Population parameters, performance and insights into factors influencing the reproduction of the black rhinoceros *Diceros bicornis* in Namibia

Jeff R. Muntifering, Abigail Guerier, Piet Beytell and Ken Stratford

Abstract Estimating the population parameters, performance and factors that influence reproduction from long-term, individual-based monitoring data is the gold standard for effective wildlife management and conservation. Yet this information is often difficult and costly to collect or inaccessible to managers. We synthesized a 20-year set of individual-based monitoring data from a subset of black rhinoceros *Diceros bicornis* subpopulations across a range of environmental conditions in Namibia. Our findings demonstrate that despite the relatively arid landscape in Namibia, the black rhinoceros metapopulation is performing well, measured by age at first reproduction, inter-birth interval, population growth and survivorship. Information-theoretic modelling revealed that a univariate model including normalized differential vegetative index had a greater influence upon age at first reproduction than population density. The inter-birth interval model set identified cumulative rainfall during the 15 months prior to the birth month as the top model, although the mean normalized differential vegetative index during the inter-birth interval was comparable. There was little evidence for density-dependence effects on reproduction. These findings suggest that although browse quality could have a greater impact on parameters spanning multiple years, shorter-term parameters could be more influenced by rainfall. Our analysis also revealed a synchronous pattern of conceptions occurring in the rainy season. Our study provides a set of population parameter estimates for Namibian black rhinoceros subpopulations and preliminary insights on factors driving their reproduction. These expand our collective knowledge of global black rhinoceros population dynamics and improve our confidence and capability to adaptively manage the black rhinoceros metapopulation of Namibia.

Keywords Black rhinoceros, demography, *Diceros bicornis*, Namibia, normalized differential vegetative index, population parameters, rainfall, reproduction

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Introduction

Once distributed widely across sub-Saharan Africa, the African black rhinoceros *Diceros bicornis* population decreased from c. 65,000 in 1970 to less than 2,500 in 1992 (Amin et al., 2006). This unprecedented decline has been driven largely by the demand for rhinoceros horn in Asia, primarily for use in traditional medicine (Amin et al., 2006; Emslie et al., 2019) and, more recently, business gifts (Milliken & Shaw, 2012) and investment opportunities (Mason et al., 2012). After more than a decade of relatively low levels of poaching between the mid 1990s and 2007 (Emslie et al., 2019), the rate at which rhinoceros poaching has escalated over the past decade once again poses a serious threat to the long-term persistence of extant rhinoceros populations (Duffy et al., 2013).

Because of the precarious status of the black rhinoceros (the species is categorized as Critically Endangered on the IUCN Red List; Emslie, 2020), many extant populations are managed intensively for maximum growth (du Toit, 2006) in fenced protected areas or on private land, with a few populations persisting on formally unprotected, open communal lands (Muntifering, 2019). For management to achieve optimal growth targets, a sound understanding of the status and drivers of the relevant population dynamics is paramount. Heeding earlier calls for a shift towards more management-relevant research (Linklater, 2003), a number of applied studies of rhinoceros demographics have helped to advance our understanding of critical population dynamic issues for rhinoceros populations in situ. These include factors affecting rhinoceros sex ratios (Berkeley & Linklater, 2010), age at sexual maturity, inter-birth intervals and fecundity (Nhleko et al., 2017; Gedir et al., 2018), population performance indicators (Ferreira et al., 2011; Law et al., 2013; Law & Fike, 2018) as well as mortality rates in rhinoceros populations. Some studies have gone further by conducting population viability assessments (Thuo et al., 2015; Subedi et al., 2017) and/or building

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more complex and sophisticated population models (Brodie et al., 2011; Soka et al., 2014). Fundamental to the quality and usefulness of the results produced by these studies are not only the collection but also the availability of the underlying rhinoceros monitoring or census data.

Black rhinoceros monitoring and management in Namibia

Namibia has a long history of monitoring and managing black rhinoceroses (Joubert, 1996), informed largely by sound research and monitoring efforts that span over 5 decades (Joubert, 1971). Individual-based rhinoceros monitoring methods, primarily using identifiable features such as ear notches and horn shape, were implemented in north-west Namibia in the late 1980s (Britz & Loutit, 1989). These basic techniques were further enhanced with digital databases in the early 1990s (Brett, 1997) and more recently with the use of *SMART* conservation software (Cronin et al., 2021). *SMART* is currently being institutionalized across the majority of the protected areas in Namibia, including a growing number of communal and private freehold rhinoceros custodians.

Namibia is home to c. one-third of the global population of the black rhinoceros and 90% of the subspecies *Diceros bicornis bicornis* (Emslie et al., 2019). Although the majority of the black rhinoceroses in Namibia persist within national parks, several subpopulations also exist on communal and private lands in other areas of the country as part of the Namibian Black Rhinoceros Custodianship Programme. This programme allows for the establishment of black rhinoceros populations outside formally protected areas and is implemented by the Ministry of Environment, Forestry and Tourism. All black rhinoceroses in Namibia belong to the state and are hosted by landowners (communal conservancies or private freeholds) under the Namibian Black Rhinoceros Custodianship Programme. The Namibian Black Rhinoceros Custodianship Programme currently has 35 land units (10 communal conservancies and 25 commercial ranches) covering an area of c. 3,400,000 ha and hosting an estimated 560 individuals on freehold land and 150 individuals on communal land (Kötting, 2020). The black rhinoceros population inhabiting the communal lands of north-western Namibia is recognized by the IUCN African Rhino Specialist Group as a Key 1 population for species recovery because of its large size (Emslie, 2008). It is also the largest population of any rhinoceros species persisting outside a formally protected area (Muntifering, 2019), heightening both its conservation and tourism importance. The growth and expansion of this population provide evidence that black rhinoceroses could not only survive but possibly thrive on communal lands outside of formally protected estates in Namibia, creating new opportunities for range expansion and metapopulation growth.

Because of security restrictions or a lack of technical capacity, the vital knowledge base collected by the Black Rhinoceros Custodians in Namibia is often not synthesized, available or presented in a manner that promotes informed decision-making in support of black rhinoceros conservation. Aligned with evidence-based management principles for more effective rhinoceros conservation (du Toit, 2006), we summarize and present black rhinoceros population parameters and performance metrics in Namibia. Using these data, we also explore and evaluate a series of alternative hypotheses on the type and magnitude of the environmental and demographic effects driving key reproductive parameters. We utilize a unique 20-year set of individual-based rhinoceros monitoring data across four subpopulations that includes both an extended wet and an extended dry period. The provision of such baseline population parameter estimates and insights into drivers of key reproductive parameters is vital to guide or refine management objectives and measures. These insights also form the basis for subsequent, more sophisticated population and parameter modelling.

Study area

Our analysis focused on four black rhinoceros subpopulations ranging from the arid, far western gravel plains of Namibia to the much denser savannah in the east of the country, covering c. 750 km from west to east. Within this context, we categorized the four subpopulations as Far West, Mid West, Central and Far East (see Table 1 for a detailed summary of the characteristics of each subpopulation). The precise locations of the subpopulations are omitted for security reasons.

Methods

Rhinoceros monitoring data

All rhinoceroses within each subpopulation have been monitored on an individual basis for a number of years, and these monitoring data have been compiled into a standardized database. For the Far West and Mid West subpopulations, individual-based rhinoceros monitoring has been operating since the mid 1980s (Britz & Loutit, 1989), carried out primarily by a local field-based NGO (Save the Rhino Trust). The Central subpopulation undergoes individual-based rhinoceros monitoring through the use of tracking teams both on foot and in vehicles, supplemented by the use of aerial surveys and camera traps. Monitoring in the Far East subpopulation is conducted by the local Conservancy Game Guards and staff from the Ministry of Environment, Forestry and Tourism who record sightings from vehicle-based patrols and remote cameras placed at water points. Rhinoceros monitoring data used for the analyses

Table 1 Summary of broad environmental characteristics at the sites inhabited by Namibian subpopulations of the black rhinoceros *Diceros bicornis*.

	Subpopulation			
Characteristics	Far West	Mid West	Central	Far East
Biome[1]	Namib Desert	Nama Karoo	Tree & shrub savannah (*Acacia*)	Tree & shrub savannah (broadleaf)
Dominant landscape[1]	Gravel plains	Kunene hills	Various	Kalahari sandveld
Dominant vegetation[1]	Sparse grassland	Varied shrubland & grassland	Karstveld	Broadleaved woodlands
Water availability	Ephemeral springs & seeps	Ephemeral springs	Human-made boreholes & ephemeral springs	Human-made boreholes

[1]From Mendelsohn (2010).

spanned 2000–2019 for all subpopulations except for the Far East subpopulation, for which monitoring began in 2008. Additional information on monitoring methods can be found in the Supplementary Materials.

Population demographic data analysis

Life stages We use the rhinoceros life stages proposed previously (Law & Linklater, 2014), with three distinct stages for male and female black rhinoceroses. Both males and females are categorized as calves from birth to separation from their mother or their fourth birthday (whichever comes first). The subadult stage follows, until the first calving or the individual's seventh birthday (whichever comes first) for females; for males this stage ends on their eighth birthday. Once the females give birth or on their seventh birthday, and for males on their eighth birthday, they enter the adult stage.

Age at first reproduction We defined age at first reproduction as the age of the female when she gave birth to her first calf. We included in our analysis only females that had their first birth within the study period and for which we had an accurate record of their date of birth.

Inter-birth interval Starting from the date of first reproduction, we calculated inter-birth intervals in months for each subsequent calf if we deemed their estimated date of birth to be accurate to within 1 month. As most breeding females gave birth to more than one calf during the study period, we used the mean inter-birth interval of each breeding female for our overall parameter estimates, to reduce bias towards females that produced more calves. We considered all inter-birth intervals for the covariate modelling (see below).

Fertility rates We used a simple calculation method for mean annual fertility rate (Nhleko et al., 2017) for each subpopulation: Fertility $\text{rate}_t = \text{Births}_t/\text{Ad Female}_{t-1}$, where Births_t is the number of known new births during the year and Ad Female_{t-1} is the number of breeding-age females surviving in the subpopulation at the beginning of the year. For the Central subpopulation we excluded the founder females arriving in 2001 and 2002 from this analysis.

Stage-specific survivorship We used the Kaplan–Meier or known fates method to estimate annual and mean stage-based survival rates (Kaplan & Meier, 1958). We then averaged annual survival estimates for each life stage (i.e. year 1 of calf stage, year 2 of calf stage, etc.) to obtain a single survival estimate for each life stage. Additional explanations of our survivorship calculations are presented in the Supplementary Materials, in the section Stage-Specific Survivorship.

Additional population metrics Using our annual population data, we also estimated population structure and growth, two key additional performance indicators. We expressed growth rates as a percentage normalized relative to the maximum population size for each subpopulation, to illustrate trends. We also assessed calf sex ratios and conception/birth months to provide an indication of any sex ratio skew, including the degree to which Namibian black rhinoceroses align with reported typical asynchronous calving (and breeding) behaviour (Hrabar & du Toit, 2005). Two additional performance metrics commonly cited by the IUCN (Rhino Management Group, 2015) are presented in Supplementary Table 1: (1) proportion of population as calves < 1 year old and (2) proportion of the population as calves < 3.5 years old at the end of each year.

Uncertainty in monitoring data Because of the long intervals between sightings for many individual rhinoceroses, the likelihood of observing and recording the precise date of a rhinoceros birth or death is small. As growing rhinoceros calves display accurately measurable key characteristics such as size relative to the cow and horn growth, it is possible to obtain reasonably accurate (± 1 month) dates of births for calves observed within the first 3–9 months of life. However, as date of birth is the critical baseline for both the age at first reproduction and inter-birth interval parameters, any uncertainty > 3–6 months could be problematic. Although modelling age at first reproduction had previously been reported as robust to uncertainties in monitoring data (Law et al., 2013), we included in our analysis only females for which we had dates of birth and dates of first calf to within 1 month accuracy, to be conservative. Obtaining precise dates of deaths is even more challenging than estimating the date of birth. However, because our survival estimates are summarized as annual rates, we only need to be confident that the mortality occurred in a given calendar year. We classified any rhinoceroses not observed during the calendar year as 'censored' and removed them from the annual survival estimates.

Reproductive performance covariate analysis and model selection In addition to our main objective of estimating parameters, we examined a set of biologically plausible hypotheses that include factors that could influence key reproductive parameters such as age at first reproduction and inter-birth interval. We chose these parameters (response variables) because their estimates could be made on a finer scale (i.e. monthly) that aligned with meaningful temporal variation in any environmental and demographic factors that could be driving them. We then selected covariates that, based on our collective knowledge of black rhinoceros biology and ecology and a literature review of other similar analyses (Hrabar & du Toit, 2005; Law et al., 2013), could influence these response variables. The covariates selected included environmental factors such as measures for rainfall, normalized digital vegetative index (NDVI) and soil content as well as biological factors such as rhinoceros population density, maternal age and experience (measured as the number of successfully weaned calves prior to the latest calf), and sex of the previous calf. Detailed descriptions of the extraction and application of each covariate in the modelling are provided in the Supplementary Materials, in the section Reproductive Performance Covariate Analysis and Model Selection. Given the complexity of reproduction and our relatively small sample size, our modelling objective was to explore the evidence for or against key variables driving reproduction and their relative influence rather than building sophisticated projection models with high predictive power. We used an information-theoretic approach (Anderson, 2008) as a model selection framework to rank the full set of all possible models and to ensure that each explanatory variable was balanced in the model set. This approach enabled both the top model to be identified (based on the lowest value of the Akaike information criterion corrected for small sample size, AICc), including the degree of evidence to support its selection (highest Akaike weight), and a measure of the relative importance of each explanatory variable. We conducted modelling analysis using *R 3.6.1* (R Core Team, 2020). For fitting models, we used the function *lm* (included in the base *R* package). We adhered to linear mixed-effects best practices (Harrison et al., 2018) and deployed the *lme4* (Bates, 2010) and *r2glmm* (Jaeger, 2017) packages for fitting and examining the mixed-effects models. We used the *MuMIn* package (Barton, 2016) for model selection.

Results

We processed a set of 20 years (2000–2019) of individual-based sighting data collected and compiled by Save the Rhino Trust for the Far West and Mid West subpopulations. For the Central subpopulation we also processed individual-based sighting data for the period 2000–2019. Data were collected and compiled by the Ministry of Environment, Forestry and Tourism for the Far East subpopulation, following the reintroduction of rhinoceroses to this area in 2008–2019. Overall parameter estimates specific to each subpopulation, age at first reproduction, inter-birth interval, fertility rate and population growth rate are summarized in Table 2, with further detail including subpopulation-specific means, medians and variation given in the Supplementary Materials.

Population demographic data analysis

Age at first reproduction A total of 32 females (Far West = 8 breeding females, Mid West = 7, Central = 15 and Far East = 2) produced their first calf during the study period, with a mean age at first reproduction of 7.4 years (95% CI = 73–105 months). This is towards the upper end of the age at first reproduction benchmark range of the IUCN of 6.0–7.5 years. The lowest age of 5.2 years was recorded in the Far East subpopulation and the oldest age of 15.8 years was in the Far West subpopulation (Fig. 1a).

Inter-birth interval Overall, 46 breeding females produced a total of 124 calves during the study period (Far West = 8 breeding females, 21 calves; Mid West = 8 breeding females, 34 calves; Central = 26 breeding females, 57 calves and Far East = 4 breeding females, 12 calves), with a mean inter-birth interval of 38 months (95% CI = 34–43 months). This falls outside the upper end of the inter-birth interval benchmark range of the IUCN of 30–36 months. The shortest inter-birth interval was 18 months recorded in the Far East subpopulation, and the longest inter-birth interval was 71 months in the Far West subpopulation (Fig. 1b).

Table 2 Summary table of population performance and environmental parameters associated with each subpopulation, and the IUCN African Rhino Specialist Group benchmark. Values are means, with 95% CIs in parentheses.

	Far West	Mid West	Central	Far East	IUCN benchmark
Population performance indicators					
Age at first reproduction (years)	9.1 (7.9–10.3)	7.7 (6.4–9.0)	7.1 (6.8–7.4)	5.8 (4.7–6.9)	6.0–7.5
Inter-birth interval (months)	44.6 (61.6–61.6)	39.1 (33.7–44.5)	33.1 (31.5–34.7)	36.4 (31.3–41.5)	30–36
Fertility rate (mean annual)	0.27 (0.17–0.37)	0.21 (0.11–0.31)	0.34 (0.14–0.54)	0.40 (0.30–0.50)	33–40
Population growth rate (mean annual %)	4.0	3.3	8.2	9.7	≥ 5
Environmental parameters					
NDVI[1]	864	2,674	3,635	8,142	
Rainfall isopleth[2] (annual mean in mm)	0–50	100–150	350–400	450–500	

[1] NDVI, normalized differential vegetative index; averaged annual estimates across the 20-year study period (2000–2019); data from USGS (2021).

[2] From Mendelsohn (2010).

Fertility rates The estimated annual mean fertility rate across the subpopulations during the study period was 31% (95% CI = 23–39%). This is slightly lower than the fertility rate benchmark range of the IUCN of 33–40%. Fertility rates of zero were recorded in both the Far West and Mid West subpopulations for a number of years (2003–2006 and 2016–2018). The Central subpopulation also recorded a single zero fertility rate in 2003. A fertility rate of 100% was recorded in the Mid West subpopulation in 2015, and two high records of 67% occurred in the Far West (2007) and Far East (2012) subpopulations.

Stage-specific survivorship Overall, the annual survival rate of Namibian black rhinoceroses was, on average, high for all stages, with mean values for calves of 0.97 (95% CI = 0.95–0.99), subadults of 0.98 (95% CI = 0.96–1.00), adult females of 0.98 (95% CI = 0.96–1.00) and adult males of 0.95 (95% CI = 0.88–1.00). The lowest mean annual survival rate was 0.85 (95% CI = 0.64–1.00) recorded in the Far West subpopulation for adult males, whereas the Far East subpopulation had a 100% survival rate across all life stages. Population numbers, normalized relative to the maximum, over time were similar across all subpopulations until 2012, when both the Far West and Mid West subpopulations experienced substantial declines. The Mid West subpopulation began to recover in 2014, whereas the Far West subpopulation continued to decline (Fig. 2a). Figure 3b illustrates the proportional change in stage-class structure over time for each subpopulation. The Far West subpopulation showed high variation in the per cent of the adult (range 50–80%) and calf stages (range 5–35%) amongst the total subpopulation, with subadults being less variable (range 5–15%). In the Mid West subpopulation, the per cent of the subadult stage was highly variable over time (range 0–30%), and there were similarly large fluctuations in the adult stage (range 35–65%) and even greater variability in the calf stage (range 15–55%). The structure of the Central subpopulation appeared more stable, especially since 2008, following a growth period during the early establishment of this subpopulation, with adult, subadult and calf ranges of 55–65%, 20–30% and 20–25%, respectively. The Far East subpopulation showed a clear increase in the per cent of subadults from c. 10–15% at establishment in 2008 to > 40% presently. In addition, the per cent of calves in this subpopulation increased from 15% in 2008 to just over 40% in 2013, but then decreased to 15% again in 2016.

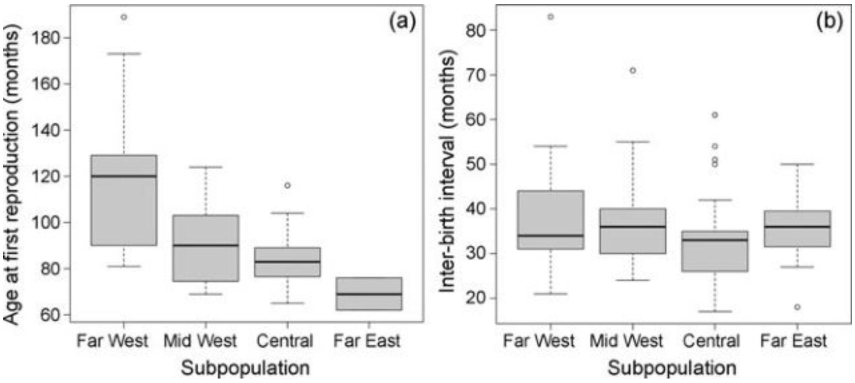
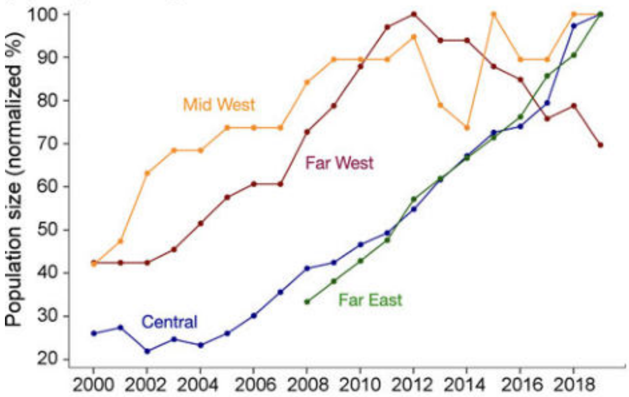


Fig. 1 (a) Age at first reproduction and (b) inter-birth interval of the Namibian black rhinoceros *Diceros bicornis* subpopulations. The black line represents the mean, the box represents the interquartile, the whiskers represent the maximum and minium and the circles show the outliers.

(a) Population growth



(b) Population structure

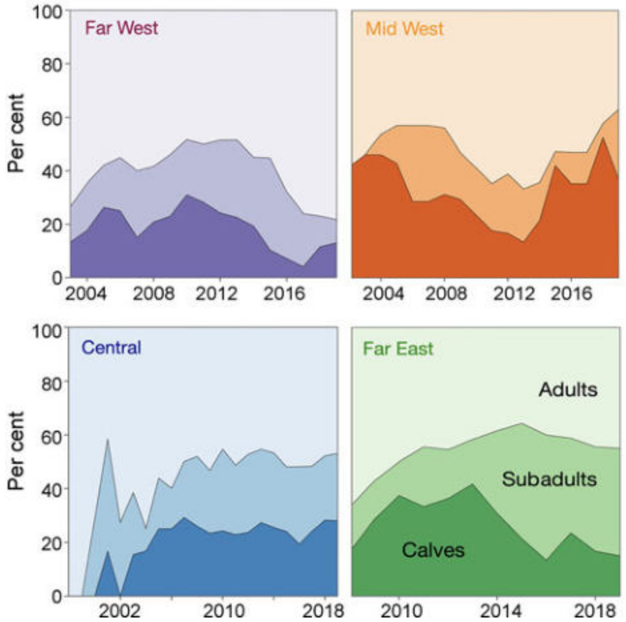


FIG. 2 Summary figures of time-series of the Namibian black rhinoceros subpopulations during 2000–2019, for (a) population growth trends using annual population size normalized by the maximum for each subpopulation and (b) annual proportional population structure (per cent of each life stage of the total subpopulation, with the shaded areas representing, from top to bottom, adult, subadult and calf stages).

Additional population metrics Calf sex ratios on average were 110 males to 100 females. However, two of the subpopulations had skewed ratios, with the Central subpopulation showing a slight bias towards females and the Far East subpopulation more noticeably skewed towards males. A total of 116 birth months exhibited some degree of seasonality overall, with 47% of births taking place during the 4 months at the beginning of the dry season, and the fewest births occurring during the end of the dry season/start of wet season. Estimated conception dates thus also exhibited seasonality, with peak conceptions occurring during the February–April wet season (Fig. 3).

Covariate analysis of key reproductive performance parameters

For age at first reproduction, our ranked candidate model set for both mean and cumulative rainfall for 6, 15 and 24 months and mean NDVI for 6, 15 and 24 months prior to first calving confirmed that mean NDVI for the prior 15 months (NDVI 15) was the top variable (Supplementary Table 2), with 58.2% of the Akaike weight. The model also performed well, with an adjusted R^2 of 0.282, which was statistically significant ($P < 0.002$). Our tests of two soil variables (carbon and nitrogen content) performed below NDVI and population density and thus we omitted these soil variables from the final model set. Because of our small sample size for age at first reproduction ($n = 32$), we restricted our final candidate model set to two explanatory variables: mean NDVI 15 and population density (Fig. 4).

The top model presented in Table 3 for age at first reproduction was mean NDVI 15 (Akaike weight = 51.2%), although a model including both NDVI and population density performed similarly well (Akaike weight = 48.8%). The relative importance of NDVI 15 was 1.000 compared to 0.488 for population density.

Following systematic reduction of highly correlated variables for the inter-birth interval dataset (Supplementary Materials), we selected five explanatory variables in the

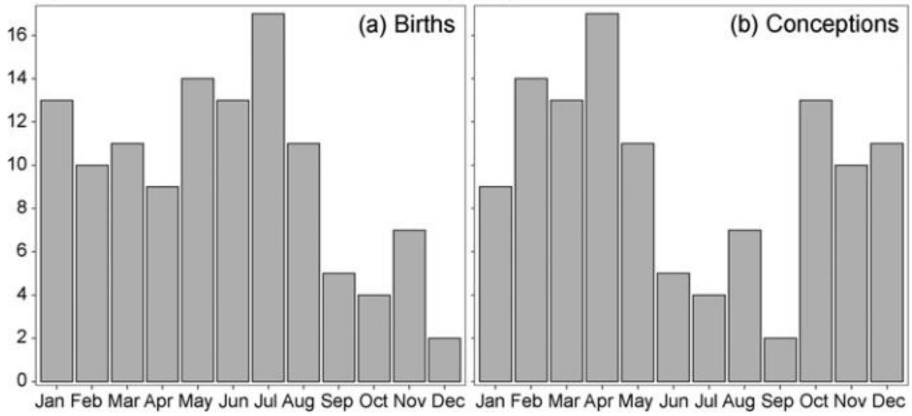


FIG. 3 Pooled frequency distribution ($n = 116$) by month of Namibian black rhinoceros (a) births and (b) estimated conceptions by backdating one gestation period (15 months) from the observed birth month.

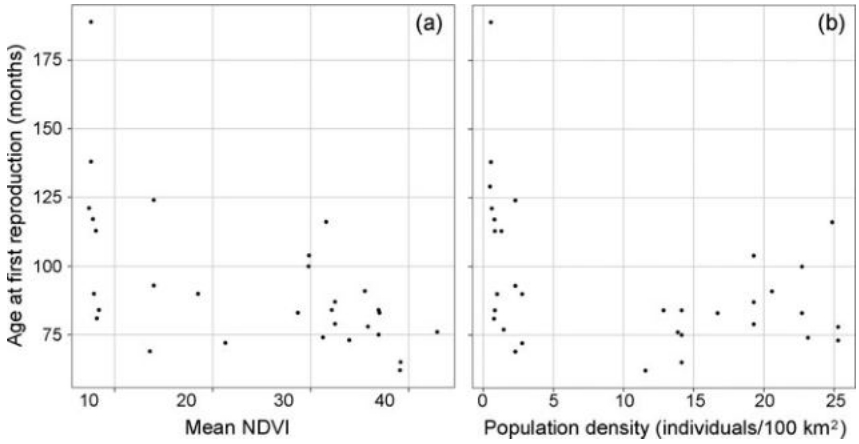


FIG. 4 Scatter plots illustrating relationships between age at first reproduction and (a) mean normalized digital vegetative index (NDVI) over a 15-month period prior to first calving and (b) population density. Three samples were removed from (a) because of missing NDVI data (Table 2).

final candidate model set: (1) maternal experience, (2) cumulative rainfall for 6 months prior to the beginning of an inter-birth interval, (3) mean NDVI during inter-birth interval, (4) population density, and (5) sex of the preceding calf. As our inter-birth interval dataset included reasonable-sized clusters of data (hierarchical) by site (n = 4) and by maternal ID (n = 35), we explored whether including random effect(s) in the models would be appropriate. However, diagnostic tests, small sample sizes within clusters (Harrison et al., 2018) and comparing both the marginal R^2 (fixed effects only) and conditional R^2 (including the random effects), as well as a likelihood ratio test to examine the significance of the random effect in the model, produced little evidence that including either or both of the random effects would improve model performance (Supplementary Table 5). Figure 5 provides scatterplots for inter-birth interval as a function of the four continuous fixed effects. The mean inter-birth interval following the birth of a male calf was 33.7 months (95% CI = 26.0–41.4 months; n = 51) and the mean inter-birth interval following the birth of a female calf was 35.8 months (95% CI = 25.2–46.4 months; n = 60).

The global linear model produced little evidence that any of our selected explanatory variables contributed to the inter-birth interval response (adjusted R^2 = 0.021), and no single explanatory variable was significant (Supplementary Table 6). The model ranking results presented in Table 4 list 23 models (out of 32 possible models) that had a ΔAICc of < 4. The Akaike weight was distributed evenly across models, with the top two models only accounting for c. 20% of the cumulative weight. The best model (see Supplementary Materials), which only included the prior rain predictor, was significant (P = 0.036) but still only explained 3.5% of the variance in the data (adjusted R^2 = 0.035).

Discussion

Our study sought to collate and analyse a unique dataset based on long-term, individual-based monitoring of black rhinoceroses in Namibia, to establish estimates of key parameters that could not only be used to revise IUCN benchmarks (particularly for populations existing in marginal or suboptimal areas) but also provide key inputs into more sophisticated population models. Overall, the means and variations of demographic parameters estimated in this study (age at first reproduction, inter-birth interval, fertility rate and annual survivorship) overlap with the IUCN benchmarks and are consistent with parameter estimates reported for South Africa (Hrabar & du Toit, 2005; Law et al., 2013; Nhleko et al., 2017; see Supplementary Table 8 for comparisons). We did observe, however, large variability across the Namibian subpopulations. We recorded below-benchmark performance across all variables

TABLE 3 Summary of general linear model ranking results for covariate effects on black rhinoceros age at first reproduction (Fig. 5), showing the number of model parameters (*K*), a measure of model goodness of fit expressed as log likelihood (logLik), Akaike information criterion corrected for small sample size (AICc), difference in AICc from the best performing model (ΔAICc), Akaike weight (ωi) and the adjusted R^2 value of each model.

Model	*K*	logLik	AICc	ΔAICc	ωi	R^2	P-value
NDVI 15[1]	3	−121.048	249.05	0.00	0.512	0.283	0.002
NDVI 15[1] + population density	4	−119.743	249.15	0.10	0.488	0.319	0.003
Population density	3	−138.697	284.25	35.20	0.000	0.100	0.043
Base (null model)	2	−140.913	286.24	37.19	0.000	0.000	N/A

[1] NDVI 15, mean normalized digital vegetative index in the 15 months prior to calving.

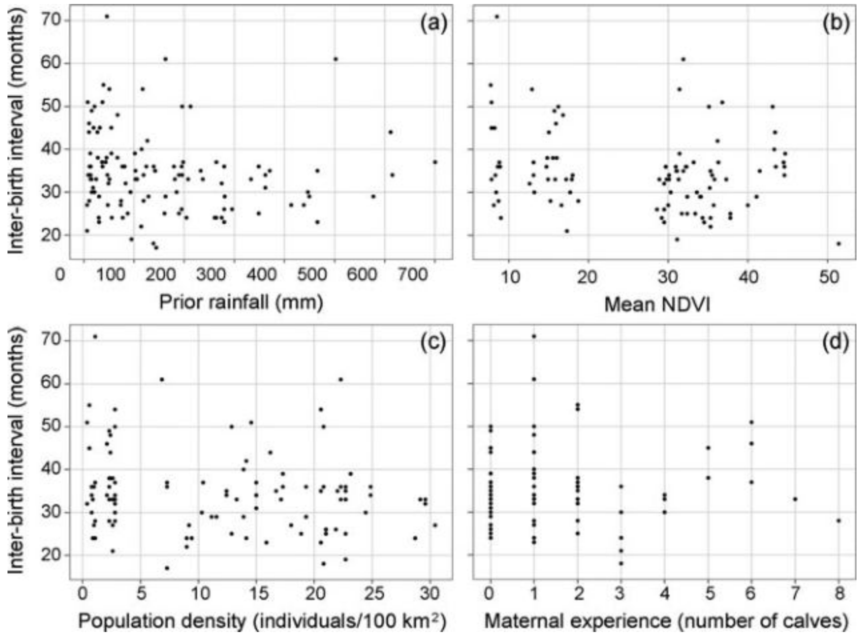


FIG. 5 Scatter plots illustrating relationships between inter-birth interval and (a) cumulative prior rainfall during the 15-month period before the inter-birth interval, (b) mean normalized digital vegetative index (NDVI) during the inter-birth interval, (c) population density and (d) maternal experience (measured in number of prior calves successfully weaned; Table 3).

in the Far West and Mid West subpopulations, especially for the key demographic parameters of age at first reproduction and inter-birth interval (Tables 1 & 2). As we found no evidence to suggest that rhinoceros population density had much influence on either age at first reproduction or inter-birth interval, we suspect that these relatively poor performance measures are more likely to be driven by lower-quality habitat linked to substantially reduced rainfall affecting browse quality and quantity. Nonetheless, these subpopulations continue to grow, and establishing such long-term parameter estimates and their variabilities across space and time is informative for broadening our understanding of black rhinoceros population dynamics in more resource-limited systems such as west Kunene.

TABLE 4 Summary table of general linear model ranking results for covariate effects on inter-birth interval of the black rhinoceros (Fig. 5).

Model[1]	K	logLik	AICc	ΔAICc	ωi
Pr	3	−361.550	729.3	0	0.112
NDVIa	3	−361.749	729.7	0.40	0.092
ME, Pr	4	−360.690	729.8	0.45	0.089
PD	3	−361.960	730.2	0.82	0.074
PD, Pr	4	−360.963	730.3	1.00	0.068
NDVIa, ME	4	−361.156	730.7	1.38	0.056
NDVIa, Pr	4	−361.163	730.7	1.40	0.056
ME, PD, Pr	5	−360.276	731.2	1.84	0.045
NDVIa, ME, Pr	5	−360.307	731.3	1.90	0.043
NDVIa, PD	4	−361.543	731.5	2.16	0.038
CS, Pr	4	−361.544	731.5	2.16	0.038
Base (null model)	2	−363.813	731.7	2.40	0.034
ME, PD	4	−361.676	731.8	2.42	0.033
CS, NDVIa	4	−361.719	731.9	2.51	0.032
CS, ME, Pr	5	−360.683	732.0	2.65	0.030
CS, PD	4	−361.900	732.2	2.87	0.027
NDVIa, PD, Pr	5	−360.936	732.5	3.16	0.023
CS, PD, Pr	5	−360.957	732.6	3.20	0.023
NDVIa, ME, PD	5	−361.054	732.7	3.40	0.020
CS, NDVIa, ME	5	−361.114	732.9	3.52	0.019
CS, NDVIa, Pr	5	−361.158	733.0	3.61	0.018
ME	3	−363.506	733.3	3.91	0.016
NDVIa, ME, PD, Pr	6	−360.207	733.3	3.97	0.015

[1] Pr, cumulative rainfall over the 15-month period prior to the month of conception; NDVIa, mean NDVI during inter-birth interval; ME, maternal experience (number of prior successfully weaned calves); PD, population density; CS, sex of previous calf.

Although age at first reproduction and inter-birth interval values are critical to understanding how breeding females are performing within a subpopulation, fertility rates provide insights about females across the entire population. Fertility rates for black rhinoceroses have been reported primarily from South Africa, with 16–45% in Pilanesberg National Park (Hrabar & du Toit, 2005), 33–41% in the Great Fish River Nature Reserve (Law et al., 2013) and 17–34% in Hluhluwe–iMfolozi Park (Nhleko et al., 2017). We found that Namibian subpopulations had fertility rates ranging between 21% (Mid West subpopulation) and 40% (Far East subpopulation, suggestive of the high-quality habitat in this area). However, the mean fertility rate in Namibia (31%) is slightly lower than the IUCN benchmark of 33%, with the two western subpopulations falling far below this benchmark. Two population performance indicators, per cent of calves < 1 year old (9%) and per cent of calves < 3.5 years old (27%), were close to the IUCN benchmarks of 8% and 28%, respectively.

The annual survivorship of rhinoceroses in Namibia fell mostly within the IUCN benchmark of 96% (du Toit, 2006), with the exception being the estimated 85%

survivorship of adult males in the Far West subpopulation. This effect might be slightly exaggerated because of the small sample size of adult males in the Far West subpopulation (10) and the greater effect of droughts, as all mortalities of adult males were natural deaths. No evidence of any fighting between males was reported at any of the located carcasses. There was also a slightly lower survivorship of adult males (97%) compared to females (99%) in the Central subpopulation, probably because of increased male-to-male fighting. Conversely, the relatively high calf survivorship across all subpopulations, with a mean annual survivorship of 97%, was noteworthy considering that black rhinoceros calf mortality rates within the first year after birth have been reported previously as 8–14% (du Toit, 2006).

Previous studies have demonstrated that stable black rhinoceros populations are composed of 60–70% reproductively mature adults, whereas increasing populations contain 45–55% reproductive mature adults (Owen-Smith, 1989). The subpopulation structures in our study differed, which can probably be attributed to the site-specific time since each subpopulation was established, with some biological management and climate conditions driving the variability in the observed growth and decline of subpopulations. For example, the Far East and the Mid West subpopulations are both characterized currently as being in a growth phase driven by the recent establishment of the Far East subpopulation and the active biological management of adult rhinoceroses in the Mid West subpopulation (i.e. translocations of individuals from this subpopulation, which may stimulate higher birth rates by reducing population density). Conversely, the Central and Far West subpopulations exhibit more stable structures as both have passed through initial rapid growth phases following their establishment, with few to no removals for translocation. The extended drought beginning in 2012 has had greater proportional impact on the structure of the Far West subpopulation compared to other subpopulations, with lower survival and fewer calves being born, resulting in a declining subpopulation.

Our modelling of the age at first reproduction and inter-birth interval parameters provided several novel insights, although with limitations because of the small sample size. Firstly, and most importantly, neither model performed particularly well. Although this suggests that we are some way from obtaining a thorough understanding of what drives these complex reproductive parameters, the model performance was similar to other studies that attempted to model these effects (Hrabar & du Toit, 2005; Law et al., 2013). There are probably other factors that we did not record that could be driving reproductive success, such as a more fine-tuned spatial and temporal alignment of environmental variables (e.g. NDVI) to specific individual space use rather than parameters averaged over the space available. Secondly, our inclusion of NDVI as a more direct measure of vegetative productivity outperformed the explanatory contribution of rainfall in the model of age at first reproduction, but this was not the case entirely in the inter-birth interval model. In the inter-birth interval model, mean NDVI outperformed rainfall during the inter-birth interval, but rainfall prior to the onset of an inter-birth interval was the most important variable in the model set, suggesting Namibian black rhinoceroses may breed synchronously. This is also supported by the fact that the majority of conceptions occur during the rainy season (October–May) in Namibia, where there is a similar seasonal pattern in rainfall across the country, although the absolute amount of rainfall varies between regions (Supplementary Fig. 9). This evidence for synchronous breeding is contrary to previous observations suggesting that black rhinoceroses are asynchronous breeders (Hrabar & du Toit, 2005), and further research is required to examine these patterns.

Our modelling results also demonstrate that reproductive performance does not appear to suffer from any negative effects of density dependence, suggesting that these populations probably remain below carrying capacity. This is in contrast with previous studies that found strong evidence for density dependence of reproductive parameters, especially at certain density thresholds (Hrabar & du Toit, 2005; Law et al., 2013). Future research could use a finer-scale approach by employing the browse available methodology (Adcock, 2006) to obtain more precise estimates of browse availability and by considering environmental explanatory variables at the individual rather than the subpopulation level.

Implications for management and conservation policy

The unique 20-year set of individual-based monitoring data provided an opportunity to estimate reproduction parameters that are often difficult and costly to obtain and process. The results presented here provide the custodians of the Namibian black rhinoceros population with a detailed and long-term benchmark of its reproductive performance, and new data points to update the range of the IUCN benchmarks. The more detailed parameter estimates also provide novel opportunities to explore more sophisticated population models to better capture the complexities inherent in black rhinoceros population dynamics. Such outputs, if applied within a management-orientated decision process, could improve and advance management strategies for the black rhinoceros in Namibia and help us to identify and evaluate opportunities to guide future range expansion. Given the past and present objective in Namibia to manage the country's black rhinoceros metapopulation actively for maximum growth, our findings are both timely and relevant to help secure a future for one of the largest remaining populations of this Critically Endangered species.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards, and the research was permitted under Ongava Research Centre's certificate number RCIV00012019 issued by the National Commission on Research, Science and Technology of Namibia.

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