

Female reproductive skew exacerbates the extinction risk from poaching in the eastern black rhino

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Supplementary Information S1

Method to estimate age-specific vital rates

We estimated vital rates using additive models because of the relatively small number of individuals used at each age, which may mean raw age-specific data are not representative of mean vital rates. An additive modelling approach enabled us to capture nonlinear trends in vital rates across an individual's lifetime at a finer-scale resolution than a stage-based approach. This was done using using generalised additive models (GAMs) implemented in the *mgcv* package [1].

We modelled the probability of birth and death separately. Reserve (factor; Lewa, Ol Pejeta or Ol Jogi) and age (numeric integer from zero to 40) were used as explanatory variables to model the occurrence of a birth or death for an individual across observation years. The response variables were binary, indicating birth/no birth and death/survival, and as such the models were fitted with binomial error structures and a logit link function. Reserve was incorporated as a factor and age as a smoothing term fit with a thin plate regression spline [2]. We used model selection based on the Akaike information criterion (AIC) [3,4] to decide the basis dimension (k value) to use for the smoothing term (Figures S1.1 and S1.2).

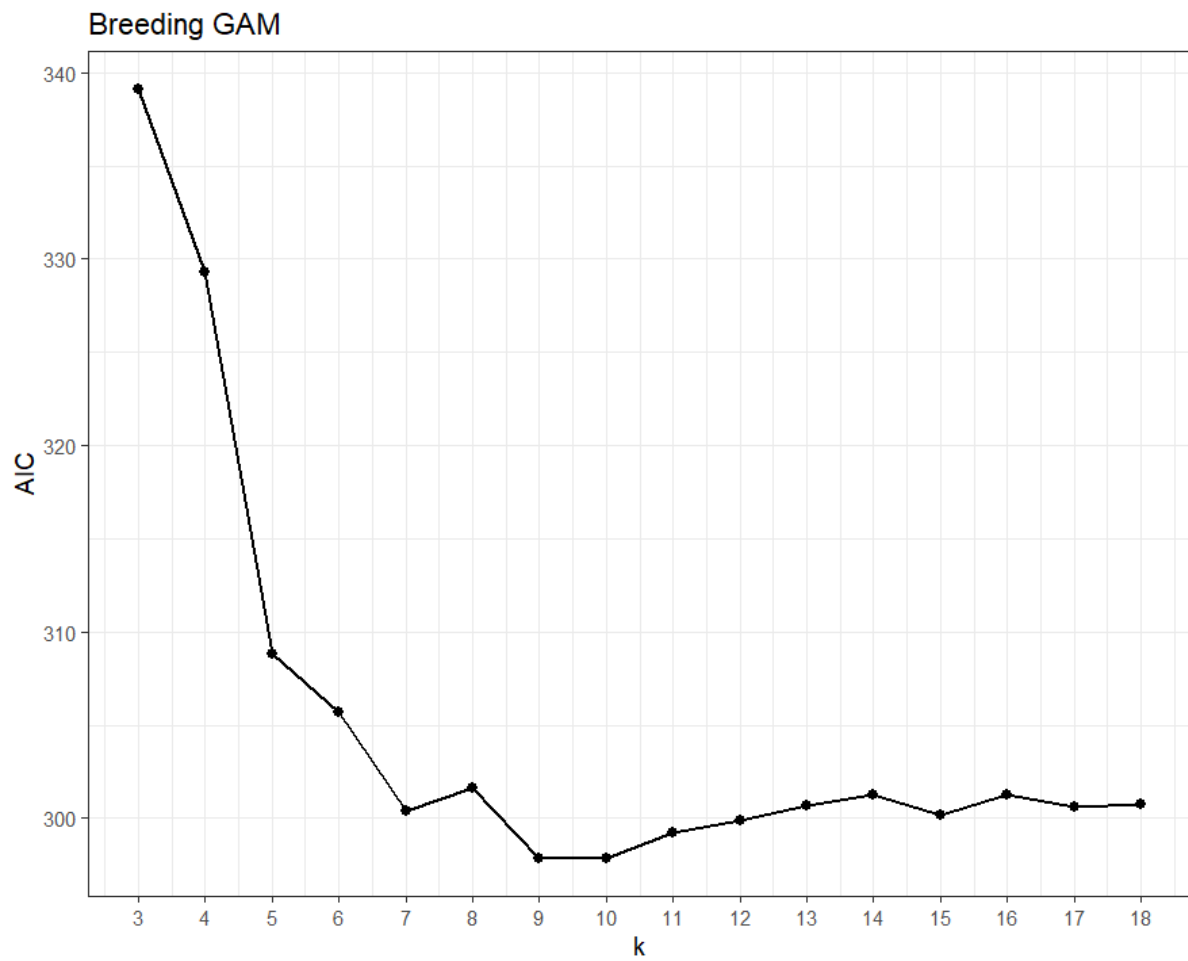


Figure S1.1 The AIC values of the breeding GAM with different k-values. A value of 9 for k was selected

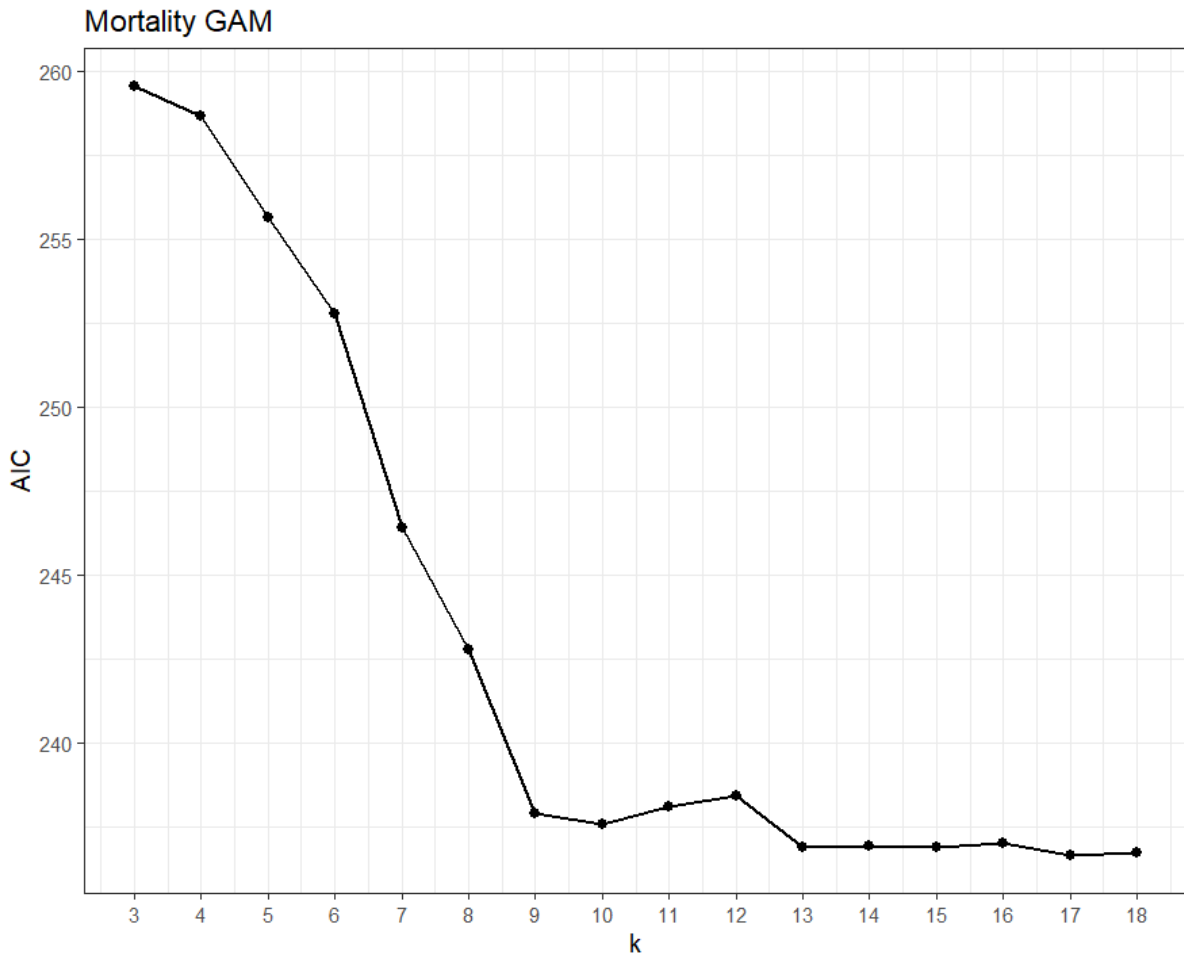


Figure S1.2 The AIC values of the breeding GAM with different k-values. A value of 9 for k was selected

The *DHARMA* package in R was used to calculate scaled model residuals in order to assess the distributional assumption of the models [5]. *DHARMA* uses a simulation-based approach to create scaled residuals for mixed effects models that are visually interpretable and allow distributional assumptions to be tested statistically. We tested for under/overdispersion and uniformity in simulated residuals using 1000 simulations (Figure S1.3-10).

Using DHARMA to test distributional assumptions

Breeding

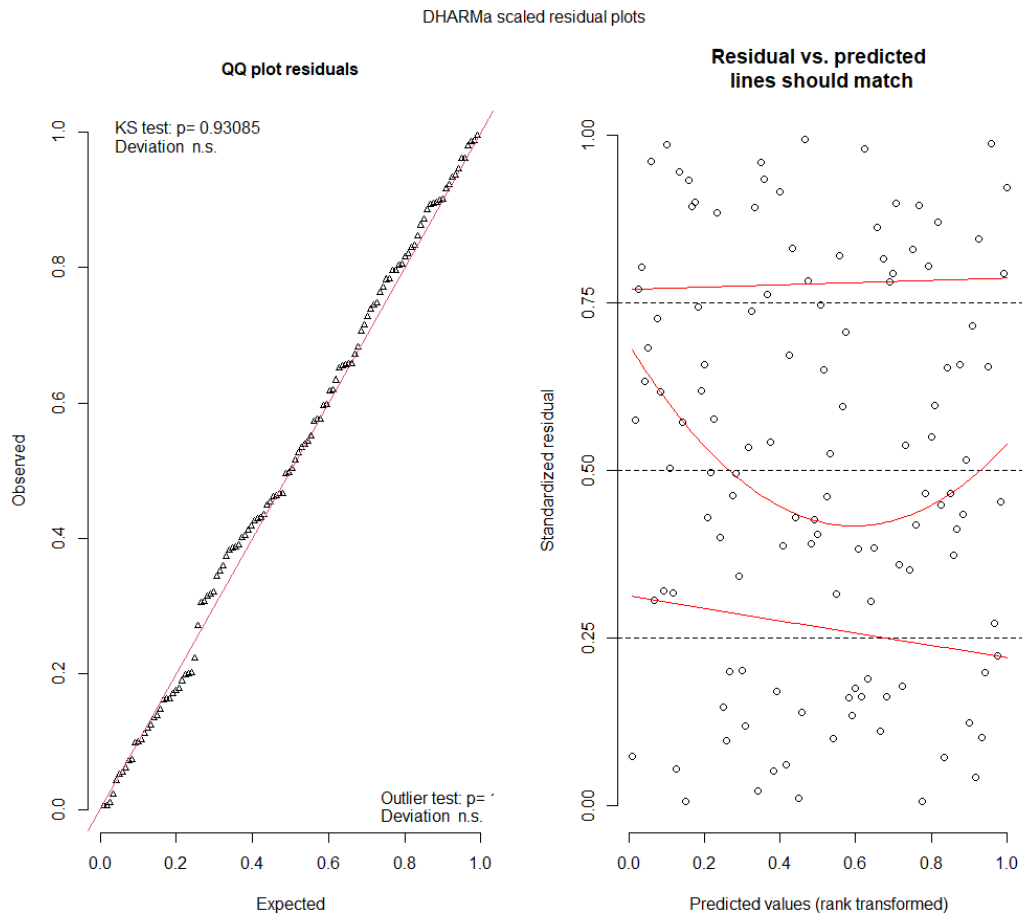


Figure S1.3 DHARMA scaled residuals were used to create a) a QQ plot (One-sample Kolmogorov-Smirnov test for uniformity. $D = 0.049456$, $p\text{-value} = 0.93085$) and b) a plot of the residuals against the predicted value. There are no outliers identified

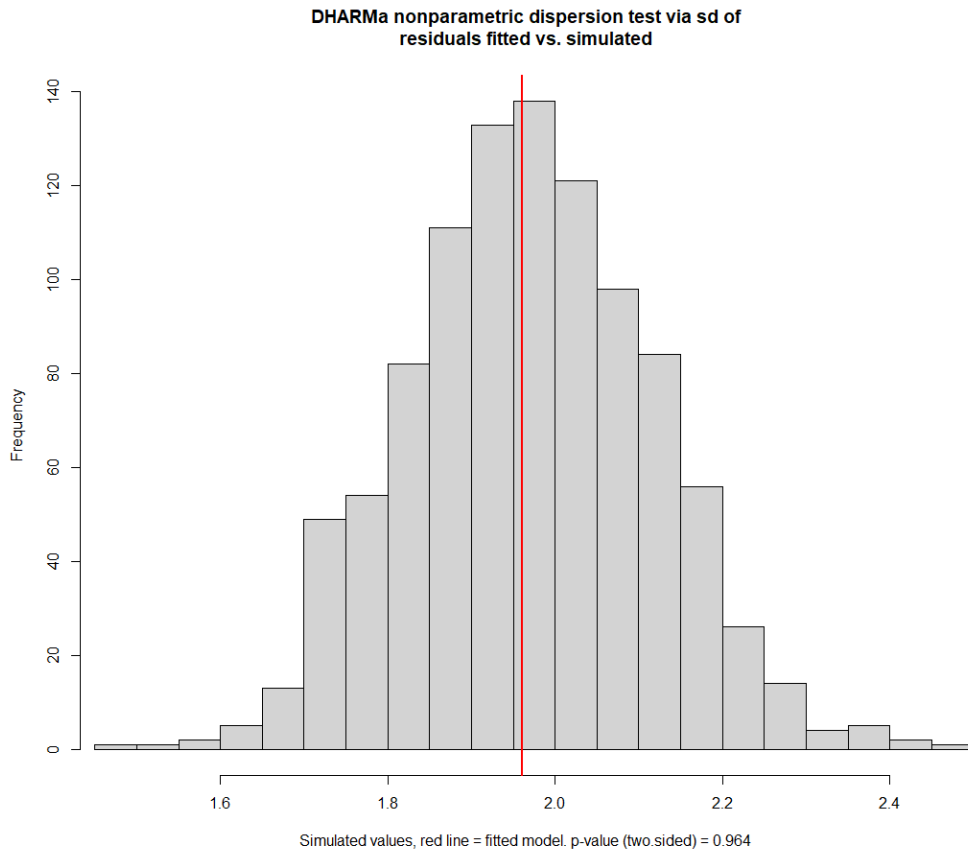


Figure S1.4 DHARMA nonparametric dispersion test via sd of residuals fitted vs. simulated. Ratio of observed to simulated = 0.99571, p-value = 0.964

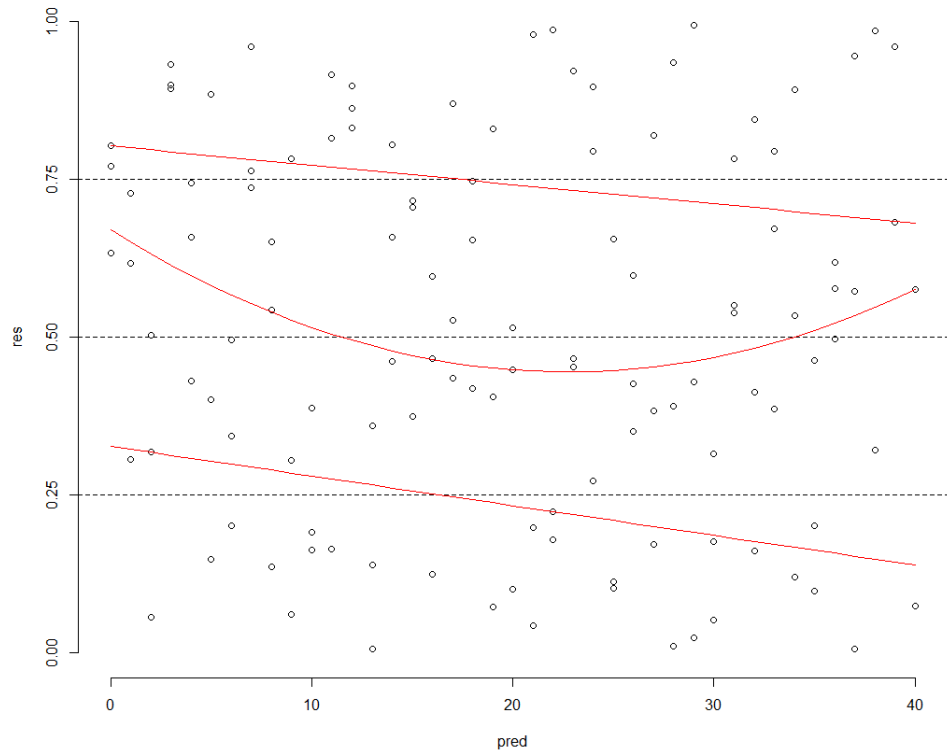


Figure S1.5 Plot of DHARMA scaled residuals for the age variable against predicted values

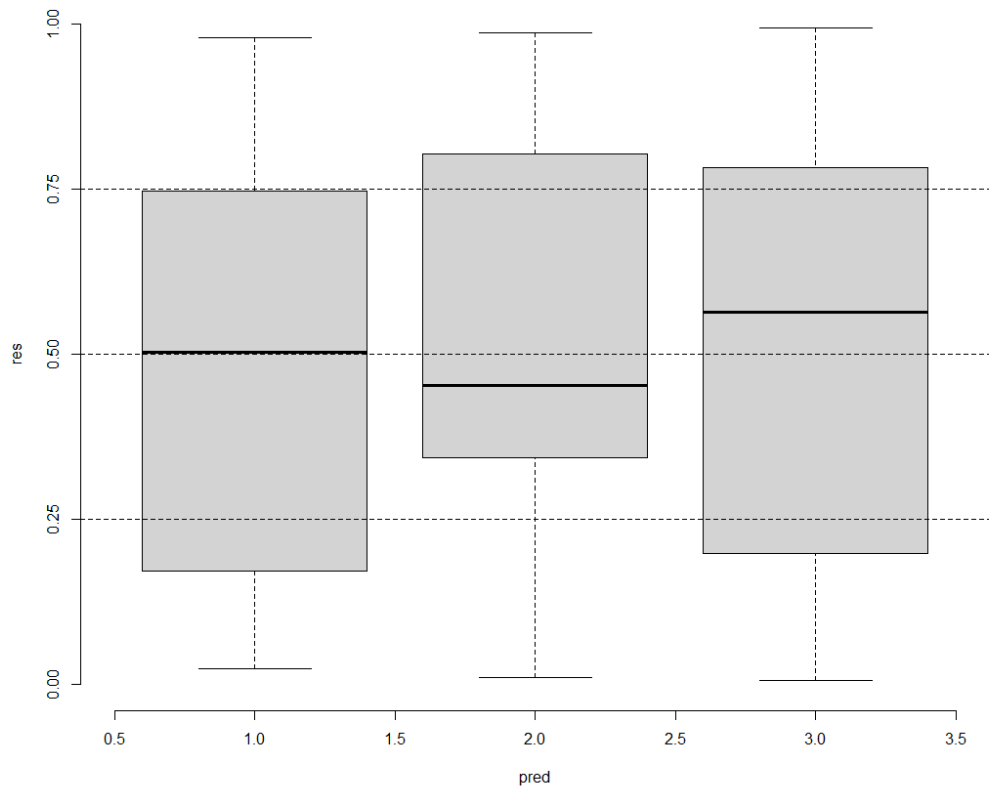


Figure S1.6 Plot of DHARMA scaled residuals for the population variable against predicted values

Mortality

DHARMA scaled residual plots

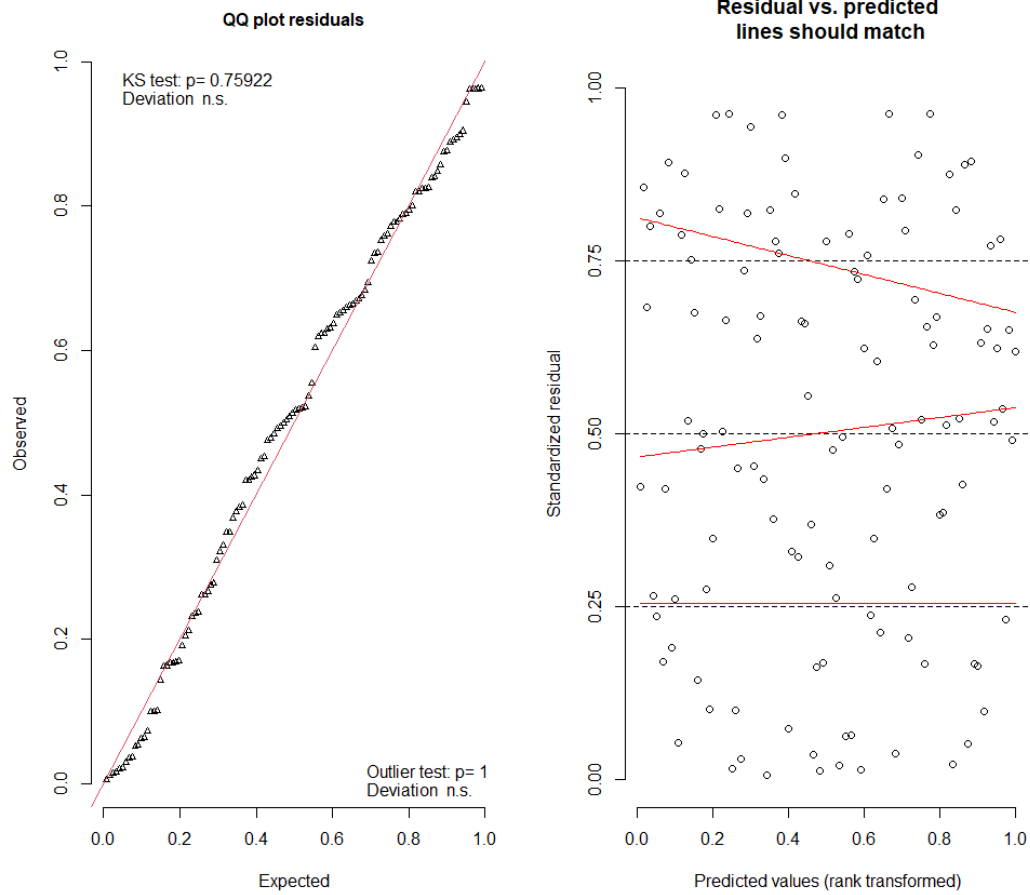


Figure S1.7 DHARMA scaled residuals were used to create a) a QQ plot (One-sample Kolmogorov-Smirnov test for uniformity. $D = 0.06123$, $p\text{-value} = 0.7592$) and b) a plot of the residuals against the predicted value. There are no outliers identified

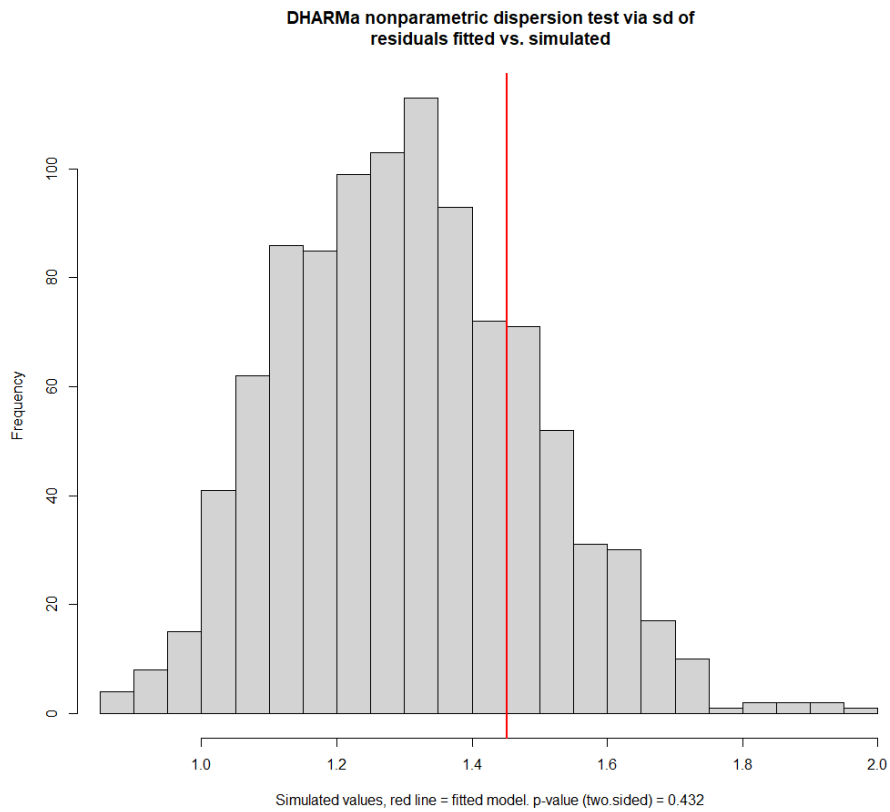


Figure S1.8 DHARMA nonparametric dispersion test via sd of residuals fitted vs. simulated. Ratio of observed to simulated = 1.1121, p-value = 0.432

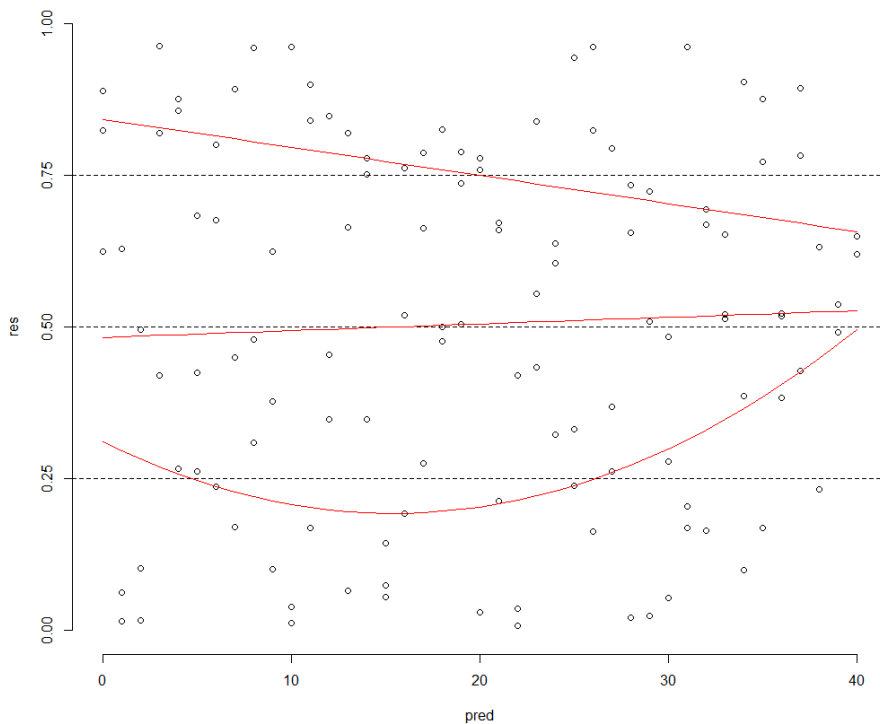


Figure S1.9 Plot of DHARMA scaled residuals for the age variable against predicted values

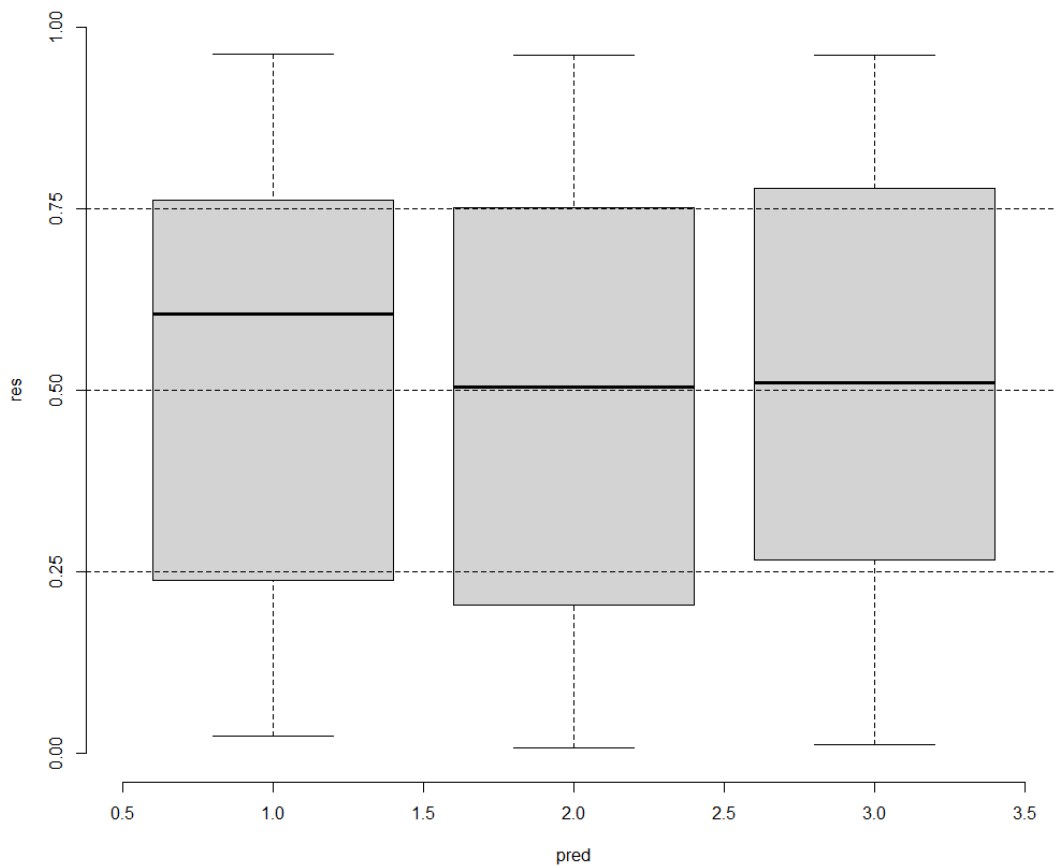


Figure S1.10 Plot of DHARMA scaled residuals for the population variable against predicted values

References

1. Wood SN. 2011 Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **73**, 3–36. (doi:<https://doi.org/10.1111/j.1467-9868.2010.00749.x>)
2. Wood SN. 2003 Thin plate regression splines. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **65**, 95–114. (doi:<https://doi.org/10.1111/1467-9868.00374>)
3. Akaike H. 1987 Factor analysis and AIC. *Psychosometrika* **52**, 317–332.
4. Burnham KP, Anderson DR. 2004 Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociological Methods & Research* **33**, 261–304. (doi:<https://doi.org/10.1177%2F0049124104268644>)
5. Hartig F. 2018 *DHARMA: residual diagnostics for hierarchical (multi-level/ mixed) regression models*. See <https://CRAN.R-project.org/package=DHARMA>.

Supplementary Information S2 - Formulation of the stochastic individual-based model

Description of the individual-based model using the ODD protocol described by Grimm et al. (2006)

Purpose

There are two main purposes of this model. The first is to evaluate the differences in population viability between three discrete Kenyan populations of eastern black rhinos. The second is to understand the effect of female reproductive skew on these populations under different poaching pressures.

State variables and scales

The models were formed at the level of individual females. Individuals are characterised by three state variables, their age (a , integer between 0 and 40 in years), the population they belong to (Lewa L , Ol Jogi J , or Ol Pejeta, P) and their reproductive value (v). As the populations were discrete, the three models were separate with no movement of individuals between them. Each population is characterised by the number of individuals at each age in each year.

Process overview and scheduling

The models proceed in annual time steps. Within each year or time step, 2 phases are processed: mortality and then birth. This order was selected as even though a female could give birth then die in the same year, a new born calf would not survive if that occurred. In each year, based on age, population and reproductive value females had a given probability of reproduction or mortality. An overview of the life-cycle and transition probabilities for Lewa is given in figure 1 L is replaced with P for Ol Pejeta and J for Ol Jogi.

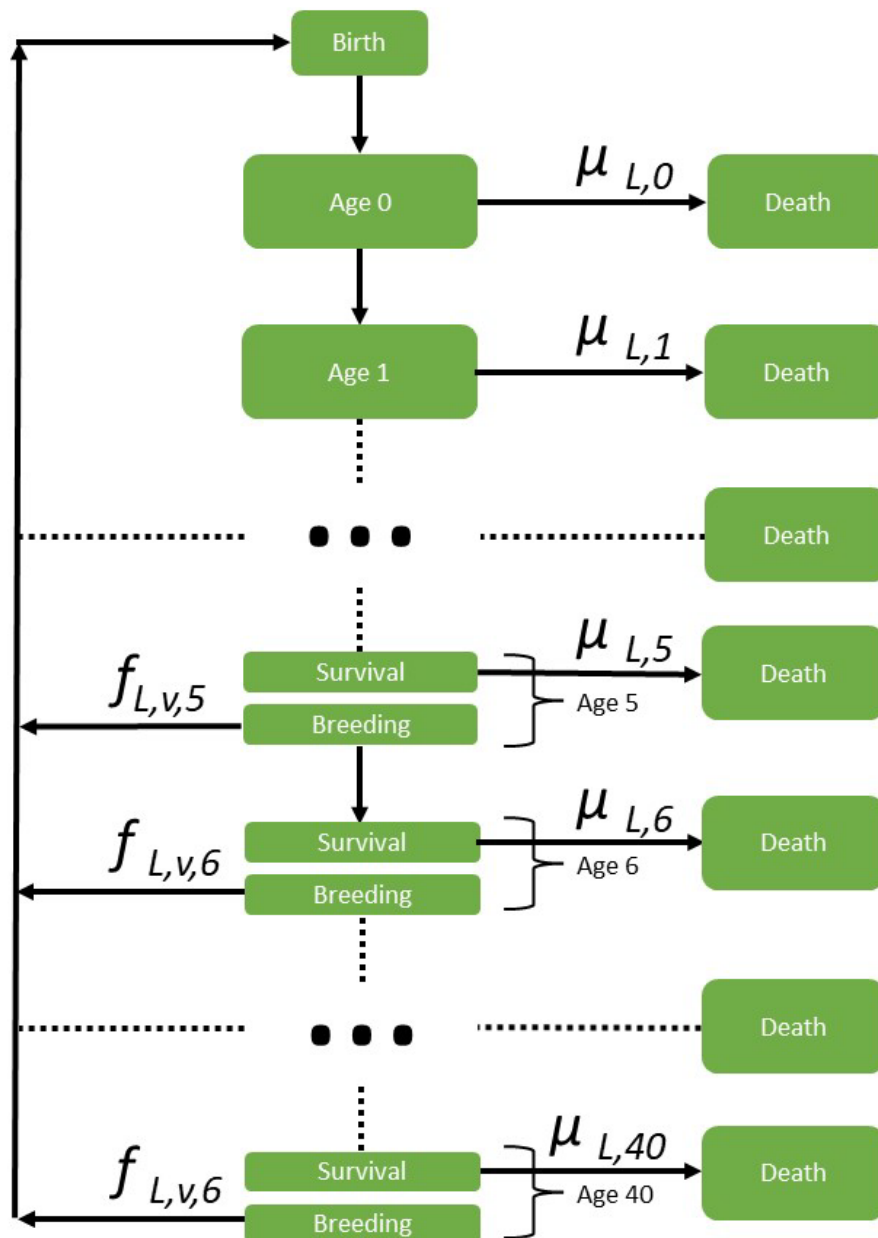


Figure S2.1 Schematic of the life-cycles for the individual-based stochastic projection model for female eastern black rhinos on Lewa. Each individual at each age (a) had mean annual predicted birth probabilities of $f_{L,v,a}$ (Lewa), $f_{J,v,a}$ (Ol Jogi) or $f_{P,v,a}$ (Ol Pejeta), and mean annual predicted mortality probabilities of $\mu_{L,a}$ (Lewa) and $\mu_{J,a}$ (Ol Jogi) or $\mu_{P,a}$ (Ol Pejeta). All individuals born were females at age 0. Individuals below the 5 were given a breeding probability of 0. For reproductive ages, survival or mortality events occurred before breeding events. Individuals living past the age of 40 were removed from the analysis.

Design concepts

Reproductive skew: A distribution of historical breeding success was created using the number of male or female calves every female in the dataset over the age of 9 had successfully raised to the

age of one year, divided by their age above 5, to give an annual rate of yearling production in their reproductive ages. This resembled a zero-inflated Poisson distribution (Supplementary Information S6). This distribution remained constant throughout the projections, therefore assuming that the distribution of reproductive success did not change. These rates were used to create a distribution of reproductive success using the `hist()` function in R. Every year, either at initialisation of the model or at birth, new individuals were assigned a reproductive value drawn from this distribution using the `sample()` function. This assigned each individual an integer of one to ten, according to the probabilities from the distribution. All reproductive values of new individuals were scaled around zero using the `scale()` function, to preserve the average breeding probability of each population. These values were divided by 100 so that the highest modifications were an order of magnitude lower than the annual breeding probabilities of reproductive age females. This reproductive value followed the individual through their entire lives and was used to modify their breeding probability every year in the simulations.

Stochasticity: The baseline size of environmental stochasticity was estimated separately for the breeding and mortality rates and separately for each reserve using the standard deviation of the total birth and mortality rates over the whole period of the dataset on each reserve. The environmental stochasticity in a particular year was drawn from a truncated normal distribution created using `rtruncnorm()`. For the breeding rate, this distribution was truncated at 0.5 and -0.5, the mean was 0 – density dependence and the standard deviation was the baseline environmental stochasticity + density dependence. For the mortality rate, this distribution was truncated at 0.5 and -0.5, the mean was 0 + density dependence and the standard deviation was the baseline environmental stochasticity + density dependence. After this we ensured that no individuals below the age of 5 bred, as this is a pre-reproductive life stage. Overall, this means that at larger population sizes, breeding rates were lower and more variable and mortality rates were higher and more variable. Birth and mortality are interpreted as binary events drawn from the Bernoulli distribution, created using `rbinom()` for each individual from each reserve, with a probability from the mean age-specific probability from the birth and mortality models, modified by the reproductive value of the individual, environmental stochasticity and density dependence.

Interaction: Interactions that cause density dependence were modelled implicitly. When the population was over 75% of the estimated ecological carrying capacity (ECC) for each reserve, mortality increased and reproduction decreased with population size. Density dependence was modelled to act on the population by affecting the environmental stochasticity. Below 0.75(ECC), environmental stochasticity was calculated as outlined below. If the population was a proportion x above ECC, then the simulation distributions from which environmental stochasticity was drawn were altered using $4(x-0.75)$. The size of the standard deviations were increased by adding $4(x-0.75)$

to the quantity calculated in section 2.5. The mean of the sampling distribution for breeding probability was decreased from zero by $4(x-0.75)$, and the mean of the sampling distribution for mortality probability was increased from zero by $4(x-0.75)$. Observation: For analysis, we recorded the population-level variable of population size. We also recorded the number of simulations that reached a population of 0 over 100 years, and the proportion of 500 simulations that reached 0 was recorded as extinction rate.

Initialisation and input

We began the projection with the age-structure present at the end of 2019 for each reserve. We cannot present the starting age-structure due to confidentiality. Demographic stochasticity was incorporated by performing 500 iterations of the projection model. We projected forward 100 years. For this projection, age-specific birth and mortality probabilities were averaged across the study period from the model predictions with the highest predictive performance. Explicitly, the mean age specific predicted birth probability, $p(\text{age specific birth})$, is given by the following binomial additive models

$$p(\text{age specific birth}) = [1 + e^{-(R_0+f(a))}]^{-1}$$

Where R_0 is the intercept dependent on the reserve, and the function $f()$ describes a thin plate regression spline smoother at age a .

The mean age-specific predicted mortality probability, $p(\text{age specific mort})$, is given by the following binomial additive model

$$p(\text{age specific death}) = [1 + e^{-(R_0+f(a))}]^{-1}$$

For a particular individual in a particular year $p(\text{birth})$ was given by the following equation

$$p(\text{birth}) = p(\text{age specific birth}) + v + b$$

Where v is the reproductive value of the female and b is the environmental stochasticity modified by density dependence.

For a particular individual in a particular year $p(\text{mort})$ was given by the following equation

$$p(\text{mort}) = p(\text{age specific mort}) + d$$

Where d is the environmental stochasticity modified by density dependence.

Supplementary Information S3 - Calculation of long-term population growth rate

Demographic potential

We created Leslie matrices for each reserve from the estimated age-specific vital rates and then using the *popbio* package [1] we calculated the asymptotic population growth rate, λ , for each population. Considering a Leslie matrix \mathbf{A} , the individual elements of the matrix a_{ij} give the transitions of individuals at age j to age i during a single year. λ is the dominant eigenvalue of \mathbf{A} , and the proportional rate of increase. The intrinsic rate of increase of the population r , which we term the demographic potential growth rate [2], is given by:

$$r = \ln\lambda$$

Long-term realised population growth rate

We calculated the proportional change, or 'realised annual population growth rate' between year t and year $t+1$ individually for each of the 500 simulations. We then plotted the mean and 95% confidence intervals of this value for each reserve over the 100 years of the population projections. We calculated the long-term realised population growth rate as the average from year 25 to year 100 and the average confidence intervals over the same time period, as transient dynamics in the early time steps of the simulations would have inflated population growth rates and at year 25 the growth rates entered a stochastic equilibrium (Figure S3.1). Here x is the long-term realised population growth rate, and if $x > 1$ then the population will increase over time. The estimated long-term intrinsic rate of increase r_{long} , is given by:

$$r_{long} = \ln x$$

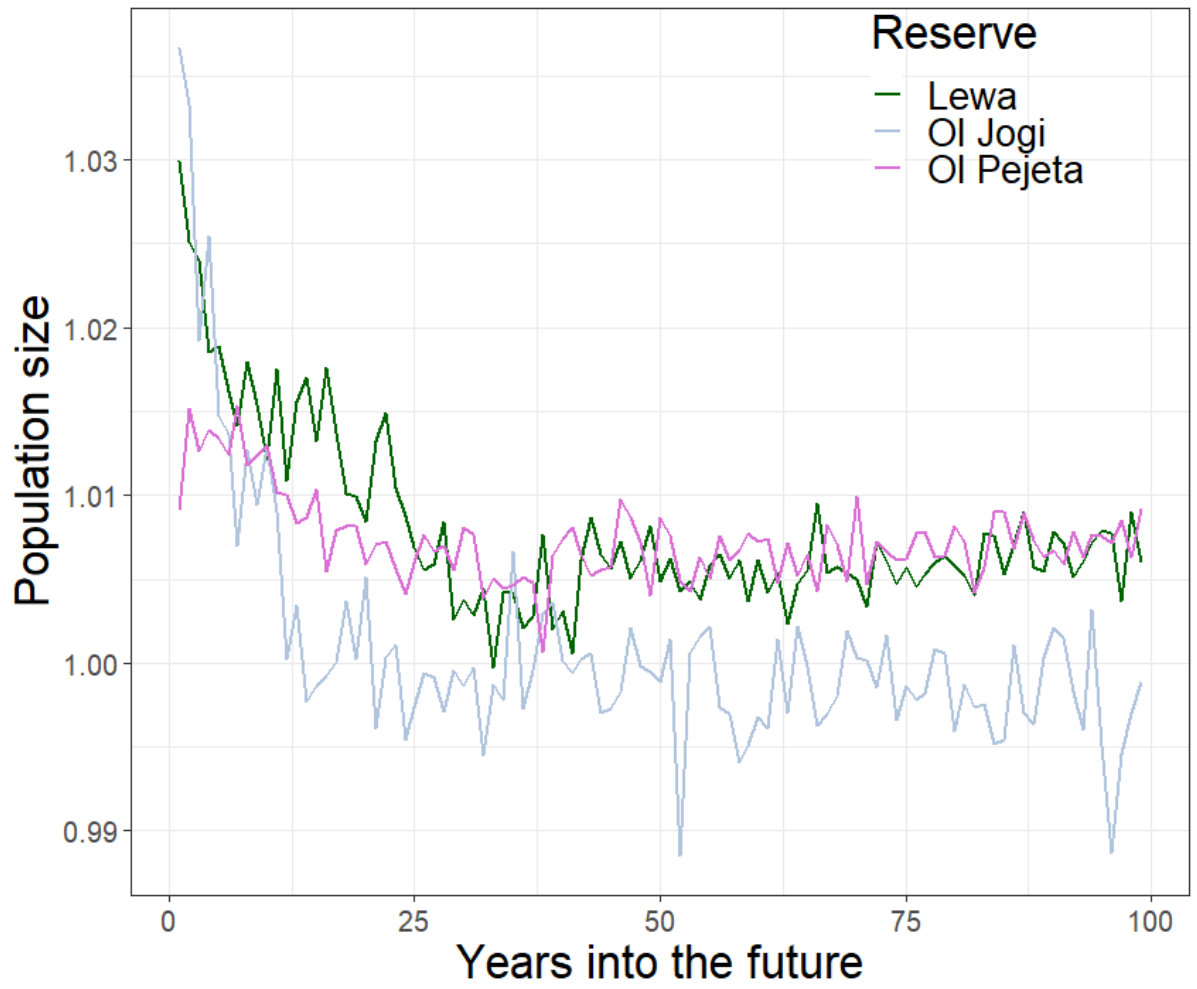
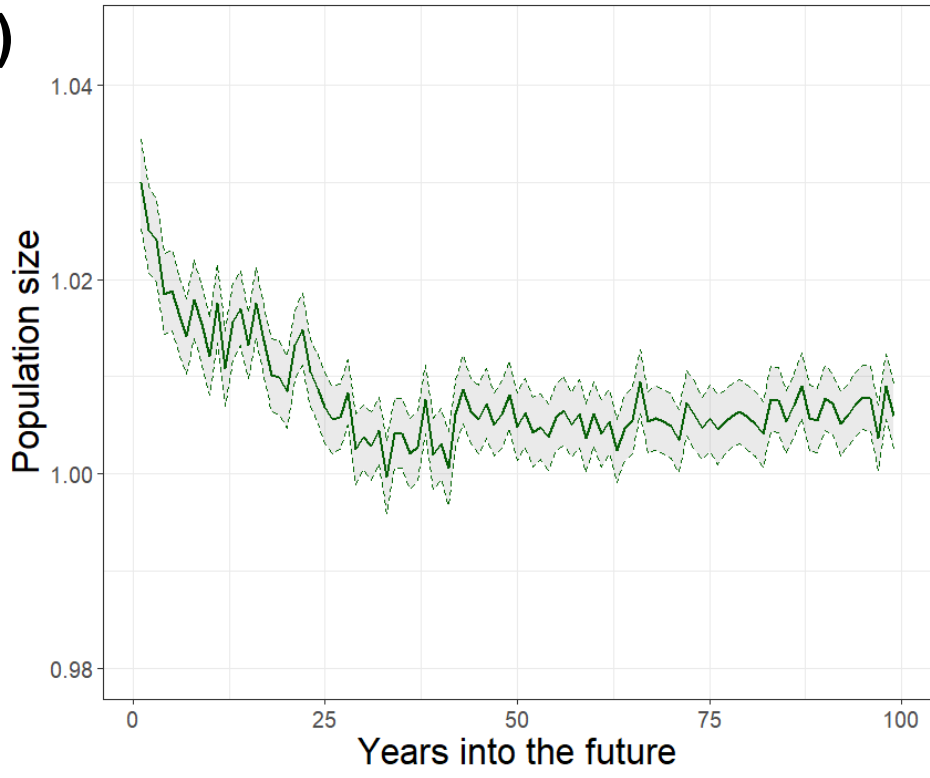
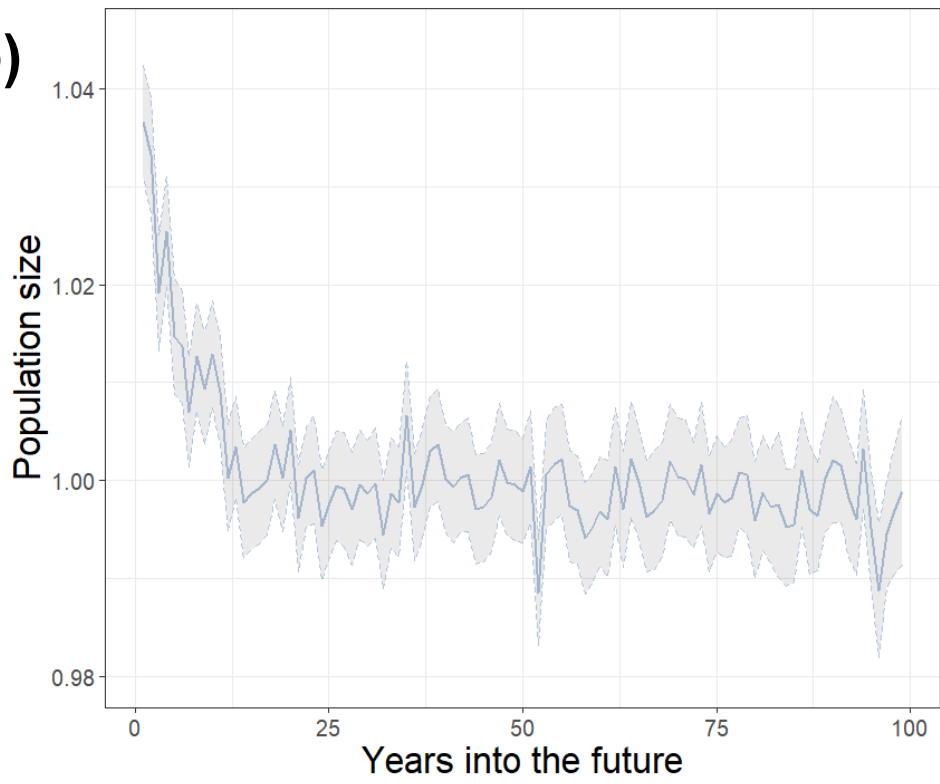


Figure S3.1 Average growth rates of the projections of each population over 500 simulations

a)



b)



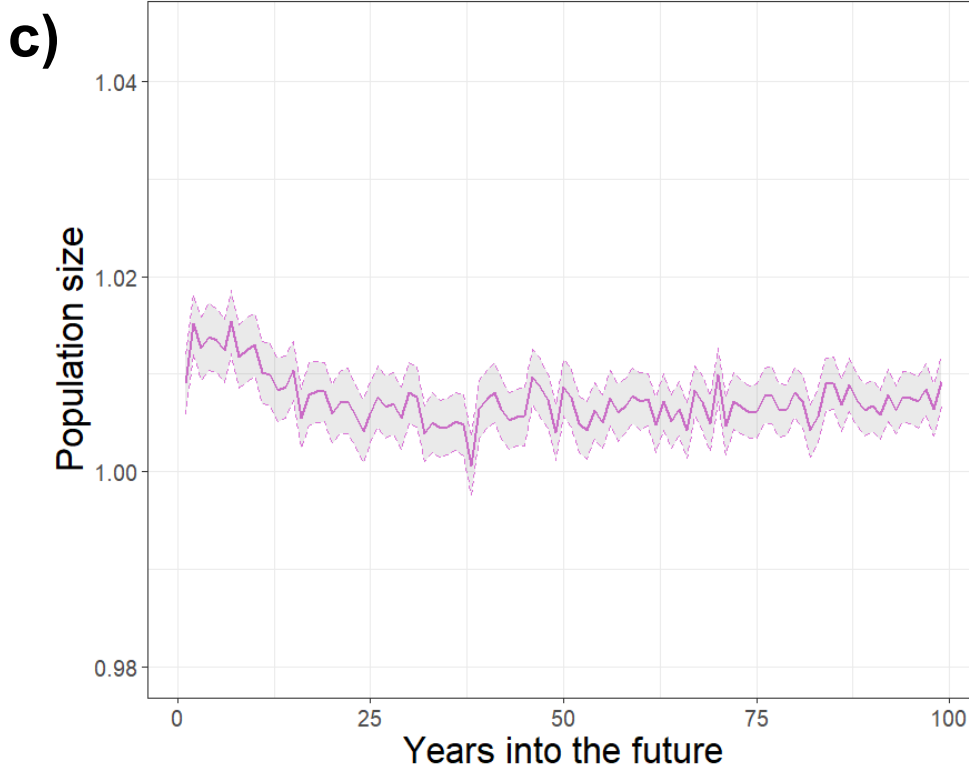


Figure S3.2 Average growth rates of the projections of over 500 simulations with 95% confidence intervals for a) Lewa, b) Ol Pejeta and c) Ol Jogi

References

1. Stubben CJ, Milligan BG. 2007 Estimating and Analyzing Demographic Models Using the popbio Package in R. *Journal of Statistical Software* **22**.
2. Caswell H. 2000 *Matrix population models*. Sinauer Sunderland, MA, USA.

Supplementary Information S4 - Lewa and OI Pejeta elasticities

Methods

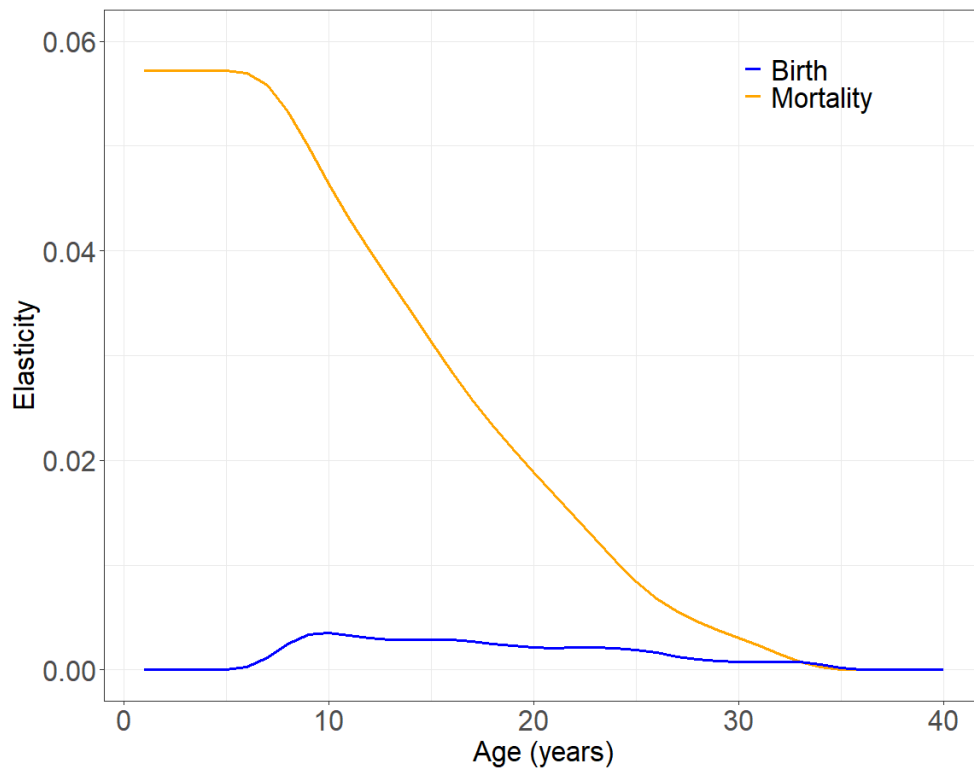
We calculated elasticities of this demographic potential for each vital rate from the Leslie matrices. Elasticities quantify the proportional change in population growth rate that results from a proportional change in one of the matrix elements [1–3]. These are calculated by:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{\partial r}{\partial \log a_{ij}}$$

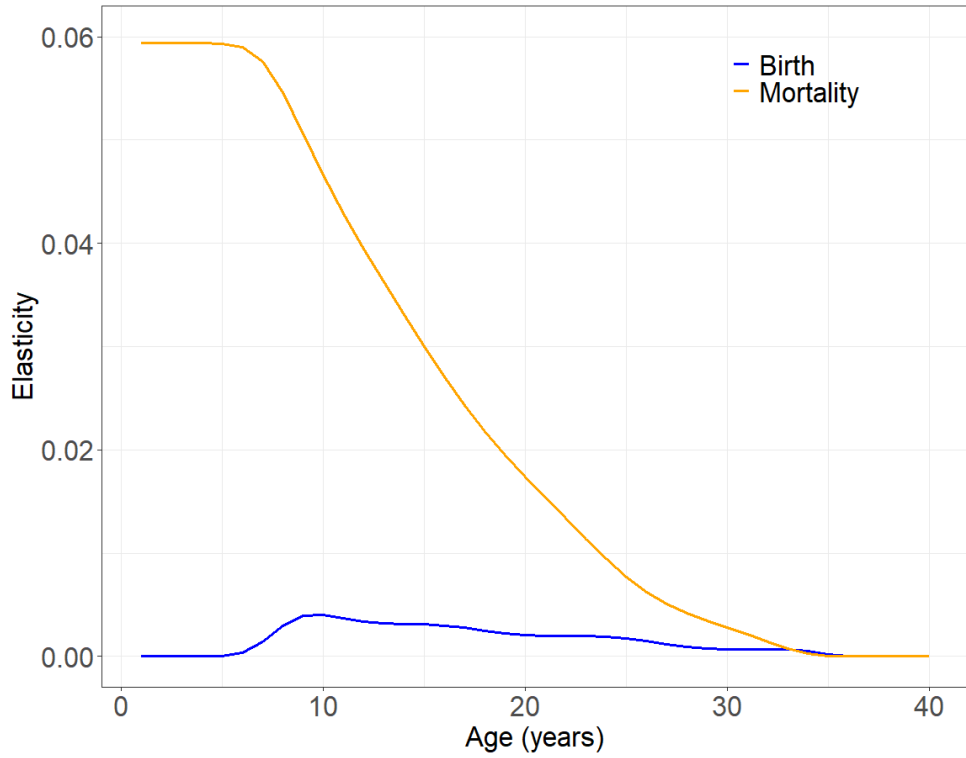
Elasticity analysis shows the relative contributions of each vital rate to λ [3] and allows for direct comparison between different vital rates. This means survival and reproduction can be compared, which is not possible when using sensitivities. Elasticities therefore give an estimate of the importance of ages and demographic rates to the populations and their management.

Results

a)



b)



c)

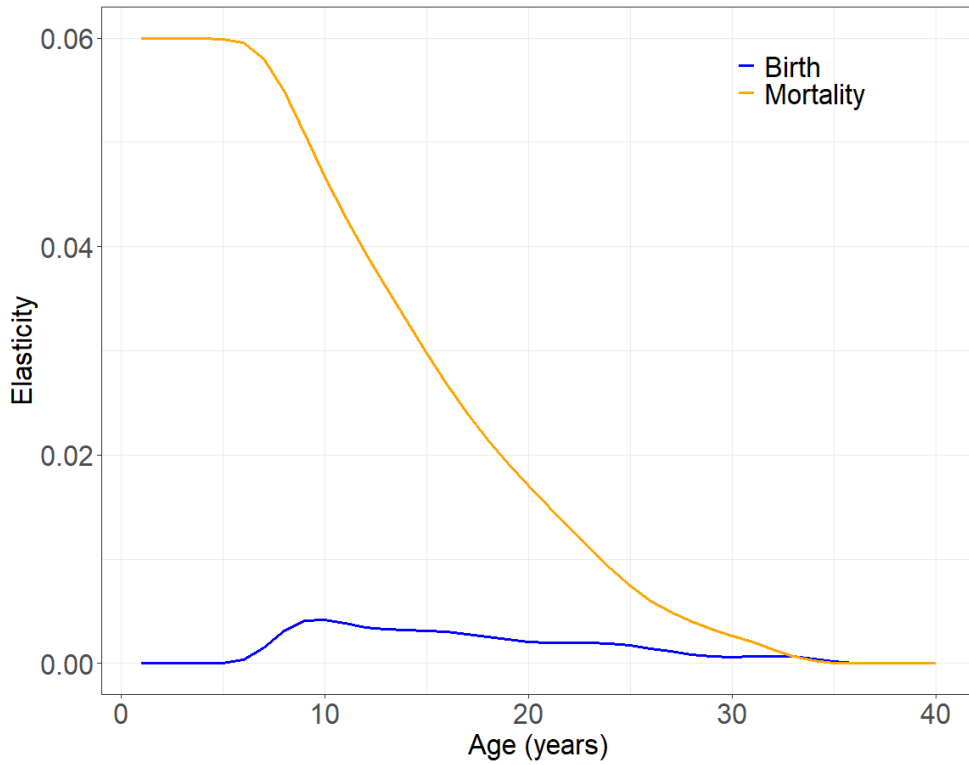


Figure S4.1 Elasticities both vital rates for a) Ol Jogi, b) Lewa and c) Ol Pejeta

We used elasticity analysis to show which ages and vital rates should be management priorities for the management of eastern black rhino populations. Mortality rates have a much greater impact on λ than fecundity rates, which is expected in mammals with late maturity and low reproductive rates

[4]. Mortality rates of younger individuals contribute more to λ , and elasticities decline gradually with age which can be understood as the younger an individual is, the greater its lifetime reproductive potential. This is an important result for the conservation of black rhinos as, coupled with this, all three populations experience high neonatal death rates (Figure 1). Calf deaths are relatively common and will have a proportionately larger effect on the growth of the population than deaths of older individuals. There are peaks in the contribution of fecundity to λ at ages that broadly correspond with the peaks in fecundity rates .

Discussion

Studies of large herbivore dynamics generally identify the survival of adult females [5] and pre-reproductive life stages [6] as the most important life stages. This study suggests that it is juvenile survival that is most important for black rhino population dynamics. While elasticity analysis shows that that mortality rates have a larger impact on population growth rates than fecundity rates, unstructured variation in survival probabilities has been theorised to have no effect on overall demographic variance [7] or extinction risk [8].

The significance of juvenile survival is important for conservation in light of the hypothesis that juvenile survival is the first vital rate to be affected by increasing density of a population or other stressors [9]. If this is true, and it is also the vital rate that is most important to future population growth, then monitoring juvenile survival is vital for conservation of black rhinos. Any increases in juvenile mortality will act as an early warning system for impacts on the population and need to be addressed quickly to prevent a depression of population growth. In Namibia and South Africa, calf mortality rates within the first year after birth have been found to range between 8% and 14% [10]. Our GAMs predict comparable rates, 12% for Lewa and Ol Pejeta and 17% for Ol Jogi. Focusing of reducing the death rate of calves should therefore be a conservation priority for these reserves, and black rhino managers. Detecting and determining the cause of calf mortalities can be difficult [86], but there are suggestions that predation may be an important factor [11,12]. Whether or not managing to reduce predation is possible or desirable is debatable, but the causes of calf mortality are an important area for future research.

References

1. Caswell H. 2000 *Matrix population models*. Sinauer Sunderland, MA, USA.
2. de Kroon H, Plaisier A, van Groenendael J, Caswell H. 1986 Elasticity: The Relative Contribution of Demographic Parameters to Population Growth Rate. *Ecology* **67**, 1427–1431. (doi:<https://doi.org/10.2307/1938700>)

3. Heppell S, Pfister C, Kroon HD. 2000 Elasticity Analysis in Population Biology: Methods and Applications. *Ecology* **81**, 605–605. (doi:[https://doi.org/10.1890/0012-9658\(2000\)081\[0605:EAIPBM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0605:EAIPBM]2.0.CO;2))
4. Oli MK, Dobson FS. 2003 The Relative Importance of Life-History Variables to Population Growth Rate in Mammals: Cole's Prediction Revisited. *Am. Nat.* **161**, 422–440. (doi:<https://doi.org/10.1086/367591>)
5. Sæther B-E, Bakke Ø. 2000 Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. *Ecology* **81**, 642–653. (doi:[https://doi.org/10.1890/0012-9658\(2000\)081\[0642:ALHVAC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0642:ALHVAC]2.0.CO;2))
6. Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C. 2000 Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores. *Annu. Rev. Ecol. Syst.* **31**, 367–393. (doi:<https://doi.org/10.1146/annurev.ecolsys.31.1.367>)
7. Kendall BE, Fox GA. 2002 Variation among Individuals and Reduced Demographic Stochasticity. *Conserv. Biol.* **16**, 109–116. (doi:<https://doi.org/10.1046/j.1523-1739.2002.00036.x>)
8. Robert A, Sarrazin F, Couvet D. 2003 Variation among Individuals, Demographic Stochasticity, and Extinction: Response to Kendall and Fox. *Conserv. Biol.* **17**, 1166–1169.
9. Eberhardt LL. 2002 A Paradigm for Population Analysis of Long-Lived Vertebrates. *Ecology* **83**, 2841–2854. (doi:[https://doi.org/10.1890/0012-9658\(2002\)083\[2841:APFPAO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2841:APFPAO]2.0.CO;2))
10. Du Toit R. 2006 Guidelines for implementing SADC Rhino conservation strategies.
11. Patton F. 2009 Lion predation on the African Black Rhinoceros and its potential effect on management. *Endanger. Species Update* **26**, 43–50.
12. Plotz R, Linklater W. 2009 Black rhinoceros (*Diceros bicornis*) calf succumbs after lion predation attempt: implications for conservation management. *Afr. Zool.* **44**, 283–287. (doi:<https://doi.org/10.3377/004.044.0216>)

Supplementary Information S5 – Age-specific vital rates and mean reserve-specific vital rates

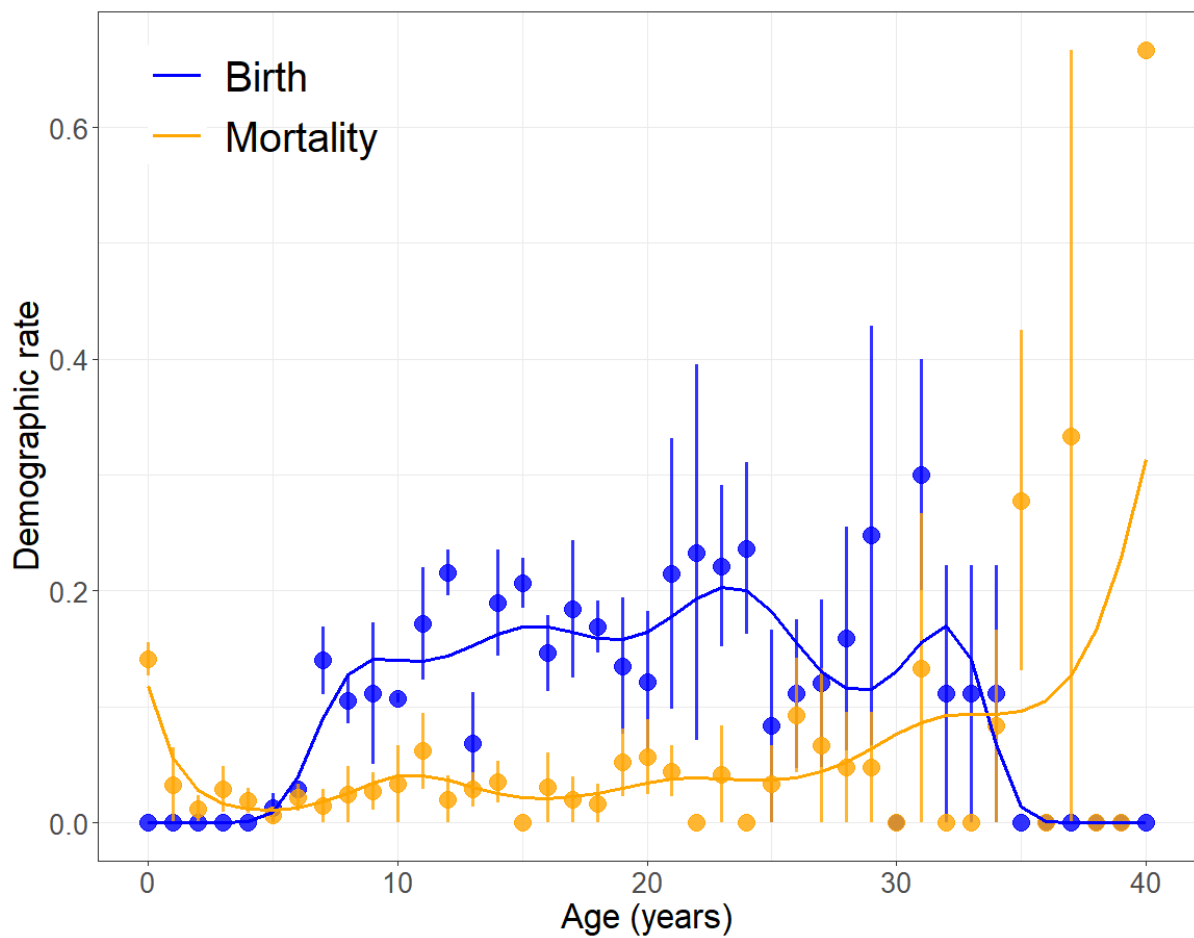


Figure S5.1 Birth and death rates for all ages, defined as the probability that an individual will breed or die in each year. Points show the raw aggregate demographic rates, with standard errors. Lines show the predicted demographic rates calculated using GAMs

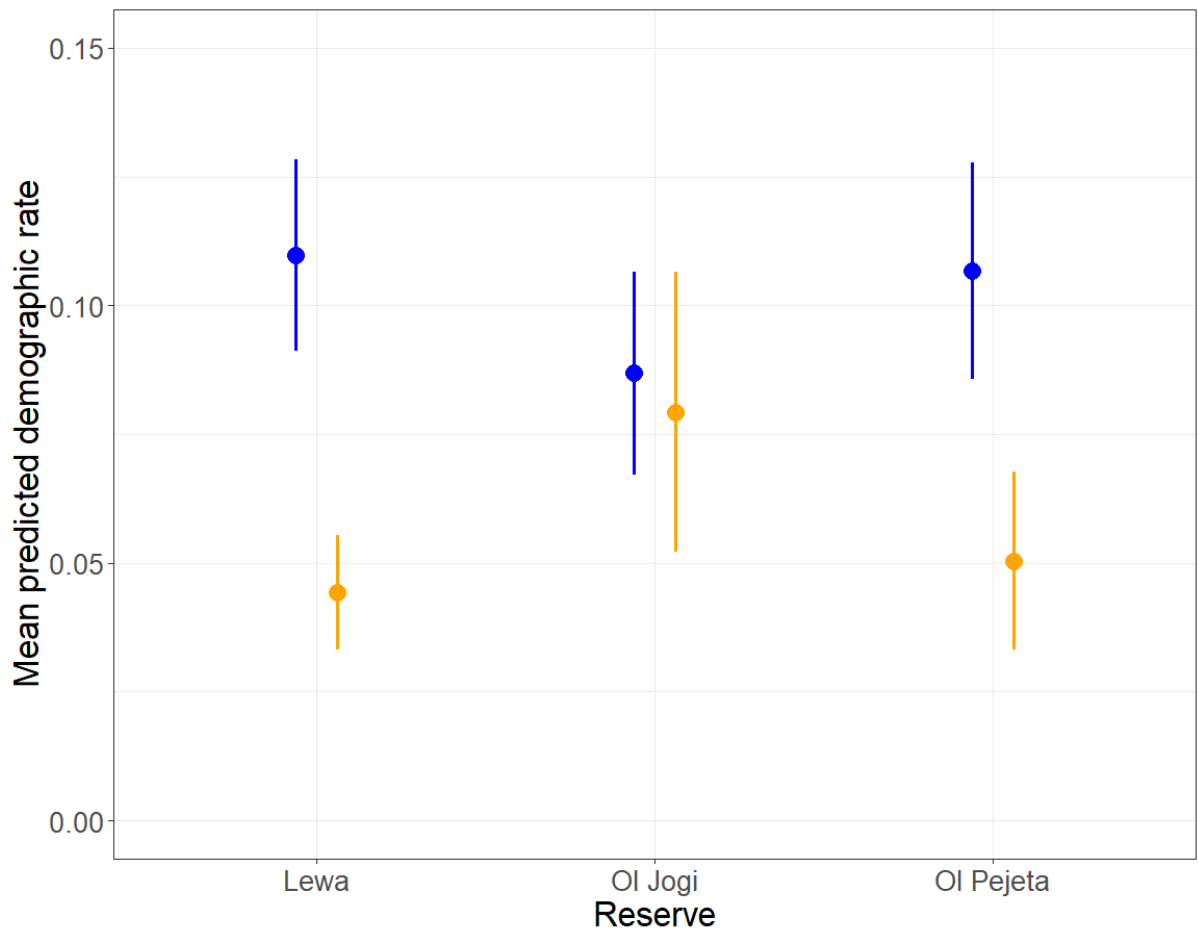


Figure S5.2 The mean demographic rates across all ages for each reserve, with standard errors.

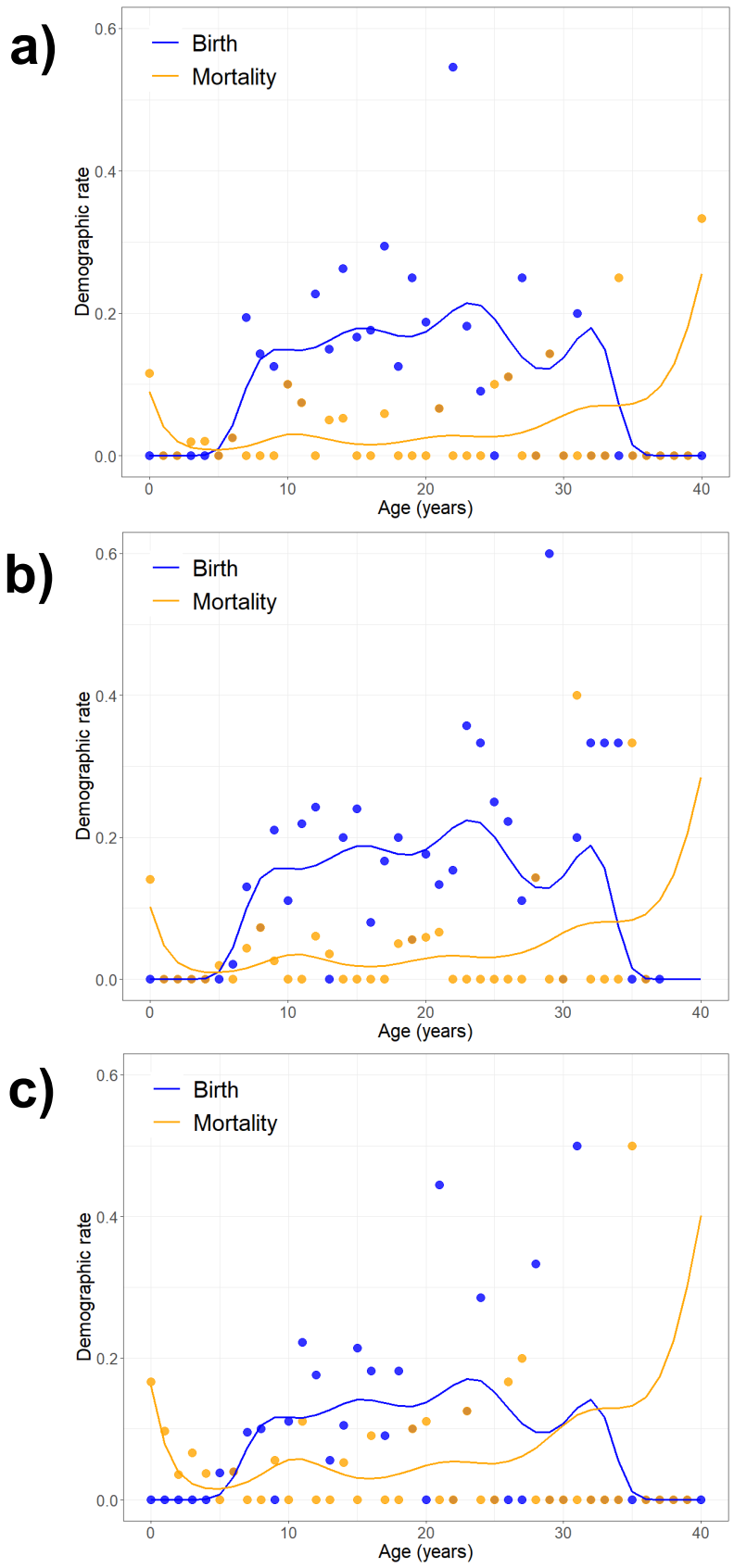


Figure S5.3 Birth and death rates for all ages for a) Lewa, b) Ol Pejeta and c) Ol Jogi. This is defined as the probability that an individual will breed or die in each year. Points show the raw aggregate demographic rates, lines show the predicted demographic rates calculated using GAMs.

Supplementary Information S6 – Female reproductive skew

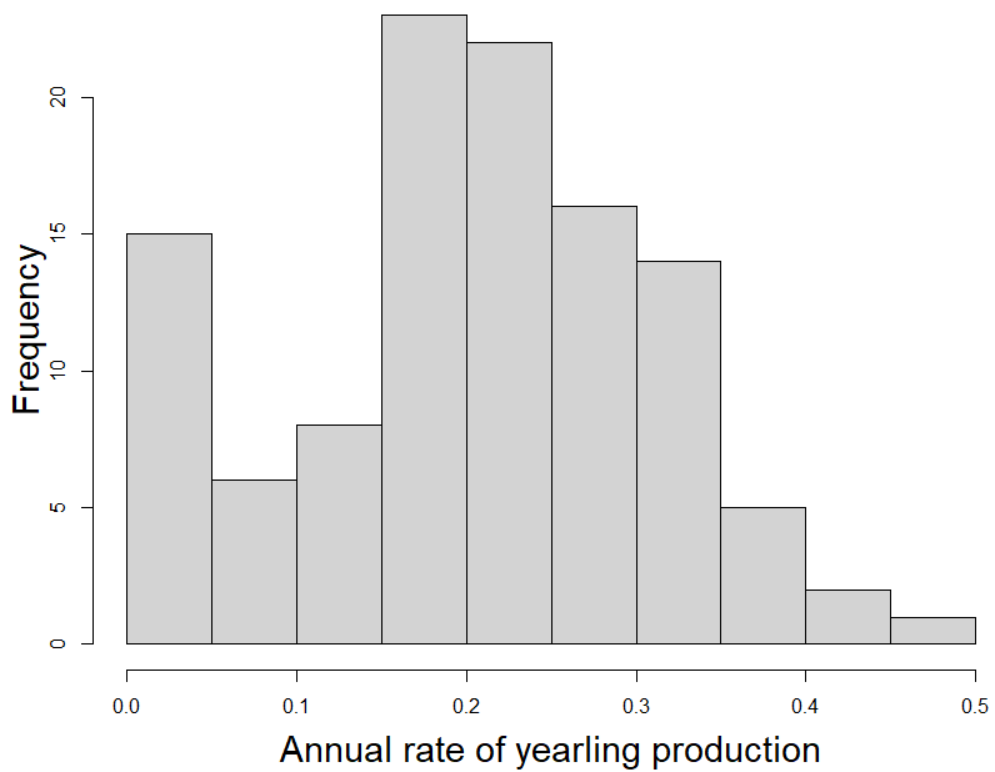
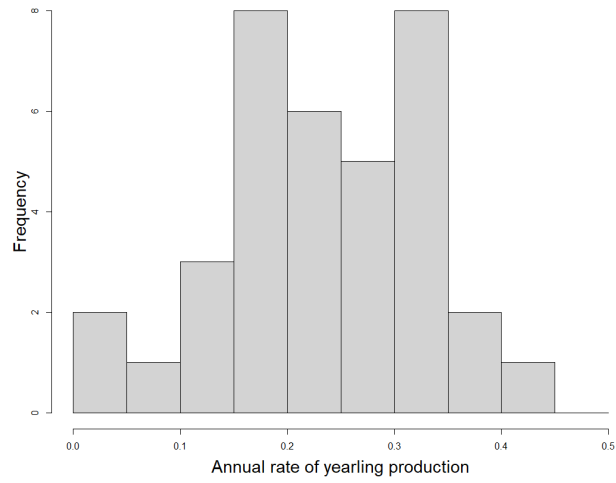
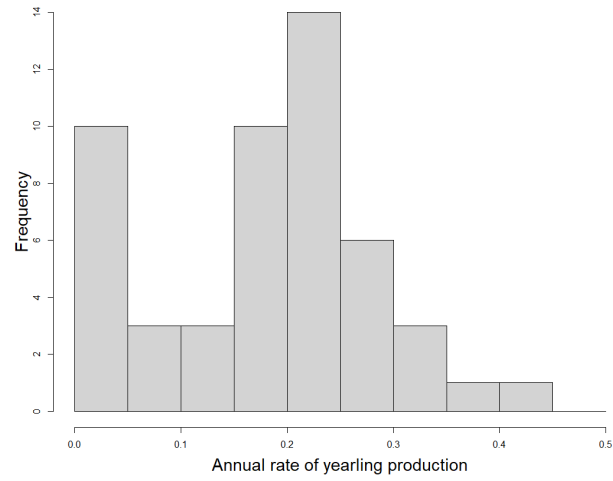


Figure S6.1 Histogram showing the variation in reproductive value of all females above the age of 9, estimated using the number of calves they raise to the age of one year annually

a)



b)



c)

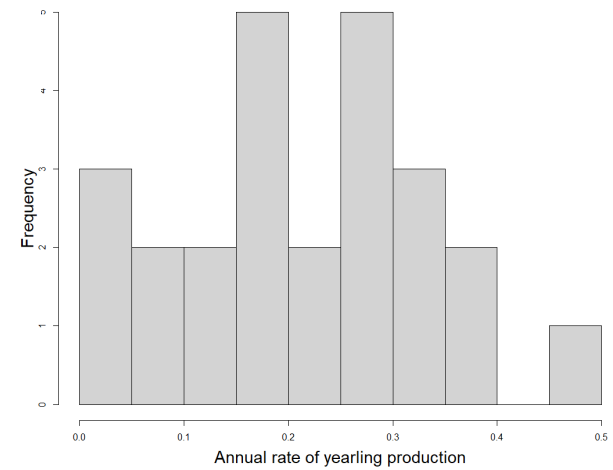


Figure S6.1 Histogram showing the variation in reproductive value of all females above the age of 9, estimated using the number of calves they raise to the age of one year annually for a) Lewa b) Ol Pejeta and c) Ol Jogi

Supplementary Information S7 – Lewa and Ol Pejeta population projections

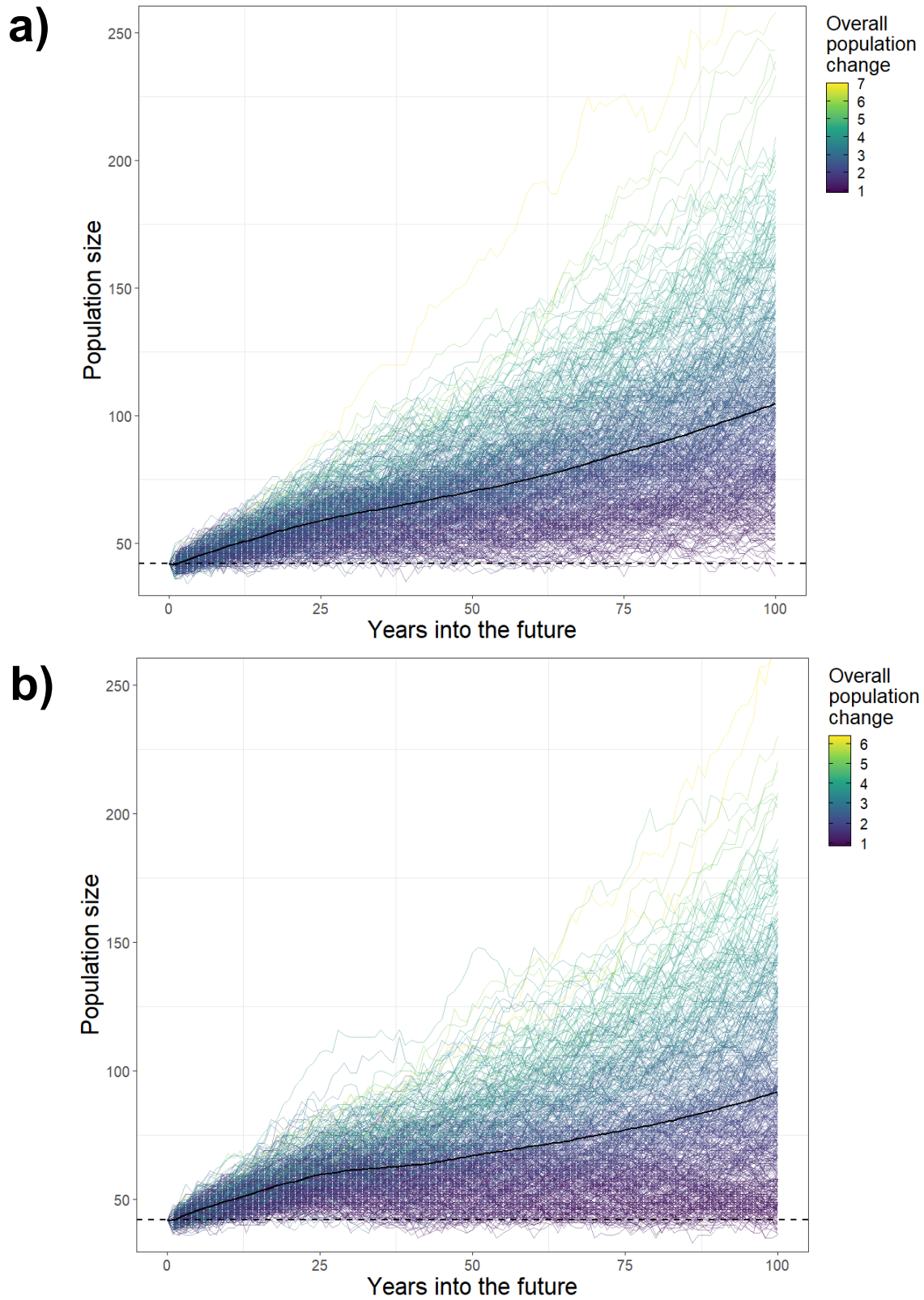


Figure S7.1 A comparison of the population projections for Lewa a) without and b) with female reproductive skew.

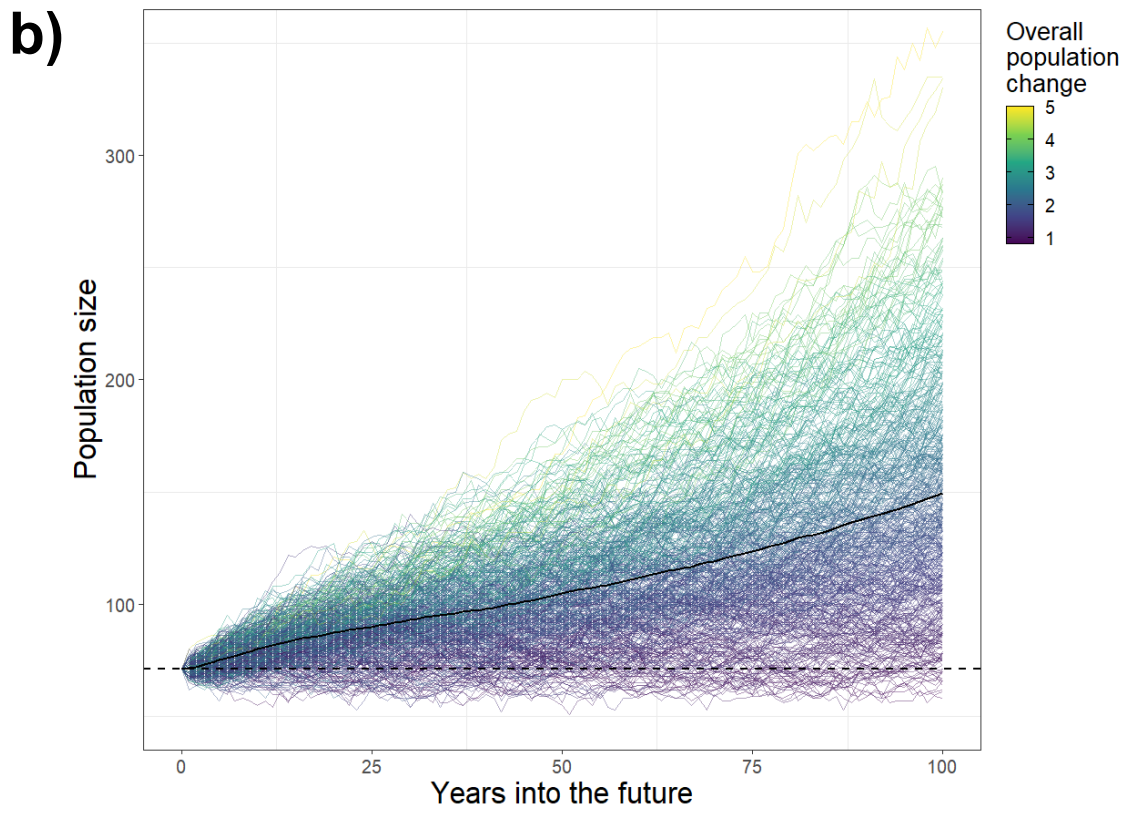
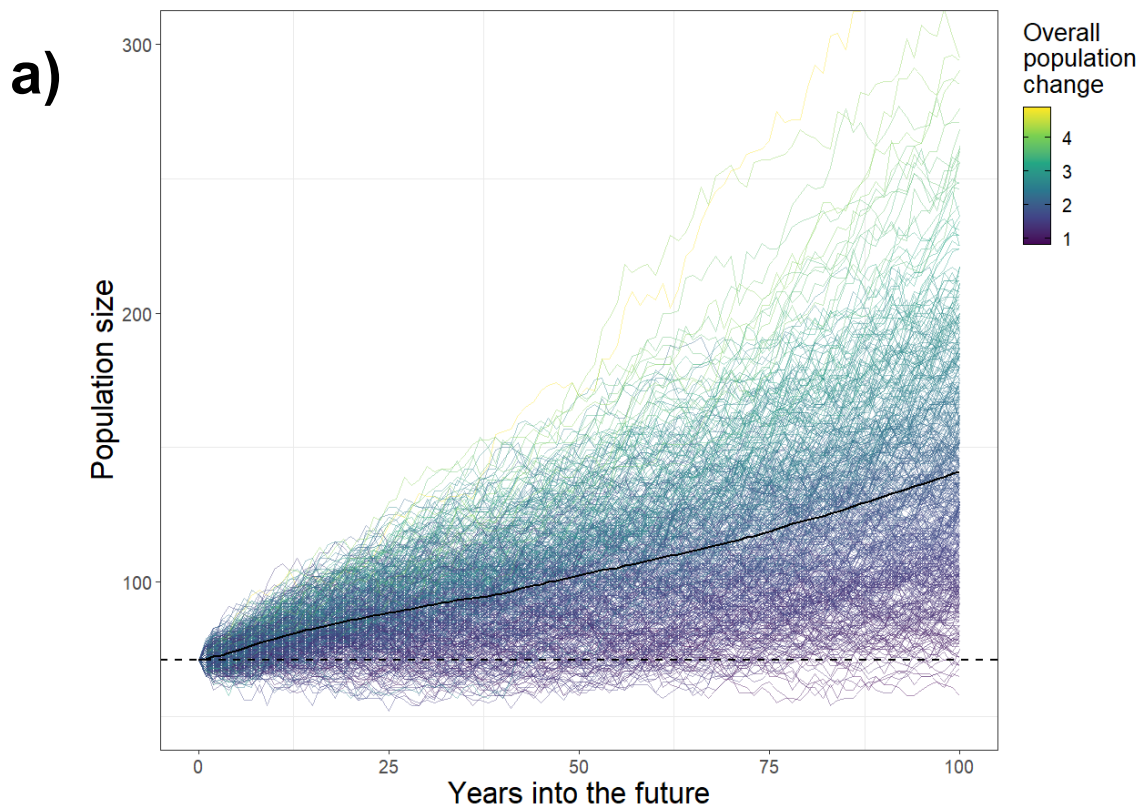


Figure S7.2 A comparison of the population projections for Ol Pejeta a) without and b) with female reproductive skew.