

RESEARCH ARTICLE

Viability analysis of Kordofan giraffe (*Giraffa camelopardalis antiquorum*) in a protected area in Cameroon

Kane P. J. Colston¹ | Caspian L. Johnson²  | Denis Nyugha³ |
Achile Mengamenya Goué⁴ | Samuel G. Penny² 

¹Bristol Veterinary School, University of Bristol, Bristol, UK

²Institute of Conservation Science and Learning, Bristol Zoological Society, Bristol, UK

³Sekakoh Organization, Ntui, Cameroon

⁴Bénoué National Park Conservation Service, Ministère des Forêts et de la Faune, Yaoundé, Cameroon

Correspondence

Samuel G. Penny, Institute of Conservation Science and Learning, Bristol Zoological Society, Hollywood Lane, Bristol, BS10 7TW, UK.
Email: spenny@bzsociety.org.uk

Abstract

Representing one of the last populations of an IUCN Critically Endangered subspecies, estimates suggest the Kordofan giraffe of Cameroon's Bénoué Complex number fewer than 300 individuals, threatened by poaching and habitat degradation. This study investigated the viability of Bénoué National Park's Kordofan giraffe and efficacy of available interventions through a population viability analysis using VORTEX. The relative impacts of anti-poaching activity, population supplementation, habitat protection and vaccination were explored, alongside a sensitivity analysis investigating parameter uncertainty. The baseline model projects a 78.6% probability of extinction (PE) within 100 years. Poaching of just two individuals every 5 years results in a 98.1% PE, highlighting anti-poaching activity as a vital intervention. Movement of a female-biased group into the park proved effective, with supplementation of 24 females reducing the PE by over 35%, sustaining a raised population size above the baseline for over 60 years on average. Annual carrying capacity reduction of 2% year⁻¹ for 20 years resulted in a 97.8% PE. Conversely, habitat restoration had little consequence unless combined with further interventions. These findings underscore the magnitude of the threat facing Bénoué National Park's Kordofan giraffe. Conservation management should prioritise strengthening existing anti-poaching activity in conjunction with protecting wildlife corridors to aid dispersal.

KEYWORDS

anti-poaching, Bénoué National Park, conservation management, extinction vortex, *Giraffa camelopardalis antiquorum*, population viability analysis

Résumé

Représentant l'une des dernières populations d'une sous-espèce en danger critique d'extinction selon l'IUCN, les girafes du Kordofan du complexe de la Bénoué au Cameroun compteraient moins de 300 individus, menacés par le braconnage et la dégradation de leur habitat. Cette étude a examiné la viabilité de la girafe du Kordofan du Parc National de la Bénoué et l'efficacité des interventions disponibles par le biais d'une analyse de viabilité de la population à l'aide de VORTEX. Les impacts relatifs des activités de lutte contre le braconnage, du renforcement de la population, de la protection de l'habitat et de la vaccination ont été étudiés, parallèlement à une analyse de sensibilité portant sur l'incertitude des paramètres. Le modèle de référence

prévoit une probabilité d'extinction (PE) de 78,6 % dans les 100 prochaines années. Le braconnage de seulement deux individus tous les cinq ans entraîne une PE de 98,1 %, ce qui montre que la lutte contre le braconnage est une intervention vitale. Le déplacement d'un groupe de femelles dans le parc s'est avéré efficace, l'apport de 24 femelles ayant permis de réduire la PE de plus de 35 % et de maintenir un effectif accru de la population au-dessus du niveau de référence pendant plus de 60 ans en moyenne. Une réduction annuelle de la capacité de reproduction de 2 % par an pendant 20 ans a entraîné une PE de 97,8 %. Inversement, la restauration de l'habitat n'a eu qu'un effet mineur, bien qu'associée à d'autres interventions. Ces résultats soulignent l'ampleur de la menace qui pèse sur la giraffe du Kordofan du Parc National de la Bénoué. La gestion de la conservation devrait renforcer en priorité les activités de lutte contre le braconnage existantes, ainsi que la protection des corridors de la faune pour faciliter la dispersion.

1 | INTRODUCTION

Giraffe (*Giraffa camelopardalis*) have experienced a rapid decline in abundance in recent years and were reclassified from least concern to vulnerable by the International Union for the Conservation of Nature (IUCN) in 2018 (Muller et al., 2018). As a species with a protracted life history (Dagg & Foster, 1976), giraffe face largely similar threats to other African megafauna. Illegal hunting (here termed 'poaching') is frequently cited as a cause of population decline, but evidence remains mostly anecdotal, with little research into its overall impact (Muller, 2010; Strauss et al., 2015). There also exists evidence that human incursion into giraffe home ranges (such as movements of livestock by indigenous pastoralist communities) can result in resource degradation and disturbance of integral social structures, which may lead to population decline (Awalu & Nformi, 2022; Bond, König, Lee, et al., 2021; Bond, Lee, Farine, et al., 2021). With such a network of interconnected influences, establishing contextual conservation priorities is paramount.

Giraffe are classified into nine subspecies discontinuously spread across sub-Saharan Africa (Muller et al., 2018). Recent genetic advances place new emphasis on the evolutionary significance of giraffe subspecies, with these geographically isolated populations now representing key genetic reservoirs (Coimbra et al., 2021; Fennessy et al., 2016; Fennessy & Marais, 2018; O'Connor et al., 2019). Kordofan giraffe (*Giraffa camelopardalis antiquorum*) are a critically endangered subspecies of giraffe found across Cameroon, Central African Republic, Chad, Democratic Republic of Congo and South Sudan, with Chad and Cameroon representing the largest populations (Fennessy & Marais, 2018).

Geopolitical instability surrounding Cameroon has left its Kordofan giraffe vulnerable to the consequences of poaching, illegal pastoralism and mining encroachment (Elkan et al., 2015; Foguekem et al., 2010). Estimates place the population between 560 and 860 individuals, with the majority residing in Waza National Park which remains largely lawless due to the ongoing conflict with Boko Haram (Elkan et al., 2015; Scholte et al., 2022), and the Bénoué Complex;

a landscape that consists of three national parks (Bénoué, Faro, Bouba N'djida) interconnected by 29 hunting zones (HZs) (Marais et al., 2019; Parks, 2021).

Population viability analyses are used to assess the relative impact of threats and conservation strategies for wild populations to guide wildlife management decisions (Beissinger & McCullough, 2002). Although vulnerable to issues of parameter uncertainty and validity of long-term projections (Gerber & González-Suárez, 2010), PVAs are largely viewed as valuable conservation tools (Brook et al., 2000). While PVAs have previously been used to model hypothetical translocation success of giraffe into unpopulated areas (Lee et al., 2020), this study represents the first PVA using VORTEX modelling software to investigate the extinction risk of an existing giraffe population.

The principle aim of this study is to assess the probability of extinction of Kordofan giraffe in Bénoué National Park by (i) establishing a baseline model using data sourced from previous population surveys and existing demographic and environmental parameters, (ii) investigating the efficacy of relevant conservation strategies on population extinction risk and growth rate and (iii) establishing the sensitivity of the model to uncertainty in parameter estimates, in order to identify key parameters for future population monitoring and model improvement. The findings of these objectives form the basis of conservation recommendations for managing small or declining populations of giraffe.

2 | MATERIALS AND METHODS

2.1 | Study area

Bénoué National Park (BeNP) is a 198,000 ha park central to the Bénoué Complex, a 3,145,700 ha region, which is characterised by mixed savannah woodland (Abrahams et al., 2022). BeNP is immediately bordered to the east by the Bénoué river and nine HZs—sites designated for commercial, legalised hunting (Elkan et al., 2015).

2.2 | Study population

This analysis focuses on the population of Kordofan giraffe that inhabit BeNP. Very little is known about this population, including their spatiotemporal distribution and demography. Giraffe exhibit considerable home range sizes, known to regularly exceed 100km² (Knüsel et al., 2019). Furthermore, facultative migration and male-biased dispersive behaviour coupled with the lack of a physical border between the park and neighbouring HZs are likely to mean that BeNP's Kordofan giraffe population size may fluctuate, representing a dynamic subpopulation within the wider BNC metapopulation (Bond, Lee, Ozgul, et al., 2021; Brown & Bolger, 2020; Le Pendu & Ciofolo, 1999). For the purposes of this PVA, owing to the uncertainty surrounding their spatial dynamics, BeNP's Kordofan giraffe were modelled as a closed population.

2.3 | Population modelling

2.3.1 | Vortex

To model the viability of BeNP's Kordofan giraffe, VORTEX v10.5.5 computer software was used (Lacy & Pollak, 2021). VORTEX is an individual-based modelling software that combines deterministic models of population growth with stochastic environmental, demographic and genetic factors. The model was run to a predetermined timestep of 100years, in accordance with IUCN guidelines (IUCN, 2022). Each model scenario was iterated 5000 times to generate statistically robust output variables. See Lacy et al. (2021) for a detailed overview of VORTEX functionality.

2.3.2 | Identification of model parameters

The initial population size was taken to be 40 individuals, established from data collected between 2016 and 2021 (Parks, 2021). We assumed a stable age distribution at year 0. For a detailed summary of chosen parameters, see Table 1; for the VORTEX input file, see Data S1.

Mortality rates were divided into four categories: Juvenile (0–1 year), subadult (1 year to sexual maturity), adult female and adult male. Elevated subadult mortality rates compared to adults are to be expected, owing to the slightly smaller body size and dispersive behaviour exhibited at this age (Leuthold & Leuthold, 1978). Juveniles <1-year-old were distinguished from other subadults due to the markedly higher mortality rate experienced as a result of predation in the first year of life (Foster & Dagg, 1972). Adult male mortality is consistently higher than females, primarily resulting from intrasexual aggression (Simmonds & Scheepers, 1996).

Mortality rates for juveniles and subadults were obtained from Manyara Ranch Conservancy (MRC) in Tanzania, as the moderate anti-poaching activity and pastoralism best matched the factors affecting BeNP (Lee, 2015; Lee et al., 2016). For adult mortality,

rates in neighbouring Tarangire National Park (TNP) were used (Lee et al., 2016). By obtaining adult mortality rates from TNP, we maintained largely consistent abiotic conditions and predation pressure across all mortality rate estimates between MRC and TNP, while removing poaching as a contributor to adult mortality because of the TNP's stricter anti-poaching infrastructure (Lee, 2015). This was necessary to ensure the baseline model did not include poaching-related adult mortality.

The age at first reproduction was taken to be 5 and 7 years for females and males, respectively (Leuthold & Leuthold, 1978; Pacifici et al., 2013). The maximum age of reproduction for males was set lower than females (20 vs. 24 years), corresponding to the highest age of peak breeding reported in captivity (Lackey, 2011). Given the polygynous rank dominance system in giraffe, wild males of this age are unlikely to be reproductively active (Owen-Smith, 1988).

Of the 26 giraffe observed by Parks (2021) within BeNP, the sex was confirmed in 19 individuals, yielding a female-biased sex ratio of 1:0.46. Despite much discrepancy in birth sex ratio estimates (e.g. Strauss et al., 2015; but see Marealle et al., 2010), this observation only accounted for 47.5% of the estimated total BeNP population ($n=40$). Additionally, evidence from Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in the Tarangire Ecosystem suggests female-biased adult sex ratios result from disparity in mortality rates from as early as 3 years old (Lee & Bond, 2022). We therefore assumed no birth sex ratio bias, in agreement with Bercovitch and Berry (2010) and Foster and Dagg (1972).

To estimate the catastrophe frequency, data from CRUTS (Climatic Research Unit gridded Time Series) was used to obtain precipitation levels for North Cameroon, in order to identify the frequency with which annual precipitation falls below two standard deviations on the mean precipitation level (Harris et al., 2020). This gave a crude estimate of drought every 40 years, which reduced survival and reproduction by an estimated 20% and 50% respectively (Owen-Smith, 1988; Walker et al., 1987).

The carrying capacity of BeNP ($K \pm SD$) was estimated using the density of a declining population of giraffe in the Seronera region of Serengeti NP between 2008 and 2010 ($0.28 \text{ km}^{-2} \pm 0.06$) and extrapolating this to the approximate size of BeNP (1980km²) (Strauss et al., 2015). The Seronera region of Serengeti NP is a 240km² unfenced area comprised primarily of *Acacia* woodland and open savannah, with 5-year averaged precipitation in 2010 comparable to 5-year averaged precipitation levels of BeNP (Mara, Tanzania = 1126.43mm; Nord, Cameroon = 1177.08mm) (Harris et al., 2020). This area therefore serves as a conservative estimate of carrying capacity, given the reduced tree cover compared to BeNP (Ruess & Halter, 1990; Sekakoh, 2020).

Given the disparity between the population size estimate and the predicted carrying capacity, density-dependent declines in reproductive rate are unlikely to influence the BeNP population. Therefore, the incorporation of an interbirth interval obtained from a growing (unsaturated) population best represents the BeNP population. This does not represent an a priori assumption

TABLE 1 Parameters chosen for the baseline model, value(s) selected, comment on rationale and source(s) used.

Parameter	Baseline value(s)	Comment	Source(s)
Number of iterations	5000		
Number of years (timestep)	100	IUCN standard	IUCN (2022)
Extinction definition	Only 1 sex remains		
Number of populations	1		
Lethal equivalents	2.5	Calculated from studbook data	Lee et al. (2020)
Percent due to recessive lethal alleles	50	Default VORTEX value	Lacy et al. (2021)
EV correlation between production and survival	0.5	Default VORTEX value	Lacy et al. (2021)
EV correlation among populations	N/A	Only one population modelled	
Dispersal	N/A	Only one population modelled	
Mating system	Polygynous		Bercovitch et al. (2006)
Age of first offspring females	5 years		Pacifici et al. (2013)
Age of first offspring males	7 years	2 years later than females	Leuthold and Leuthold (1978)
Maximum lifespan	28 years		Western (1979)
Maximum number of broods per year	1		
Maximum number of progeny per brood	1		
Sex ratio at birth—in % males	50		Bercovitch and Berry (2010), Foster and Dagg (1972)
Offspring dependent on their dam for x years	x = 1	Rounded to nearest integer	Leuthold and Leuthold (1978)
Maximum age of female reproduction	24 years		Bercovitch and Berry (2010)
Maximum age of male reproduction	20 years	Upper end of peak breeding age estimate in captivity	Lackey (2011)
Density dependent reproduction	N/A	Not included	
% adult females breeding	63.8	(12/Mean calving interval)*100 Mean calving interval = 18.8 months	Pellew (1983)
SD in % breeding due to EV	6.86	Estimation using SD of mean calving interval	Pellew (1983), Ramirez and Cox (2012)
Distribution of broods per year	0 Broods: 0 1 Brood: 100		
Distribution of number of offspring per female per brood	1 Offspring: 100		
Mortality of females as %	Mortality from age 0 to 1 = 28 SD in 0–1 mortality due to EV = 7 [Annual] Mortality from age 1 to 5 = 13 SD in 1–5 mortality due to EV = 3.25 Annual mortality after age 5 = 11 SD in mortality after age 5 = 2.75	SD set at 25% of mortality estimate	Lee (2015), Lee et al. (2016)

TABLE 1 (Continued)

Parameter	Baseline value(s)	Comment	Source(s)
Mortality of males as %	Mortality from age 0 to 1=28 SD in 0 to 1 mortality due to EV=7 [Annual] Mortality from age 1 to 7=13 SD in 1 to 5 mortality due to EV=3.25 Annual mortality after age 7=16 SD in mortality after age 7=4	SD set at 25% of mortality estimate	Lee (2015), Lee et al. (2016)
Number of types of catastrophes	1	Simulation of drought	
[Catastrophe] Frequency %	2.5	Once every 40 years	Harris et al. (2020)
[Catastrophe] Severity	Reproduction=0.5 Survival=0.8	Proportion of normal values	Owen-Smith (1988), Walker et al. (1987)
% Males in breeding pool	50		
Initial population size	40		Parks (2021)
Age distribution	Stable age distribution		
Carrying Capacity (K)	504	Calculated using giraffe density estimate and Bénoué National Park size	Strauss et al. (2015)
SD in K due to EV	146	Transformation of giraffe density estimate confidence interval	Strauss et al. (2015)
Trend in K	N/A	Not included in baseline	
Harvest	N/A	Not included in baseline	
Supplementation	N/A	Not included in baseline	
Genetics	N/A	Not included	

of growth in the modelled population but serves to eliminate density-dependent influences on reproductive rate. An interbirth interval of 18.8 months was chosen to estimate the percentage of females breeding annually (see Table 1), obtained from a growing population recorded in the Serengeti National Park, Tanzania (Pellew, 1983).

2.3.3 | Intervention scenarios

Four intervention strategies were simulated individually and in combination to investigate their relative influence on population viability.

The 'supplementation' function within VORTEX was used to simulate the movement of giraffe into BeNP, either through translocations or net dispersal influx from surrounding HZs. Translocations of giraffe across sub-Saharan Africa are not uncommon, with up to 30 individual animals moved in a given event (Fennessy et al., 2020). To investigate the impact of supplementation, the following scenarios were simulated: 2♀2♂, 4♀4♂ and 12♀12♂ in year 1 (even sex ratio); 24♀0♂, 18♀6♂, 6♀18♂ and 0♀24♂ in year 1 (biased sex ratio); 12♀12♂ in year 1 and 11 (repeat supplementation after one generation). All supplemented individuals were at or above the sex-specific age of sexual maturity (Table 1).

With a zero-poaching baseline, simulations of increasing poaching pressure were conducted to assess the impact of improved

anti-poaching measures. To survey a range of poaching pressures, the following scenarios were run: 1♀1♂, 2♀0♂ and 2♀2♂ 'harvested' every year; 1♀1♂ 'harvested' every 2, 3 and 5 years. All harvested individuals were adults, as these are most often targeted by poaching (Strauss et al., 2015).

To simulate habitat restoration, scenarios with annual incremental increases in K were conducted. Further runs involving incremental reduction in K were also investigated, to explore the impact of continued illegal pastoralism and deforestation. The following scenarios were inspected: +10% year⁻¹, +2% year⁻¹, -1% year⁻¹, -2% year⁻¹, -5% year⁻¹ and -10% year⁻¹. All incremental changes to K were implemented for 20 years. Current rates of habitat degradation within the Bénoué Complex are varied, with unprotected areas having experienced approximately 6% gross forest loss between 2000 and 2018, compared to 1% for protected areas (Abrahams et al., 2022). Changes of +10% year⁻¹ and -10% year⁻¹ equate to a 611% increase and an 86.5% decrease over 20 years respectively, representing drastic changes to the habitat of BeNP over the modelled time course. The low- and high-end scenarios are useful to understand giraffe population responses to extreme habitat changes. This can occur through sudden, dramatic climate catastrophe or human intervention, for example through civil conflict, similar to that observed in the DRC from 1990 to 2010 (Nackoney et al., 2014).

A further scenario reducing the annual adult mortality by 5% was conducted, to investigate the benefit of modest veterinary

intervention (Kaitho et al., 2013). We chose to model modest reductions in the adult mortality rate as a result of pre-emptive vaccination against pathogenic agents like anthrax or black quarter, with a 5% annual reduction representing a longer term average.

Four scenarios were also trialled in combination to explore the additive effect of simultaneous interventions. The scenarios trialled in combination were:

- K + 2% year⁻¹, 20 years (Table 2, Scenario 10)
- Adult mortality -5% (Table 2, Scenario 23)
- Supplementation; 4♀ + 4♂, year 1 (Table 2, Scenario 3)
- Supplementation: 12♀ + 12♂, year 1 and 11 (Table 2, Scenario 9).

Scenarios (a) to (c) were chosen to represent modest carrying capacity increases, reduction in mortality and supplementation, respectively, with scenario (d) selected to examine a more optimistic supplementation regime. To investigate the statistical significance of each scenario combination in comparison to the baseline or other scenarios, permutation tests were conducted on the mean end population size (N_{100}).

2.4 | Sensitivity analysis

To address concerns around parameter uncertainty and the consequences for model projections, we included a sensitivity analysis of the input parameters (Chaudhary & Oli, 2020), whereby all parameters were tested individually. A random value from within a ±50% range of the baseline value was applied to 100 iterations, recording the mean stochastic growth rate (stoch-r). This process was repeated 100 times to generate a stoch-r distribution across the ±50% range for each parameter. For each distribution, a linear regression using R statistical software (v4.1.2; R Core Team, 2022) was used to identify parameters with statistically significant ($p < 0.05$) linear correlations and large (>0.5) r^2 goodness-of-fit values. Uncertainty in these parameters was likely to have significant influence on model outputs.

The parameters meeting the specified criteria from the individual sensitivity testing were next varied simultaneously, using Latin hypercube sampling to obtain near-random combinations while ensuring unbiased sampling of multidimensional sample space (McKay et al., 1979). Each parameter combination was iterated 1000 times, with 1000 separate parameter combinations tested. Variance partitioning was conducted using a multiple linear regression model in R (v4.1.2; R Core Team, 2022) to obtain adjusted- R^2 goodness-of-fit values for each parameter.

3 | RESULTS

Table 2 summarises the results for each of the 29 scenarios investigated.

3.1 | Baseline model

The baseline model indicated a substantial population decline over the next 100 years, with a stoch-r of -0.0306 (SD=0.1429) and a 78.6% probability of extinction (PE). The mean time to extinction (T_E) was 61.0 years.

3.2 | Intervention scenarios

3.2.1 | Supplementation

All supplementation scenarios resulted in a lower PE and a higher N_{100} when compared to the baseline model (Table 2). The addition of two male and two female giraffes in the first year (scenario 2) was sufficient to yield a statistically significant increase in the N_{100} (permutation test, $p < 0.0001$).

Figure 1 illustrates the influence that supplementation sex ratio has on the N_{100} . The addition of 24 males only in the first year (scenario 8) produces N_{100} comparable to the baseline scenario. Conversely, the addition of 24 females only (scenario 6) raises the population above its initial size for over 60 years. The addition of 12 giraffes in year 1 and year 11 (scenario 9) results in the lowest PE (34.0%) and largest population size after 100 years (20.25, SD=26.25).

3.2.2 | Poaching

The impact of poaching on the mean probability of survival is shown in Figure 2. Low poaching levels—one adult male and one adult female every 5 years (scenario 21)—reduce the probability of survival from baseline projections by 20%. All poaching scenarios result in high PE; the removal of one adult male and one adult female per year (scenario 17) results in a T_E of approximately 15 years.

3.2.3 | Change in carrying capacity (K)

Figure 3 shows the influence of changes to K on mean probability of survival. Increases of 10% year⁻¹ for 20 years (scenario 11), equivalent to a 6.11-fold increase, had no significant effect on the probability of survival (permutation test, $p = 0.9422$). A reduction in K of 10% year⁻¹ for 20 years (scenario 15) resulted in a 100% PE. Even modest decreases of -1% year⁻¹ (scenario 12), equivalent to an 18% reduction after 20 years, increase the PE by 6.6%.

3.2.4 | Intervention combinations

The influence of simultaneous intervention strategies on population viability is shown in Figure 4. An increase in K of 2% year⁻¹ had no

TABLE 2 Conservation intervention scenarios investigated and output variables generated. All values given to three significant figures.

Scenario number	Scenario name	VORTEX parameter modification(s) to baseline	Stochastic growth rate (stoch-r) \pm SD	Probability of extinction (PE)	Mean end Population size (N_{100}) \pm SD	Genetic diversity \pm SD	Mean time to extinction (T_E , Years)
1	Baseline	N/A	-0.031 \pm 0.143	0.786	3.87 \pm 10.6	0.648 \pm 0.162	61.0
2	Supplementation: 2♀ + 2♂, year 1	Supplementation: 2 females, 2 males, year 1.	-0.0278 \pm 0.140	0.749	4.94 \pm 12.2	0.665 \pm 0.163	64.4
3	Supplementation: 4♀ + 4♂, year 1	Supplementation: 4 females, 4 males, year 1	-0.0259 \pm 0.139	0.714	5.88 \pm 13.7	0.671 \pm 0.168	66.2
4	Supplementation: 12♀ + 12♂, year 1	Supplementation: 12 females, 12 males, year 1	-0.0197 \pm 0.138	0.567	10.7 \pm 19.0	0.714 \pm 0.152	71.8
5	Supplementation: 18♀ + 6♂, year 1	Supplementation: 18 females, 6 males year 1	-0.0161 \pm 0.133	0.467	14.8 \pm 23.4	0.736 \pm 0.140	73.9
6	Supplementation: 24♀ + 0♂, year 1	Supplementation: 24 females, year 1.	-0.0139 \pm 0.130	0.409	17.5 \pm 24.9	0.749 \pm 0.139	75.9
7	Supplementation: 6♀ + 18♂, year 1	Supplementation: 6 females, 18 males, year 1	-0.0240 \pm 0.144	0.660	7.18 \pm 15.1	0.690 \pm 0.157	68.0
8	Supplementation: 0♀ + 24♂, year 1	Supplementation: 24 males, year 1	-0.0294 \pm 0.152	0.776	4.53 \pm 12.2	0.664 \pm 0.163	62.7
9	Supplementation: 12♀ + 12♂, year 1 and 11	Supplementation: 12 females, 12 males, year 1; 12 females, 12 males, year 11	-0.0119 \pm 0.132	0.340	20.3 \pm 26.3	0.769 \pm 0.131	76.5
10	K + 2% year ⁻¹ , 20 years	Carrying capacity: 2% annual increase over 20 years	-0.0309 \pm 0.143	0.788	3.81 \pm 10.3	0.651 \pm 0.161	62.8
11	K + 10% year ⁻¹ , 20 years	Carrying Capacity: 10% annual increase over 20 years	-0.0311 \pm 0.144	0.786	3.89 \pm 10.8	0.640 \pm 0.163	62.1
12	K - 1% year ⁻¹ , 20 years	Carrying capacity: 1% annual decrease over 20 years	-0.0302 \pm 0.143	0.852	2.38 \pm 7.75	0.643 \pm 0.167	58.0
13	K - 2% year ⁻¹ , 20 years	Carrying capacity: 2% annual decrease over 20 years	-0.0271 \pm 0.139	0.978	0.300 \pm 2.51	0.595 \pm 0.193	43.4
14	K - 5% year ⁻¹ , 20 years	Carrying capacity: 5% annual decrease over 20 years	-0.0168 \pm 0.119	1.00	0.00 \pm 0.00	0.00 \pm 0.00	15.8
15	K - 10% year ⁻¹ , 20 years	Carrying capacity: 10% annual decrease over 20 years	-0.0154 \pm 0.114	1.00	0.00 \pm 0.00	0.00 \pm 0.00	9.50
16	♀ + 10	Supplementation: 12 females, 12 males, year 1; 12 females, 12 males, year 11. Carrying capacity: 2% annual increase over 20 years	-0.0116 \pm 0.130	0.295	24.2 \pm 30.5	0.777 \pm 0.131	80.2
17	Poaching: 1♀ + 1♂, every year	Harvest: first year: 1, last year: 100; interval between harvests: 1; 1 adult female, 1 adult male	-0.165 \pm 0.190	1.00	0.00 \pm 0.00	0.00 \pm 0.00	15.3
18	Poaching: 2♀ + 2♂, every year	Harvest: first year: 1, last year: 100; interval between harvests: 1; 2 adult female, 2 adult male	-0.289 \pm 0.227	1.00	0.00 \pm 0.00	0.00 \pm 0.00	8.60
19	Poaching: 1♀ + 1♂, every 2 years	Harvest: first year: 1, last year: 100; interval between harvests: 2; 1 adult female, 1 adult male	-0.0938 \pm 0.173	1.00	0.00 \pm 0.170	0.601 \pm 0	26.0
20	Poaching: 1♀ + 1♂, every 3 years	Harvest: first year: 1, last year: 100; interval between harvests: 3; 1 adult female, 1 adult male	-0.0704 \pm 0.165	0.998	0.0500 \pm 1.27	0.699 \pm 0.106	33.9
21	Poaching: 1♀ + 1♂, every 5 years	Harvest: first year: 1, last year: 100; interval between harvests: 5; 1 adult female, 1 adult male	-0.0535 \pm 0.159	0.981	0.320 \pm 2.82	0.695 \pm 0.129	43.4
22	Poaching: 2♀ + 0♂, every year	Harvest: first year: 1, last year: 100; interval between harvests: 1; 2 adult females	-0.155 \pm 0.146	1.00	0.00 \pm 0.00	0.00 \pm 0.00	10.7
23	Adult mortality -5%	Mortality: female annual mortality after age 5 = 10.45; male annual mortality after age 7 = 15.2	-0.0257 \pm 0.138	0.696	6.81 \pm 15.3	0.674 \pm 0.154	63.5

(Continues)

TABLE 2 (Continued)

Scenario number	Scenario name	VORTEX parameter modification(s) to baseline	Stochastic growth rate (stoch-r) \pm SD	Probability of extinction (PE)	Mean end Population size (N_{100}) \pm SD	Genetic diversity \pm SD	Mean time to extinction (T_E , Years)
24	3 + 10	Supplementation: 4 females, 4 males, year 1. Carrying capacity: 2% annual increase over 20years	-0.00730 \pm 0.124	0.696	38.0 \pm 43.9	0.808 \pm 0.114	67.1
25	3 + 23	Supplementation: 4 females, 4 males, year 1. Mortality: female annual mortality after age 5 = 10.45; male annual mortality after age 7 = 15.2	-0.0215 \pm 0.134	0.605	9.92 \pm 19.2	0.692 \pm 0.155	67.6
26	3 + 10 + 23	Supplementation: 4 females, 4 males, year 1. Carrying capacity: 2% annual increase over 20years. Mortality: female annual mortality after age 5 = 10.45; male annual mortality after age 7 = 15.2	-0.0211 \pm 0.132	0.572	11.2 \pm 21.0	0.708 \pm 0.148	69.1
27	9 + 23	Supplementation: 12 females, 12 males, year 1; 12 females, 12 males, year 11. Mortality: female annual mortality after age 5 = 10.45; male annual mortality after age 7 = 15.2	-0.00750 \pm 0.125	0.256	31.1 \pm 36.6	0.797 \pm 0.120	77.4
28	10 + 23	Carrying capacity: 2% annual increase over 20years. Mortality: female annual mortality after age 5 = 10.45; male annual mortality after age 7 = 15.2	-0.0267 \pm 0.139	0.705	6.47 \pm 14.6	0.665 \pm 0.168	65.0
29	9 + 10 + 23	Supplementation: 12 females, 12 males, year 1; 12 females, 12 males, year 11. Carrying capacity: 2% annual increase over 20years. Mortality: female annual mortality after age 5 = 10.45; male annual mortality after age 7 = 15.2	-0.00730 \pm 0.124	0.208	37.0 \pm 43.9	0.808 \pm 0.114	81.6

significant influence on the N_{100} compared to the baseline (permutation test, $p=0.766$). In combination with reduced adult mortality and supplementation of eight individuals, an increase in K does have a significant impact on N_{100} ('b+c' vs. 'a+b+c', permutation test,

$p=0.0015$). A combination of high supplementation, a reduction in adult mortality and an increase in K had the greatest impact on N_{100} and genetic diversity, reducing the PE by 57.9% (Table 2).

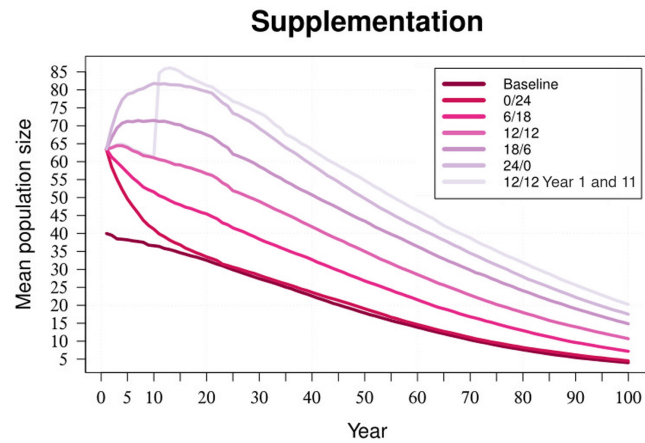


FIGURE 1 Effect of supplementation of BeNP population with adult giraffe on mean population size. Number of giraffes of each sex translocated represented as #M/#F.

3.3 | Sensitivity analysis

Of all parameters tested, 10 met the significance criteria outlined (shown in Figure 5). Further sensitivity testing preceded the partitioning of variance using adjusted R^2 goodness-of-fit values obtained from the multiple linear regression (Table 3). This revealed that '% adult females breeding', 'Sex ratio', 'Adult female mortality rate' and 'Subadult mortality rate' were responsible for 87.6% of the observed variation between iterations in stoch-r, with a third of which was explained by '% adult females breeding' alone. 6.6% of the variance was unexplained by the included parameters and is attributable to the inherent demographic stochasticity. 'Lethal equivalents' and 'Initial population size' made no contribution to the total variance in stoch-r in the model.

The relative impact on stoch-r of varying each selected parameter by $\pm 50\%$ of their baseline is shown in Figure 5. Steeper lines signify a greater level of influence on stoch-r and therefore on uncertainty in

Effect of poaching on population survival probability

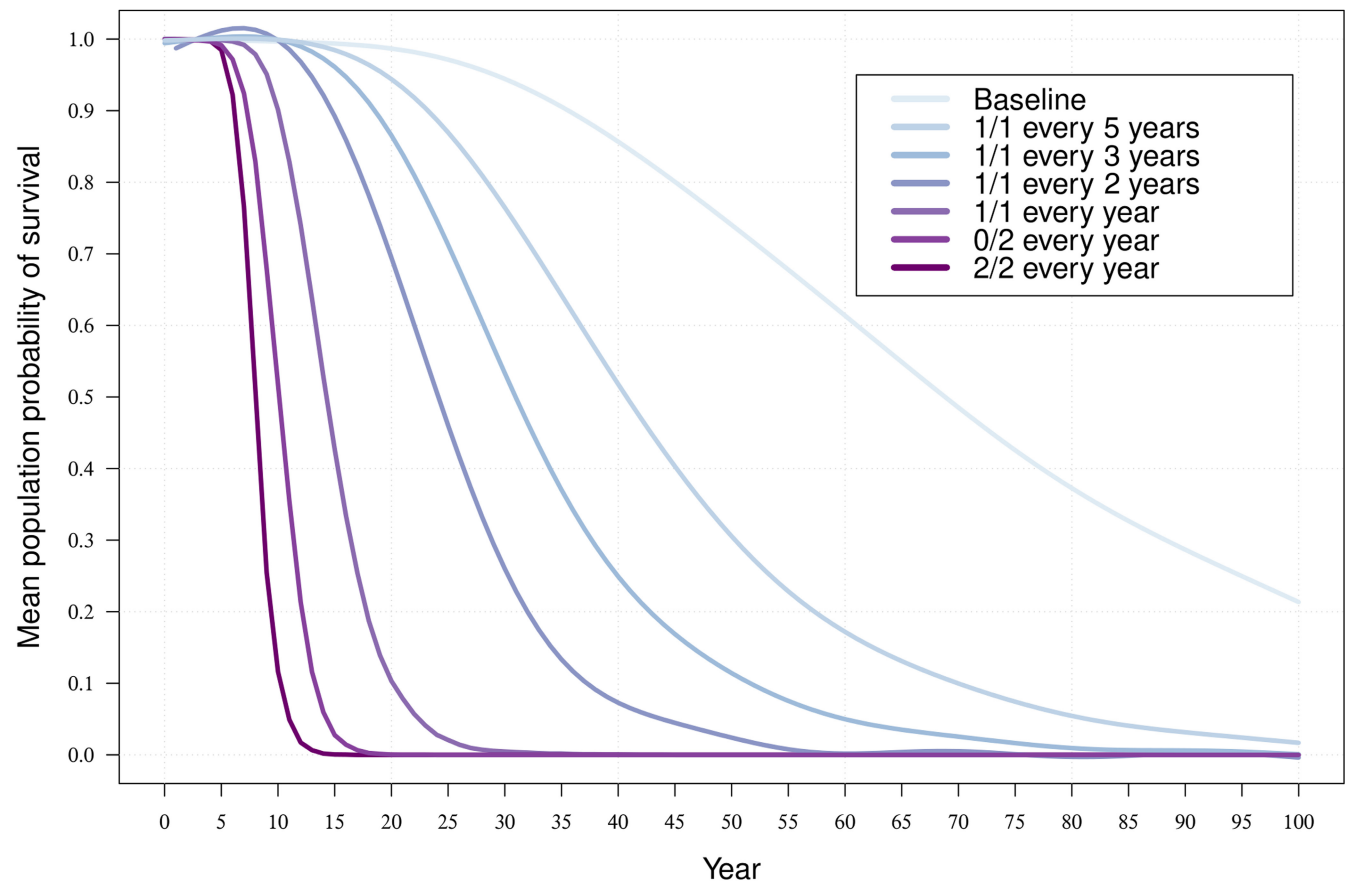


FIGURE 2 Effect of poaching rate on mean population probability of survival. The mean population probability of survival is defined as the probability that the population survives from a given time to a specified future time, here given as year 100. Number and sex of giraffe poached represented as #M/#F. All poached animals are above the age of sexual maturity.

Effect of change in carrying capacity on population survival probability

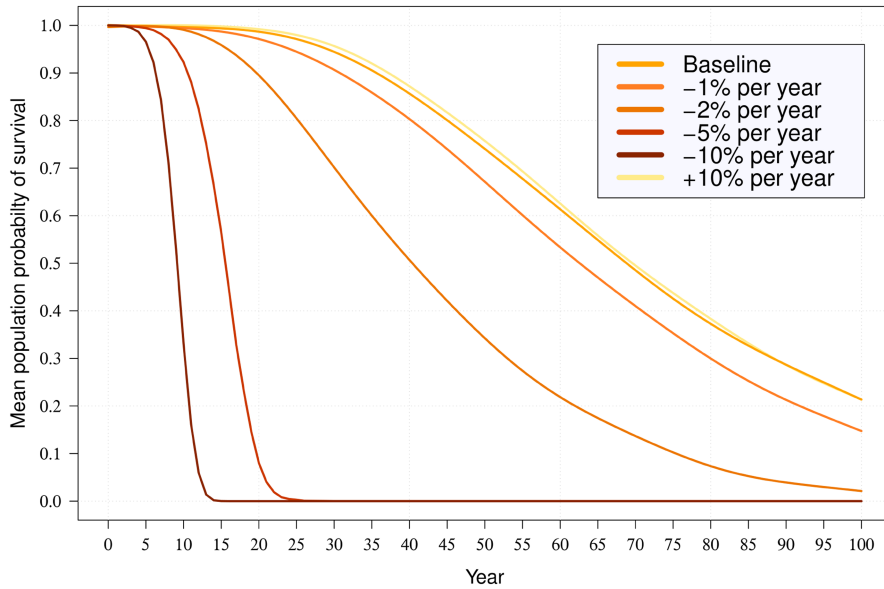


FIGURE 3 Effect of annual change in carrying capacity on mean population probability of survival. Standard deviation due to environmental variation (EV) set to 0 for each scenario. Percentage change applied every year for the first 20 years.

Effects of conservation intervention on population size and genetic diversity

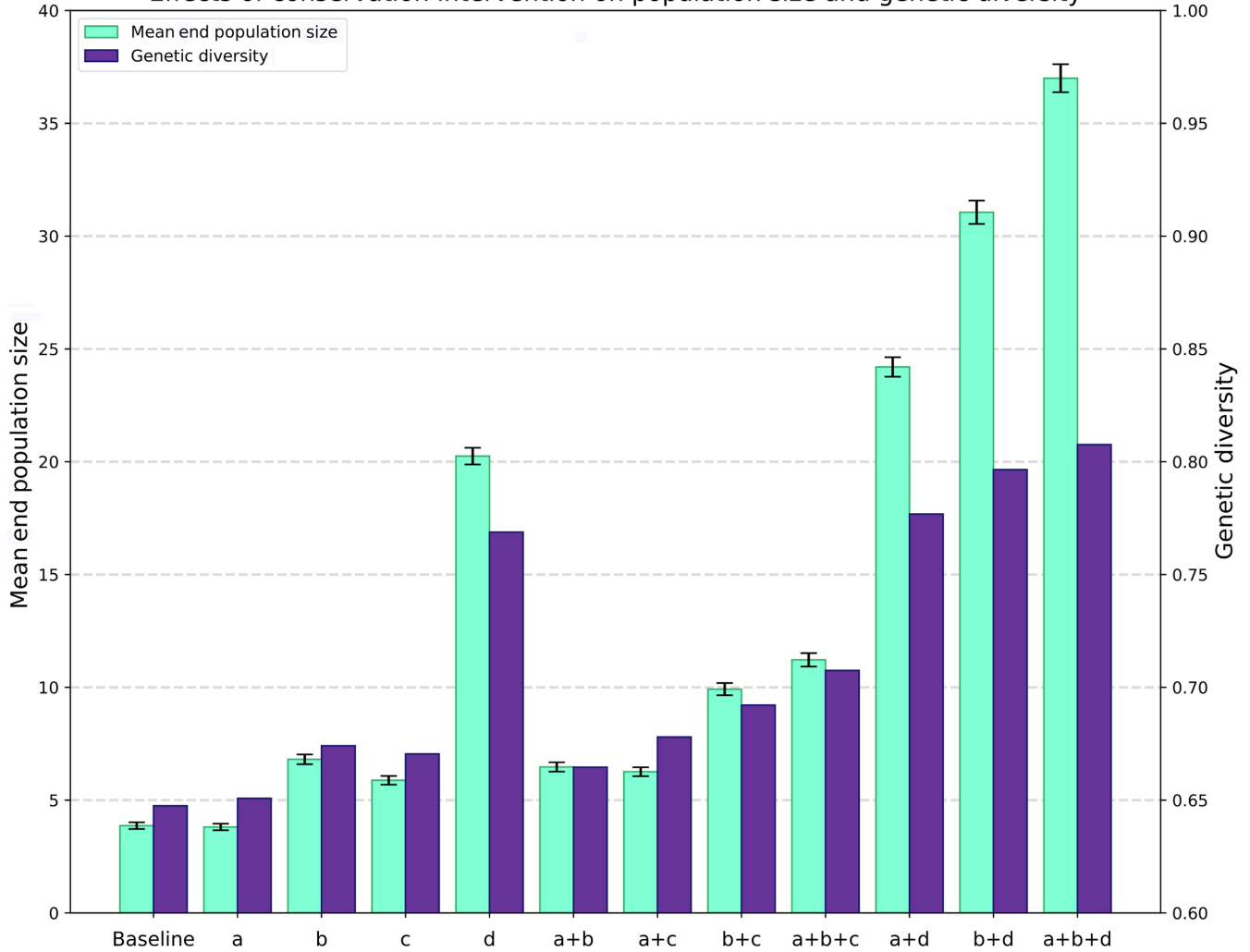
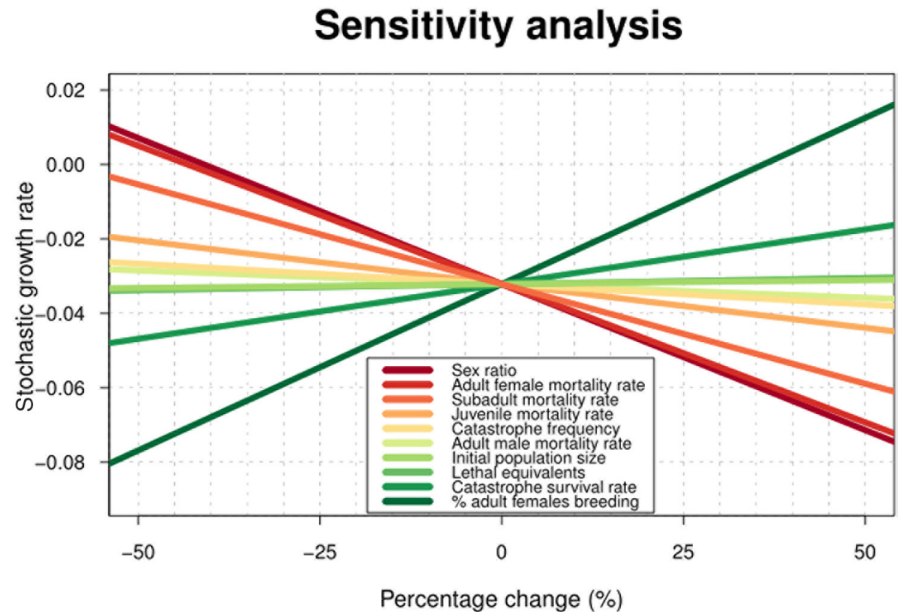


FIGURE 4 Influence of conservation interventions in combination on mean end population size (N_{100}) and genetic diversity. Standard error (SE) bars shown for N_{100} . SE for genetic diversity too small to be displayed. a = $K + 2\% \text{ year}^{-1}$, 20 years (Table 1, Scenario 10). b = Adult mortality -5% (Table 1, Scenario 23). c = supplementation; $4\varphi + 4\delta$, year 1 (Table 1, Scenario 3). d = supp: $12\varphi + 12\delta$, year 1 and 11 (Table 1, Scenario 9).

FIGURE 5 Relative impacts of uncertainty on parameter estimates. Percentage change (%) represents deviation from baseline value (see Table 1). 'Initial population size' is superimposed on top of 'Lethal equivalents', both with gradient ≈ 0 . Sex ratio given as % males at birth.



the baseline estimates. Again, '% adult females breeding' has the greatest positive correlation; however, an increase of above approximately 25% is biologically impossible owing to the 15-month gestational period of giraffes (Lackey, 2011). The greatest negative correlations were 'Sex ratio' and 'Adult female mortality rate'. The uncertainty range of 'Adult female mortality rate' was 5.5–16.5%, well within the range of values reported in the literature (Lee et al., 2016; Pellew, 1983). Again, 'Initial population size' and 'Lethal equivalents' have very little influence on the stoch-r over the range of values investigated.

4 | DISCUSSION

Population viability analyses are widely used to model the effects of conservation management decisions and environmental change on endangered species (Akçakaya & Sjögren-Gulve, 2000). However, the reliability and utility of longer term predictions and point estimates of extinction probabilities may be diminished if there is a lack of robust demographic and environmental data (Coulson et al., 2001). It is therefore crucial that appropriate steps—such as clear objectives, justified parameter estimates and a sensitivity analysis—are taken when conducting a PVA, particularly when applied to small or data-deficient populations that are often in need of modelling (Chaudhary & Oli, 2020). While we consider our approach to have taken such necessary steps, we continue to prioritise the relative comparison of intervention scenarios and our sensitivity analysis as the most pertinent to future conservation decisions, in line with recommendations on the interpretation of PVAs by Reed et al. (2002).

4.1 | Baseline model

The findings of the PVA indicate a significant and immediate threat of extinction to BeNP's Kordofan giraffe. The baseline model

represents an optimistic projection, owing to the exclusion of poaching and positive density dependence, as well as potentially overestimating the percentage of females breeding (Lacy et al., 2021). Without historical data of BeNP's giraffe population nor the inclusion of future climate change scenarios, the baseline model cannot be appropriately validated and must be interpreted with caution. Nevertheless, the baseline model still suggests a marked average decrease in population size over the modelled time course and a high PE, which should be examined further.

Even with the exclusion of positive density-dependent growth, small populations are disproportionately influenced by demographic stochasticity inherent to the VORTEX model (Fagan & Holmes, 2006; Lacy et al., 2021; Lande, 1998). This may be heightened by our inclusion of catastrophe estimates associated with periodical drought. The BeNP Kordofan giraffe population may be approaching, or have crossed, a 'demographic tipping point', with our baseline model serving as a potential early warning sign of an extinction vortex (de Silva & Leimgruber, 2019; Gilpin & Soulé, 1986). Continued scrutiny of population structure and demographic trends are necessary to establish accurate near-term projections and avoid irreversible decline.

While our baseline scenario suggests a high risk of extinction for BeNP's giraffe, this could be the result of inherent inaccuracies in our parameter estimates. The findings of the sensitivity analysis indicate that the primary sources of error that may explain erroneous projections of baseline population decline are overestimates of sex ratio, overestimates of adult female & subadult mortality rates and underestimates of catastrophe survival rate. Our model used a 50:50 sex ratio at birth as this is commonly observed in both captive and wild settings (Bercovitch et al., 2004). Female-biased sex ratios at birth as a result of small population inbreeding and paternal genetic effects have been observed in another Critically Endangered African ruminant, the Eastern Bongo (IUCN SSC Antelope Specialist Group, 2017; Malo et al., 2019). This observation could explain the adult sex ratio bias in BeNP's

population indicated by Parks (2021), but the data are far more easily accounted for by unequal sex-specific survival rates commonly observed in giraffe, as accounted for within the model (Lee & Bond, 2022).

An overestimate of adult mortality within the model is also possible, given the unaccounted-for higher density of predators in Serengeti NP than BeNP (Croes et al., 2011; Massawe et al., 2022). Overly conservative estimates of carrying capacity are unlikely to be the cause of baseline model decline, given the influence of annual increases in K (Figure 3).

4.2 | Impact of poaching

Of the interventions investigated, anti-poaching measures appear the most significant for population viability. Removal of one male and one female every 5 years was sufficient to cause a 98.1% PE. Far higher giraffe poaching rates have been reported in other national parks (e.g. Caro, 2008). The extent of poaching in BeNP is still unclear, but recent confirmed reports of the poaching of two giraffe in a period of just 3 months highlight not only the urgency of conservation intervention but the need for further modelling to examine the impact of juvenile and subadult 'harvest', given the model's sensitivity (Figure 5). Poaching of females had a more significant impact on population viability than males (Figure 2). This agrees with previous modelling, highlighting the sensitivity of giraffe populations to adult female mortality (Strauss et al., 2015). This finding may be explained by the removal of non-breeding males, buffering the population from subsequent impacts on reproductive rate (Bercovitch et al., 2006).

4.3 | Impact of changes to carrying capacity (K)

Investigation into changes in K revealed an asymmetric response due to the relatively small initial population size. Incremental increases in K had little impact, whereas modest annual reductions of 2% year⁻¹ (a 33% reduction over 20 years) resulted in T_E comparable to the poaching scenarios. Transhumance pastoralism is widespread across northern and central Cameroon (Motta et al., 2018), with incursions onto BeNP resulting in destruction of vital resources such as *Afzelia africana* (Sekakoh, 2020), with further potential consequences on the giraffe's sociability (Bond, König, Lee, et al., 2021; Bond, Lee, Farine, et al., 2021). Prevention of resource degradation is therefore vital to preventing further decline in BeNP's Kordofan giraffe.

Carrying capacity is incorporated into the model through the annual truncation of population size above the predetermined annual capacity (selected from a binomial distribution of mean and SD as specified in Table 1). This does not account for density-dependent declines in reproductive rates close to K , nor compensatory dispersal behaviours (Owen-Smith, 1988, 2014), and therefore, this truncation may result in greater mortality than should be expected in years when K is low. Although this may have consequences on estimates

of genetic diversity and cause catastrophes to be overrepresented, the sensitivity analysis found that uncertainty in estimates of SD in K had little consequence on stochasticity.

4.4 | Impact of supplementation

The supplementation of genetically unrelated adults resulted in a decrease in PE. As with poaching, alteration to the number of adult females had a greater impact on model outputs than comparable changes to the adult male population. As shown in Figure 1, the supplementation of 24 female giraffe (Table 2, scenario 6) generated a 10-year period of population growth, not seen under scenarios with even sex ratios. Although the movement of 48 individuals into BeNP across 10 years (Table 2, scenario 9) resulted in the lowest probability of extinction, it did not generate sustained population growth.

Practically, translocations of Kordofan giraffe may be unfeasible given their scarcity, while supplementation using different subspecies would raise fundamental questions around conservation ethics (Galindo-Leal & Weber, 1994). Furthermore, current IUCN conservation translocation guidelines emphasise that strong evidence is required that the threat(s) causing any prior extinction has been identified and adequately mitigated (IUCN/SSC, 2013, p. 14). Given present concerns around poaching within BeNP, underscored by the findings of the VORTEX model, translocation of individuals at this current time would be unjustifiable. Translocation should therefore not be considered until sufficient evidence indicates that the threats of poaching and habitat degradation have been sufficiently and sustainably curtailed.

An alternative interpretation of supplementation, as a net influx of individuals through dispersal into the park, offers another avenue for conservation intervention. Very little is currently understood about the connectivity of different regions within the Bénoué Complex, nor the extent of genetic isolation from other sub-Saharan populations. Should the interconnectivity of different subpopulations prove restricted, increasing the prevalence and protection of wildlife corridors may reverse the population decline in BeNP through net immigration, reducing edge effects and increasing the rate of genetic exchange (Akçakaya et al., 2007). This may prove a more sustainable, lower risk intervention strategy for both giraffe and other threatened species within BeNP, should these corridors remain undisturbed.

4.5 | Impact of intervention combinations

Intervention strategies implemented in parallel always had a greater effect than that of each constituent intervention individually (Figure 4). Only for combinations 'b+d' and 'a+b+d' (Figure 4) was the N_{100} greater than the sum of the constituent interventions. This may be due to the greater initial population sizes (as a result of supplementation) in 'b+d' and 'a+b+d' than in the individual interventions 'a' and 'b', resulting in a greater number of deaths prevented

over the 100-year timestep through the 5% adult mortality reduction. Combinations involving female-biased supplementations were not investigated but may be sufficient to generate a self-sustaining, long-term population.

4.6 | Sensitivity analysis

Of all parameters investigated for sensitivity, few proved as significant as '% adult females breeding'. Our model used a relatively optimistic estimate for interbirth interval of 18.8 months in order to exclude density-dependent reproductive rate decline from our model. Interbirth intervals are, however, a highly variable aspect of a female giraffe's lifetime fitness, with the coefficient of variation approximately 27% in wild populations (Bercovitch and Berry, 2010). Multiple studies approximate the interbirth interval for giraffe to 20 months (Bercovitch & Berry, 2010; Foster & Dagg, 1972; Hall-Martin & Skinner, 1978), with some estimates exceeding 22 months (Strauss et al., 2015). Findings of the sensitivity analysis suggest an interbirth interval of 20 months ('% adult females breeding' = 60.0%) would reduce the stoch-r by 8.82×10^{-3} , while 22.6 months ('% adult females breeding' = 53.1%), quoted by Strauss et al. (2015), yields a reduction in stoch-r of 1.58×10^{-2} from the baseline growth rate (a -51.63% change in the stochastic growth rate). In view of the notable population decline exhibited by the baseline model under our interbirth interval, this finding

further stresses the urgency of conservation action, with priority also given to establishing a more accurate estimate for this parameter in the BeNP population. This may prove difficult, owing to the long gestation periods of giraffe and behavioural difference between breeding and non-breeding females that may complicate survey efforts (Nichols et al., 1994).

The uncertainty in sex ratio was also found to significantly influence model output, representing roughly a quarter of explained variance (Table 3). Increased population growth rates associated with female-biased sex ratios (Figure 5) agree with observation of wild ungulates, however the linearity observed between sex ratio and stoch-r is unlikely to extrapolate to female-biased extremes, once the operational sex ratio no longer remains male-biased (Bessa-Gomes et al., 2004).

Of significance was the finding that uncertainty in initial population size estimates had little consequence on stoch-r . As with supplementation, even sex ratio increases in population size result in slightly larger N_{100} , but the rate of population decline is comparable to the baseline scenario (Figure 1).

5 | CONCLUSIONS

Of the conservation interventions investigated, this study places emphasis on the importance of anti-poaching activity as the primary route to preventing further population decline. Anti-poaching efforts must, however, be conducted in conjunction with further interventions in order to eliminate risk of extinction completely. This study points towards female-biased population supplementation as an effective avenue. Although supplementation through translocation reduces extinction risk, it is an expensive intervention that is often cost prohibitive. The more feasible alternative would be to strengthen the connectivity of the Bénoué Complex through better protection of wildlife corridors to facilitate supplementation through immigration. We therefore emphasise that the identification and protection of corridors should be a priority action. Extinction risk is further reduced when combined with the prevention of declines in the carrying capacity from illegal pastoralism and reductions in adult mortality. Ecoguard patrols, coupled with community engagement and strengthened law enforcement, are necessary to stem pastoralist incursion and the decline in suitable habitat. Despite no immediate imperative to increase carrying capacity, the growth rate of trees favoured by giraffe (such as *Azelia Africana*) being approximately 1 m year^{-1} (Gérard & Louppe, 2011) necessitates forward planning to improve habitat quality and increase carrying capacity should other strategies result in population growth.

The significance of uncertainty in estimates of 'Sex ratio', '% adult females breeding' and 'Adult female mortality' parameters highlights the need for long-term population monitoring in BeNP. Further use of aerial and ground-based surveys should be considered to establish population-specific approximation of the aforementioned parameters and continued population estimates. Alongside existing anti-poaching patrols, survey efforts should

TABLE 3 Partitioning of variance from the sensitivity analysis.

Parameter	% Variance in stochastic growth rate (stoch-r)	% Variance as a proportion of total explained variance
Juvenile mortality rate	2.06	2.21
Subadult mortality rate	11.1	11.9
Adult female mortality rate	21.5	23
Adult male mortality rate	0.111	0.119
Catastrophe frequency	0.367	0.393
Catastrophe survival rate	3.28	3.52
Lethal equivalents	0	0
Sex ratio	23.9	25.6
Initial population size	0	0
% Adult females breeding	31.1	33.3
Total	93.4	100
Residual	6.6	0

Note: Calculated using adjusted R^2 goodness-of-fit values generated from the multiple linear regression model.

quantify the exact poaching rate in BeNP to adjust model inputs. Long-term monitoring efforts may reveal more precise age–sex distributions in the population, which may help to improve the accuracy of model predictions—given that a stable age distribution was assumed in this study.

The spatiotemporal distribution of BeNP's Kordofan giraffe remains uncertain. Establishing the extent of dispersive movements across the park and the interconnectedness with both adjacent HZs and other Cameroonian National Parks will be pivotal to the long-term viability of this population. These efforts will also help to identify priority areas for protected wildlife corridors and may help to establish whether the BeNP population is either (a) in decline partly because of genetic isolation or (b) in spite of cross-boundary dispersal (suggesting the park's giraffe are a sink population within the wider BNC metapopulation). Further research is also required on the changing ecological landscape of Bénoué National Park. Habitat suitability modelling, accounting for future climate projections and human-induced habitat destruction, should be conducted to more accurately gauge how the carrying capacity of the park will change over the next century. This should serve as the basis for habitat restoration efforts once other intervention strategies have resulted in sustained population growth.

These findings have wider implications, furthering our understanding of how large bodied, k-selected mammals respond to extinction threats and conservation strategies at very low population sizes. These populations' growth rates are particularly sensitive to reproductive rates (more so than juvenile mortality, indicated by the sensitivity analysis), as seen by intervention scenarios that modelled changes in adult female population size through supplementation or poaching. Our findings further emphasise this sensitivity of population growth in k-selected species to changes in reproductive rates, as well as illustrating the scale and persistence of intervention required to reverse population declines in large-bodied, slow-reproducing species. Our analysis demonstrates the importance of population modelling in conservation—efficacies of intervention strategies are context-specific and non-uniform, and therefore should not be implemented blindly.

AUTHOR CONTRIBUTIONS

KC and SP conceptualised the study; KC conducted the modelling; KC, CJ and SP contributed to writing the original draft; all authors contributed to writing—review and editing. The authors declare no conflicting or financial interests. All authors accepted the final version of the manuscript.

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DATA AVAILABILITY STATEMENT

The PVA VORTEX input file used in this study is available in Data S1.

ORCID

Caspian L. Johnson  <https://orcid.org/0000-0001-6990-7952>

Samuel G. Penny  <https://orcid.org/0000-0002-7485-7897>

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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