in black rhinoceros is determined more by quantity of forage than are inter-calving interval and yearly percentage of females calving. These findings contribute to more understanding on the different influence of PAM and PAN in the quantity and quality of different plant guilds which in turn support reproductive performance in mega-herbivores. Besides the requirement of sufficient woody cover, the finding that black rhinoceros can thrive in area of low soil fertility and high precipitation is exciting as it has positive implications for what sort of habitats to use for the conservation of this mega-herbivore. Lands that are of low PAN and high PAM are generally not favourable for human habitation or for agriculture. Selection of such areas for conservation of black rhinoceros would benefit the animal and at the same time lead to a reduction in human-wildlife conflicts. Our findings thus contribute a new criterion on use of PAM and PAN to selecting conservation areas for maximising the reproductive performance of black rhinoceros. With these findings, our study can improve the conservation of mega-browsers and their habitat.

6 | DISCLAIMER

Findings, opinions conclusion and recommendation expressed in this material are those of the author(s) and the funding agencies do not accept any liability in this regard.

ACKNOWLEDGEMENTS

The Kenyan rhinoceros monitoring team collected and stored the demographic data. Kenya Wildlife Service provided the lead author with the time to carry out this research when he was an employee at the organisation. Financial and in-kind support was received from Leibniz Institute of Zoo Biology and Wildlife Research in Germany, Mohamed Bin Zayed Species Conservation Fund, Save the Elephants, Wageningen University, World Wide Fund for Nature in Kenya, Zoo D'Amneville in France and Zoological Society of London. Kenya Soil Survey and ISRIC-World Soil Information in Wageningen provided information on soils. Priya Koduganthi and Yoganand Kandasamy provided helpful insights. We thank Kevin Davey for writing the algorithms for efficient extraction of demographic data from KIFARU©, the Kenya Rhino Information System. Adrian Shrader, Farshid Ahrestani, Marcus Clauss, Rajan Amin and Shelley Waterland provided helpful comments. The authors have no conflict of interest in relation to this work.

CONFLICT OF INTEREST

The authors have no conflict of interest in relation to this work.

AUTHORS' CONTRIBUTIONS

B.O.-O. and H.T.T.P. initially thought of the PAM and PAN approach to population performance. F.v.L. helped with the statistical analyses and extraction of woody cover data. B.O.-O. collated all the rhino and soil nutrient data from the relevant sources. P.M. helped with the extraction of precipitation and temperature data and production of maps. B.O.-O. led the writing of the manuscript with extensive contributions and supervision from I.H. and H.T.T.P. S.v.W. provided useful comments and supervision. All authors have commented and approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

All data used in this research are available on request from the corresponding author. Data especially on individual rhino numbers and performance may be shared or made public by the permission from the Kenya Wildlife Service due to the sensitivity surrounding conservation of a critically endangered and protected species.

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How to cite this article: Okita-Ouma B, van Langevelde F, Heitkönig IMA, Maina P, van Wieren SE, Prins HHT. Relationships of reproductive performance indicators in black rhinoceros (*Diceros bicornis michaeli*) with plant available moisture, plant available nutrients and woody cover. *Afr J Ecol*. 2020;00:1–15. https://doi.org/10.1111/aje.12779

APPENDIX

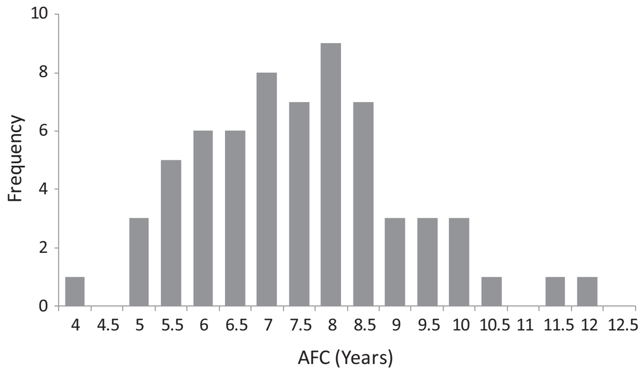

FIGURE A1 Frequency histogram of Ages at First Calving (AFC) for female black rhinoceroses ($n = 64$) of ±1 year birthdate accuracies in six populations in Kenya namely Nakuru, Mara, Ngulia, Nairobi, Ol Jogi and Ol Pejeta, between 1993 and 2010. Aberdare is excluded due to lack of data for females with ±1 year birthdate accuracies

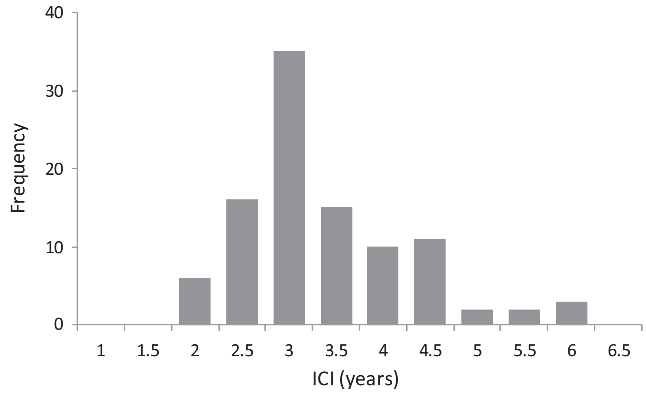

FIGURE A2 Frequency histogram of average Inter-calving Interval (ICI) for female black rhinoceroses ($n = 100$) with ≥2 calves in seven populations in Kenya namely Aberdare, Nakuru, Mara, Ngulia, Nairobi, Ol Jogi and Ol Pejeta between 1993 and 2010

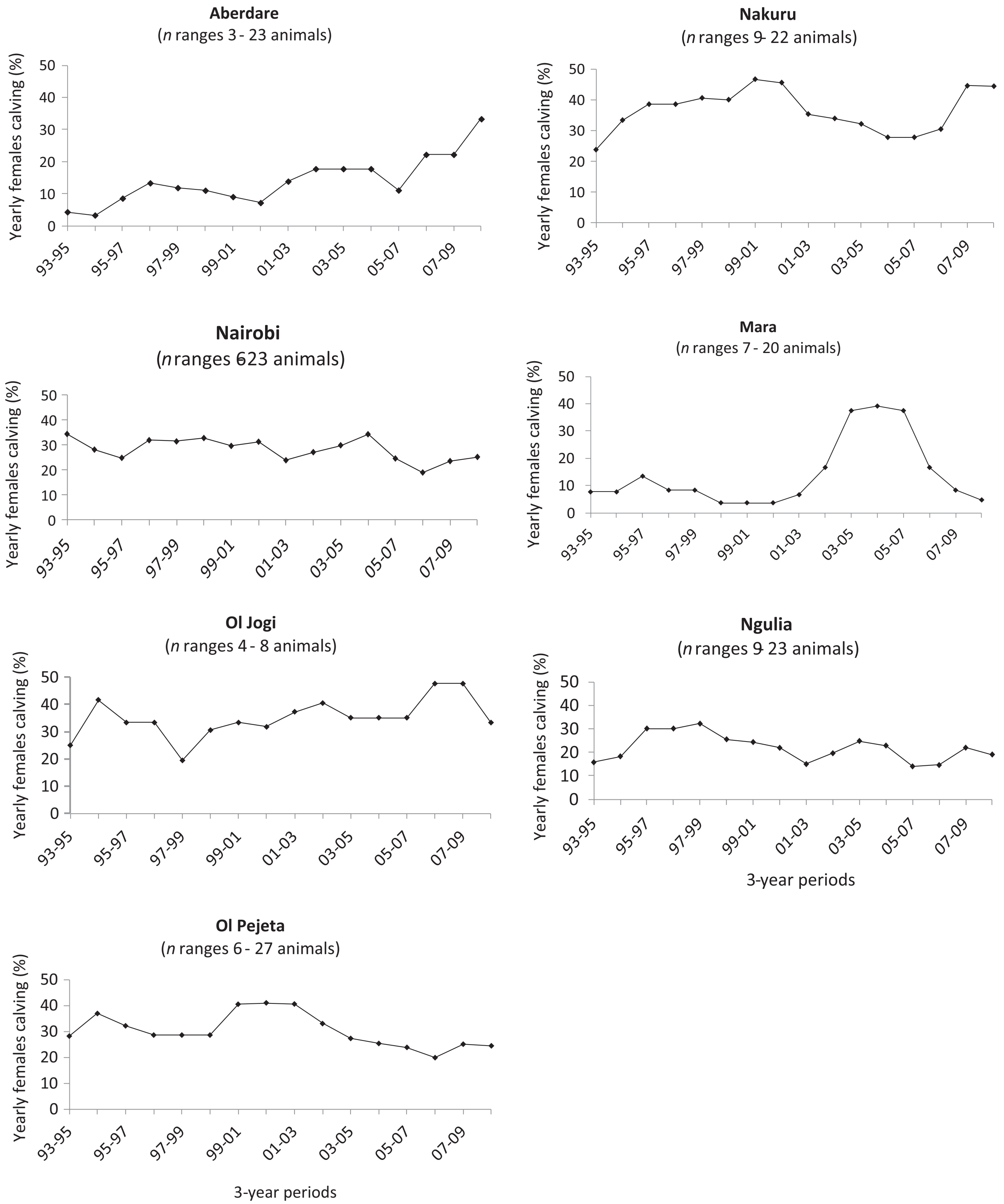

FIGURE A3 A 3-year moving average of yearly percentage of female black rhinoceros calving between 1993 and 2010 in seven study areas in Kenya. A FC >40% is excellent, 33%–40% is good, while <33% is below average performance