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Demographic responses of an insular elephant population to removal as a management intervention

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Abstract

Disturbances that change population structure may evoke transient dynamics that can be assessed within a demographic resilience framework. Conservation management interventions are conceptually disturbances that can be evaluated through such a framework to inform management actions and goals. The Main Camp in Addo Elephant National Park in South Africa presents a case study. Here management reduced the size of the elephant (*Loxodonta africana*) population by ∼26%. We compared population growth, modelled trends, constructed life tables and parameterized population projection matrices from data collected before, during and after the interventions. The interventions reduced population size and density, but co-occurring droughts may have reduced subsequent population growth and stage-specific survival. Transient dynamics followed the interventions and droughts and were associated with an unstable stage structure. The effect of adult survival on modelled asymptotic growth (its elasticity) was greater than a change in fertility. However, lowered juvenile survival contributed most to changes in transient growth. Management plans for elephant populations should consider the length of transients induced by interventions and environmental disturbances such as droughts. Our approach can benefit the assessment of population responses of elephants to disturbances such as poaching and persistent droughts elsewhere in Africa.

KEYWORDS
demographic resilience, demography, disturbance, *Loxodonta africana*, management, savanna elephants, transient dynamics

1 | INTRODUCTION

Southern Africa has a long history of efforts to curtail population size and growth of savanna elephant (*Loxodonta africana*) populations (van Aarde et al., 1999; Pimm & van Aarde, 2001; Robson et al., 2017). In fenced-off protected areas, elephant populations grow at high rates (Gough & Kerley, 2006; Slotow et al., 2005; Mackey et al., 2006), probably due to the lack of dispersal opportunities and in response to water supplementation (van

Aarde & Jackson, 2007; Purdon & van Aarde, 2017). Here, conservation practitioners often attempt to achieve conservation goals by reducing population size through culling, inducing dispersal, or reducing fecundity (Owen-Smith et al., 2006; van Aarde et al., 2006; Kerley & Shrader, 2007; Hayward, 2009; Hayward & Slotow, 2016). However, fenced-off elephant populations are also vulnerable to adverse environmental conditions, such as droughts, that may reduce survival, especially among juveniles (e.g., Foley et al., 2008; Shrader et al., 2010).

Elephants may withstand environmental disturbances, but are slow to recover from intense exploitation that occurs elsewhere in Africa (e.g., Wittemyer et al., 2013; Turkalo et al., 2017). Their slow life histories and the assumptions of constant rates of change associated with asymptotic (long-term) dynamics might misinform

conservation authorities on the effects of management practices on populations (see Stott et al., 2011; Koons et al., 2016). Consequently, transient (short-term) dynamics displayed within a conceptual framework of demographic resilience (Capdevila et al., 2020), may best reflect the response of populations to disturbances and management practices (Stott, 2016). Transient dynamics are the response of a population to regain stability in its age structure after a disturbance (Capdevila et al., 2020). Transient dynamics are likely in an environment that is temporally unstable, such as frequent droughts in savannas (Ogutu & Owen-Smith, 2003).

The elephant population of the Main Camp (MC) section of Addo Elephant National Park (AENP) in South Africa typifies such a case and is the focus of the present study. High elephant density, possibly due to a lack of
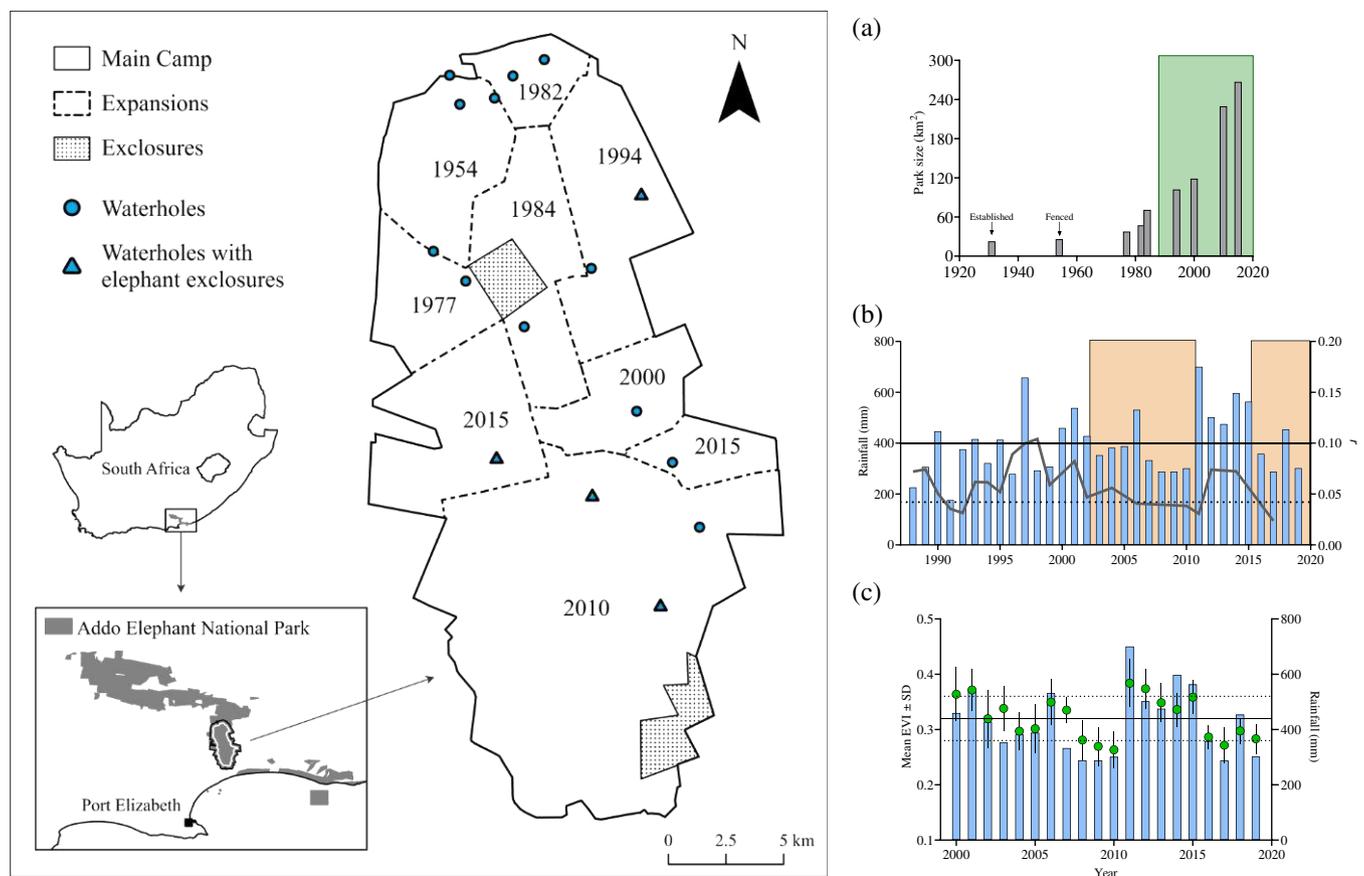

FIGURE 1 The study area (Main Camp [MC]) is part of the Addo Elephant National Park (AENP) in South Africa. The cartogram shows the expansion of MC and the location of 16 waterholes that provide water for wildlife. (a) the study area (MC) expanded from 38 km² in 1977 to 267 km² in 2015, and the green box shows our study period (1988–2019). (b) the mean yearly (Oct. in year x to Sept. in year x + 1) rainfall (solid line) at MC from 1988–2019 was 399 mm ± 125 (SD). The orange boxes reflect the two periods of below-average yearly rainfall for 2003–2010 (358 mm ± 80) and 2016–2019 (350 mm ± 75). The stippled line represents the mean growth of the elephant population for the study period (1988–2019: $r = 0.042 \pm 0.012$) and the gray line represents the moving yearly growth. During the two dry periods the population growth was below that for the study period (for 2003–2010: $r = 0.039 \pm 0.031$ and for 2016–2019: $r = -0.004$). (c) the mean (± SD) yearly enhanced vegetation index (EVI, green circles) across MC for 2000–2019 tracked the mean yearly rainfall. The solid line represents the mean (0.32 ± 0.04) EVI (see Figure S1 for the EVI composite layers for 2000–2019). This map was created using ArcGIS® software by Esri®.

dispersal (Whitehouse & Hall-Martin, 2000; Gough & Kerley, 2006) and habitat deterioration (see Landman et al., 2012; Smit et al., 2016), prompted management to reduce the population by a quarter (~26%) and to increase the size of the park (see Figure 1). Due to density independence (see Gough & Kerley, 2006), we expected that the interventions should have reduced population size, but not population growth, or changed its age structure, or demographic rates unless environmental conditions changed during the study and amplified the effect of the intervention. Here we evaluate this expectation.

The analytical framework developed by Wauchope et al. (2021) that compares trends in time series of numbers before and after interventions with that of a null model is a concrete approach to obtain evidence for the effectiveness of management interventions. We compared population growth and modelled trends based on counts for 16 years before and 16 years during three removal events. Furthermore, we constructed life tables from our demographic surveys of the population before and after the interventions, to parameterize population projection matrices and assessed transient dynamics within a framework of demographic resilience (Capdevila et al., 2020). We then performed a life table response (simulated) experiment to illustrate which vital rate(s) contributed most to a change in modelled transient population growth. Our study shows that transient dynamics followed after the removal of elephants. Irregular rainfall, with droughts that affected resource quantity and quality, reduced population growth, possibly through a reduced survival of juvenile elephants, destabilized the age structure, and induced transient dynamics that may last for 28 years. The duration of transient dynamics complicates assessing the effectiveness of interventions and renders asymptotic projections of limited value to plan or evaluate the consequences of management interventions. Managers should adopt their conservation goals and management activities accordingly and consider demographic resilience that may negate short-term interventions.

2 | STUDY AREA

AENP is situated in the subtropical Albany Thicket Biome (Vlok et al., 2003) in South Africa. The vegetation (low-growing shrubs dominate the woody species) is degraded around waterholes (Landman et al., 2012; Smit et al., 2016), secondary grasslands (Landman et al., 2014), and remnants of cultivated fields (SANParks, 2015). The mean yearly (Oct. in year x to Sept. in year $x + 1$) rainfall at MC from 1988–2019 was $399 \, mm \pm 125$ (SD) (Figure 1b). Enhanced vegetation index (EVI) as a proxy of resource quality (Loarie et al., 2009; Tsalyuk et al., 2019) responded to rainfall (Figure S1), with years of below-average rainfall having below-average EVI values (Figure 1c).

Following extensive hunting in the region (Hoffman, 1993), the MC section of AENP was established in 1931 and fenced to protect 11 elephants that consisted of two adult bulls, one subadult bull, and the remainder of adult females and their young (Whitehouse & Kerley, 2002). The two adult bulls were shot, the last remaining subadult bull was killed by a train, and subsequently 9 years went by without recruitment after the first fences were installed. Breeding only commenced again in 1948 (Whitehouse & Kerley, 2002). The construction of an "elephant proof" fence (park size was $23 \, km^2$) in 1954 prevented elephants from dispersing. The area of MC has since been extended from $38 \, km^2$ in 1977 to $267 \, km^2$ in 2015 (SANParks, unpublished data) (Figure 1a).

3 | ELEPHANT MANAGEMENT

Management removed 61 (of unknown sex and age in breeding herds) out of a total of 374 elephants from MC in 2003 (16.3% of the population), 11 adult bulls (a 3.6% reduction) in 2005, and 28 elephants (two bulls, nine adult cows, and 17 juveniles: a 5.9% reduction) in 2018 (SANParks, unpublished data). Management introduced two bulls from Kruger National Park in 2002 and another bull from Tembe Elephant Park in 2019. He died a year later. Our study focussed on the recent history of the population, thus minimizing potential founder effects on our assessment. We, therefore, cover 32 years from 1988 (the population size was then 140 elephants, see Whitehouse & Kerley [2002]) to 2019, starting some 34 years after the fencing of MC in 1954.

4 | METHODS

4.1 | Population counts

Helicopter-based surveys conducted by SANParks between February and June from 1988 to 2019, with flight paths at 400 m intervals, covered the entire MC and yielded a single total population count (with no error estimates) for nearly every year (the five missing survey years included 2001, 2008–2010, and 2014). At a ground speed of $80–120 \, km.h^{-1}$ (pending weather conditions and vegetation density) and with the pilot accompanied by

three observers, it took ∼3 hrs to cover all of MC (Whitehouse et al., 2001; SANParks, unpublished data). The counts were completed before the removal of elephants (SANParks, unpublished data).

4.2 | Rapid Elephant Population Assessment

Our Rapid Elephant Population Assessment (REPA) in January 2020 was based on a series of digital images of elephants ($n = 261$, ∼50% of the population) in breeding herds along a flight path that covered the entire MC. Our modelling routines converted the back-length measurements to an estimated sex-specific age using the Von Bertalanffy curvilinear growth function and Monte Carlo simulations (Shrader et al., 2006; Ferreira & van Aarde, 2008; Trimble et al., 2011). Our REPA in September 2003 was based on shoulder heights of elephants ($n = 163$, ∼44% of the population) measured from ground level. Trimble et al. (2011) validated the conversion of shoulder heights to back lengths and the estimated age of each elephant. We used the estimated ages of the elephants to construct an age structure of the female segment of the population. From the ages and cow-calf associations we calculated the mean age at first calving, the calving interval (the mean difference in the ages of calves associated with cows), and the number of breeding females (f_b) as described by Ferreira and van Aarde (2008) and used by others (e.g., Trimble et al., 2009; Shrader et al., 2010; Young & van Aarde, 2010).

5 | ANALYSES

5.1 | Population growth

We calculated population growth from 1988 to 2019, 1988 to 2003, and 2004 to 2019 from a time series of the total counts using the density-independent diffusion approximation (DA) method (Dennis et al., 1991). This method accounts for missing survey years, returns an estimate of variation of the growth rate (and not the variation of the ln abundance values, as is a common practice), and minimizes autocorrelation (Mills, 2007). Here, population growth $\widehat{r}$ was the slope of an ordinary least-squares linear regression of the ln-transformed population change $y_{(i)}$ over a time interval $x_{(i)}$ as:

$$x_{(i)} = \sqrt{t_{(i+1)} - t_{(i)}},\qquad(1)$$

and:

$$y_{(i)} = \frac{\left[ln\left(N_{(i+1)}/N_{(i)}\right)\right]}{x_{(i)}},\qquad(2)$$

where $N_{(i)}$ was the population size in year $t_{(i)}$, $N_{(i+1)}$ was the population size in the following year $t_{(i+1)}$, $y_{(i)}$ was the population change divided by the time interval $x_{(i)}$, and forcing the regression intercept through 0 (Mills, 2007). Variance of population growth was the residual mean square of an ordinary least-squares linear regression. Two of the 27 population counts were identified as outliers (2016 and 2017) by a Bonferroni Outlier Test (Fox, 2016) and removed from all analyses (see Supplementary Material).

5.2 | Population trends

To determine the likely trend in population numbers, we fitted five candidate models to the complete time series and for that before (1988–2003), and during the interventions (2004–2019). We included the logistic and Gompertz dynamic models to represent asymptotic trends. The linear and exponential models accounted for increasing or decreasing population size without reaching an apparent asymptote, and the null model indicated no trend (i.e., fluctuations around the mean). We selected the best-fit model according to the lowest corrected Akaike Information Criteria (AICc) and assessed the relative strength of each model using Akaike weights AIC (wi) (Burnham & Anderson, 2002). We used the "minpack.lm" package in R version 4.0.5 to fit models (R Core Team, 2021; Elzhov et al., 2016).

5.3 | Evaluation of effects of intervention

We compared population growth for the periods before (1988–2003) and during (2004–2019) management interventions using the approach of Wauchope et al. (2021). We fitted a generalized linear model with a Poisson distribution to elephant numbers over time and tested for autocorrelation before proceeding with analyses (Liboschik et al., 2017). We included a binary variable (Before/During) to represent the pre-intervention (1988–2003: assigned a value of 0) and during intervention (2004–2019: assigned a value of 1) time periods. We added an interaction term between time and Before/During (time x Before/During) to estimate changes in numbers during the interventions. To allow the model to

compare immediate change between the last time step in the period before the interventions and the first-time step in the period during interventions, we centred time around 0, with zero reflecting the first year after the interventions began (i.e., in 2004; see Wauchope et al., 2021).

The numbers from 2004 to 2007 may reflect a delay in population growth after elephants were removed in 2003 and 2005. To test this, we included a third-factor level to our Before/During variable (2004–2007: assigned a value of 2) and refitted the generalized linear model with a Poisson distribution. We compared the models with and without the time-lag effect and selected the best model based on corrected AICc and Akaike weights AICc (*wi*) (Burnham & Anderson, 2002). To assess whether the interventions had a significant impact on population growth, we compared the null model (without the Before/During term) to both the models with and without the time-lag effect. We inspected standard diagnostic plots for deviations from model assumptions and assessed model fit using a chi-squared goodness-of-fit test. Models were run in R version 4.0.5 (R Core Team, 2021) using the *glm* function from the MASS package (Venables & Ripley, 2002).

5.4 | Demography

We used the age structures and estimates of reproductive variables returned by REPAs in life table analyses (e.g., Caughley, 1977) to parameterize population projection matrices (Caswell, 2001; Fujiwara & Diaz-Lopez, 2017) (see flow diagram in Supplementary Materials). Here an age structure comprised the number of female elephants $f_{(x)}$ for 16 age classes (x) from 0 to 15 years old, and a single adult age class from 16 to 60 years (Ferreira & van Aarde, 2008; see Table S5). We used a Pearson's Chi-square statistic to test if the age structures of 2003 and 2020 differed (see de Silva et al., 2017), and Pielou's evenness index (J') (see Cecchini et al., 2019) as a measure of heterogeneity in age-specific proportional abundances ($f_{(x)}$ as a proportion of 1). We used the Student's *t*-test to evaluate if age at first calving and calving interval differed in 2020 from those recorded in 2003.

We defined six life stages for the female segment of the population that included infants (0–3 years), juveniles (4–7 years), subadults (8–11 years), primiparous females (12–15 years), adult females (16–53 years), and post-reproductive females (54–60 years) (Figure S4). For each life table (Table S5), we included the age at first calving $x_{(afc)}$ and assumed age at last calving $x_{(alc)}$ of 53 years (Ferreira & van Aarde, 2008). We estimated fecundity as:

$$m_{(x)} = \left(\frac{0.5}{CI}\right), \tag{3}$$

where CI was the calving interval and assuming an equal sex ratio at birth (see Visscher et al., 2004). We derived the number of new-born calves as:

$$f_{(0)} = m_{(x)} * f_{(b)}, \tag{4}$$

where $f_{(b)}$ was the number of breeding females. Stage-specific survival probability was:

$$l_{(x)} = e^{-\alpha_1 x}, \tag{5}$$

where α_1 was the stage-specific exponential decay rate of $f_{(x)}$ (Fujiwara & Diaz-Lopez, 2017), and we assumed a constant mortality rate for adult females (16 to 60 years) (Gaillard et al., 2000; Hilde et al., 2020). Survival probability $l_{(x)}$ was then multiplied with e^r where r was the era-specific (1988–2003 and 2004–2019) population growth returned from counts (Fujiwara & Diaz-Lopez, 2017).

5.5 | Parameterizing the population projection matrices

The number of individuals $f_{(x)}$ of each life stage $f_{(stage)}$ formed the vector $N_{(t)}$ in the matrices, where (t) represented the year of a REPA. Elephants breed throughout the year (Trimble et al., 2009), and we used a birth-flow model to construct deterministic stage-structured (Lefkovitch) population projection matrices (e.g., Caswell, 2001). Age-specific survival rate from age (x) to $(x + 1)$ was:

$$s_{(x)} = l_{(x)} + l_{(x+1)} / l_{(x-1)} + l_{(x)}. \tag{6}$$

We calculated stage-specific survival rates $S_{(i)}$ using the weighted geometric mean of age-specific survival rates and the matching proportion transitioning method as the conditional stage-transition rate $P_{(j,i)}$ (Fujiwara & Diaz-Lopez, 2017). The probability of remaining within a stage $S_{(i,i)}$ was:

$$S_{(i)} * \left(1 - P_{(j,i)}\right), \tag{7}$$

and the probability of transitioning to the next stage $P_{(j,i)}$ was:

$$S_{(i)} * P_{(j,i)}. \tag{8}$$

(Fujiwara & Diaz-Lopez, 2017). Age-specific fertility rates $f_{(x)}$ for primiparous and adult females was:

$$f_{(x)} = l_{(0.5)} \left(m_{(x)} + s_{(x)} m_{(x+1)} / 2\right), \tag{9}$$

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where:

$$l_{(0.5)} = l_{(0)} + l_{(1)}/2. \tag{10}$$

For the age class before maturity ($x_{[afc-1]}$), we multiplied fecundity with 0.34 (one standard deviation of the mean age at first calving). We calculated stage-specific fertility $F_{(i)}$ using the weighted arithmetic mean of age-specific fertility (Fujiwara & Diaz-Lopez, 2017). Tables S6a, S6b gives our stage-structured population projection matrices, and MATLAB R2020b (MATLAB 2020) returned the dominant eigenvalue as the asymptotic population growth $\lambda_{(a)}$.

5.6 | Sensitivity and elasticity

We calculated the sensitivity of asymptotic population growth $\lambda_{(a)}$ to stage-specific survival $S_{(i)}$ and stage-specific fertility $F_{(i)}$ by reducing each vital rate by 1% while keeping the other rates constant (Morris & Doak, 2002). Sensitivity of $\lambda_{(a)}$ to survival was:

$$\Delta\lambda_{(a)}/\Delta S_{(i)}, \tag{11}$$

and to fertility was:

$$\Delta\lambda_{(a)}/\Delta F_{(i)} \tag{12}$$

(Caswell, 2001). To compare the relative influence of stage-specific vital rates for $\lambda_{(a)}$ we converted sensitivity to elasticity by:

$$\Delta\lambda_{(a)}/\Delta lnS_{(i)}, \tag{13}$$

and:

$$\Delta\lambda_{(a)}/\Delta lnF_{(i)} \tag{14}$$

(Caswell, 2001).

5.7 | Population projections

We multiplied the population projection matrix with the vector $N_{(t)}$ to obtain $N_{(t+1)}$ and estimated transient population growth $\lambda_{(t)}$ as:

$$N_{(t+1)}/N_{(t)}. \tag{15}$$

We projected $\lambda_{(t)}$ forward in time by one time-step (i.e., 1 year) until the contribution of the dominant eigenvalue to $\lambda_{(a)}$ becomes 99 times greater than that of the subdominant eigenvalue (Capdevila et al., 2020). This projection of $\lambda_{(t)}$ was the time for a population to converge to a modelled stable stage structure (i.e., the transient period using a damping ratio, Capdevila et al., [2020]). For each projected time-step, we extracted $\lambda_{(t)}$ and stage-specific abundance $f_{(stage,t)}$ and used Keyfitz's Δ (Caswell, 2001) to compare the observed $f_{(stage)}$ in 2003 and 2020 with their respective modelled stable stage structures.

We constructed transient envelopes as a visual presentation of demographic resilience following Stott et al. (2011) and Capdevila et al. (2020) and calculated reactivity and first-step attenuation, maximum amplification and attenuation, inertia amplification and long-term attenuation, and the reactivity and inertia envelope metrics. A transient envelope represents a hypothetical scenario where all the individuals in the female cohort consisted of adult females (to calculate amplification; upper bound) or infants (attenuation; lower bound) following a disturbance. A larger envelope indicates that the population is less resilient to changes in its age structure (Capdevila et al., 2020). We evaluated if the yearly population size ($\log_{10}$) predicted by $\lambda_{(a)}$ or $\lambda_{(t)}$ matched those returned by the yearly population counts.

5.8 | Life table response experiment

We followed Haridas et al. (2009) and Koons et al. (2016) to estimate the contribution of stage-specific vital rates for transient population growth $\lambda_{(t)}$. The contribution of each stage-specific vital rate comprises the direct effects (elasticity of yearly population growth due to changes in vital rates [$e_{R,t}$]), and the indirect effects (elasticity of yearly population growth due to changes in population structure [$e_{U,t}$]). For the two surveys, we calculated yearly transient population growth $\lambda_{(t)}$ for 17 years (i.e., for 2003: 2003–2020 and for 2020: 2020–2037) and calculated the geometric mean transient population growth separately for the two time periods as:

$$log\lambda_g = \frac{1}{T}\sum_{0}^{17-1} log\lambda_t, \tag{16}$$

and the difference between the two time periods as:

$$\Delta log\lambda_g = log\lambda_{2003} - log\lambda_{2020}. \tag{17}$$

We constructed perturbation matrices for the 2003 survey by reducing each stage-specific vital rate by 1%. Using these perturbation matrices, we projected each yearly

unperturbed vector forward by one time-step and calculated yearly population growth $\lambda_{(R)}$. The difference between the transient population growth $\lambda_{(t)}$ and the recalculated yearly population growth $\lambda_{(R)}$ served to calculate $e_{R,t}$.

We used the 2003 vector $N_{(t)}$ and projected it forward for 17 years, this time using the perturbation matrices to calculate the indirect effects. The outcome here was a series of perturbed vectors specific to a change in each vital rate. Each perturbed vector was projected forward by one time-step with the original (unperturbed) 2003 matrix, and we calculated yearly population growth $\lambda_{(U)}$. The difference between transient population growth $\lambda_{(t)}$ and the recalculated yearly population growth $\lambda_{(U)}$ served to calculate $e_{U,t}$.

We summed the elasticity values for each stage-specific vital rate E_t as:

$$E_t = e_{R,t} + e_{U,t}, \tag{18}$$

and calculated the mean elasticity E^S as:

$$E^S = \left(\frac{1}{N}\right) \sum_{t=1}^{N} E_t. \tag{19}$$

The change in a stage-specific vital rate between 2003 and 2020 was multiplied with its stage-specific mean elasticity E^S to estimate its contribution to the geometric mean transient population growth change.

6 | RESULTS

6.1 | Population growth

The elephant population in MC increased from 140 in 1988 to 519 in 2019 at 4.2% per year ($\widehat{r} = 0.042 \pm 0.012$, 95% CL: 0.017–0.068, $F_{1,23} = 11.6$, $p = 0.003$) (Figure 2a). Over the 16 years (1988–2003) before the removal of elephants, the population grew at 6.6% per year ($\widehat{r} = 0.066 \pm 0.009$, 95% CL: 0.046–0.086, $F_{1,13} = 49.9$, $p < 0.0001$), and for the 16 years during the removals (2004–2019) at 3.5% per year ($\widehat{r} = 0.035 \pm 0.015$, CL: 0.001–0.070, $F_{1,8} = 5.42$, $p = 0.048$) (Figure 2a). During the two dry periods, the population growth was below that for the study period (for 2003–2010: $\widehat{r} = 0.039 \pm 0.031$ and for 2016–2019: $\widehat{r} = -0.004$: Figure 1b). Yearly EVI tracked rainfall directly (Figure 1c; Figure S1).

6.2 | Population trends

A linear model best described the trend in elephant numbers across the full time series (1988–2019: AICc = 174.1, AICc (wi) = 0.75, $R^2 = 0.93$), whereas the exponential model was selected for both before (1988–2003: AICc = 71.7, AICc (wi) = 1.00, $R^2 = 0.99$) and during (2004–2019: AICc = 69.7, AICc (wi) = 0.77, $R^2 = 0.94$) the interventions (Table 1; Table S2; Figure S2). These exponential rates imply a lack of density dependence during our study period.
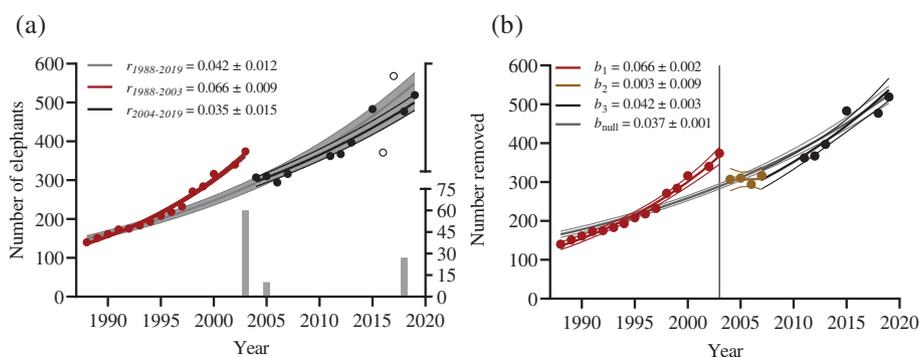

FIGURE 2 (a) Elephant numbers in Main Camp increased at a rate of 0.042 ± 0.012 from 1988 to 2019 (gray curve). Population growth ($\pm$ SE) before (red circles and curve) the removal of elephants was higher ($r = 0.066 \pm 0.009$, 95% CL: 0.046–0.086, $F_{1,13} = 49.9$, $p < 0.0001$) than thereafter (black circles and curve; $r = 0.035 \pm 0.015$, CL: 0.001–0.070, $F_{1,8} = 5.42$, $p = 0.048$). Population growth (r) and standard error (SE) in 2(a) was calculated using the density-independent diffusion approximated method (Mills 2007). Counts for 2016 and 2017 were identified as outliers (white circles) and removed before analyses (Table S1). Sixty-one elephants of unknown age were removed from MC in 2003, 11 bulls in 2005, and 28 elephants (two adult bulls, nine adult cows and 17 juveniles) in 2018. (b) Population growth ($\pm$ SE) before (red curve) the intervention was higher ($b_1 = 0.066 \pm 0.002$) than for both the time-lag period (brown curve, $b_2 = 0.003 \pm 0.009$) and thereafter (black curve, $b_3 = 0.042 \pm 0.003$), which also was higher than for the time-lag period. The population growth for the null model (i.e., without intervention; gray curve) was $b_{null} = 0.037 \pm 0.001$. Population growth ($b$) and standard error (SE) in 2(b) was calculated using a time lag Poisson generalized linear model following Wauchope et al. (2021). The vertical line separates the pre-intervention era (1988–2003) from the intervention era (2004–2019).

TABLE 1 Model selection returned the linear model to describe the trend in elephant numbers for the full study time series and the exponential model for before and during interventions

Time series	Best-fit model	Parameters	AICc	AICc (w_i)	R^2
Full (1988–2019)	Linear	3	174.1	0.75	0.93
Before (1988–2003)	Exponential	3	71.7	1.00	0.98
During (2004–2019)	Exponential	3	69.7	0.77	0.93

Note: AICc selected the best fit model. The model parameters included the intercept, slope, and the intercept residual variance. The best model was selected by the Akaike information criteria adjusted for small sample size AICc and the AICc weights. Refer to Table S2 for the complete set of model selection statistics.

TABLE 2 Demographic variables for the elephant population in Main Camp of Addo Elephant National Park in 2003 (before) and 2020 (after interventions) as returned by REPA and life table analyses

Variable	2003	2020
Age at first calving (mean $\pm$ SE years)[e]	13.8 ± 0.85[a]	14.0 ± 0.40[c]
Calving interval (mean $\pm$ SE years)[e]	3.96 ± 0.34[b]	4.05 ± 0.22[d]
Age-specific fecundity $m_{(x)}$	0.126	0.123
Primiparous fertility (12–15 years)	0.086	0.085
Adult fertility (16–53 years)	0.123	0.122
Infant survival (0–3 years)	0.995	0.964
Juvenile survival (4–7 years)	0.964	0.766
Subadult survival (8–11 years)	0.785	0.844
Primiparous survival (12–15 years)	0.995	0.995
Adult survival (16–53 years)	0.995	0.995
Post-reproductive survival (54–60 years)	0.853	0.853

Abbreviation: SE, standard error.

[a]$n = 18$.
[b]$n = 20$.
[c]$n = 81$.
[d]$n = 59$.
[e]Difference between 2003 and 2020 was not significant based on Student's t-test ($\alpha = 0.05$).

6.3 | Impact of management interventions

Model comparison identified the time-lag model (AICc $= -3.78$, AICc (wi) $= 0.52$, $R^2 = 0.99$) as best for evaluating the impact of removing the 61 elephants from the population in 2003 (Table S3). The relatively large difference in AICc between the null and time lag models (ΔAICc $= 38.9$) confirmed model robustness and suggested that the intervention and/or associated environmental conditions reduced population growth.

TABLE 3 Sensitivity and elasticity of asymptotic population growth to stage-specific survival and fertility for 2003 (before) and 2020 (after) the interventions

Stage-specific vital rate	Sensitivity		Elasticity	
	2003	2020	2003	2020
Infant survival	0.12	0.09	0.12	0.09
Juvenile survival	0.11	0.05	0.11	0.04
Subadult survival	0.06	0.06	0.05	0.05
Primiparous survival	0.12	0.10	0.12	0.10
Adult survival	0.56	0.66	0.55	0.66
Primiparous fertility	0.04	0.02	0.003	0.002
Adult fertility	0.23	0.16	0.03	0.02

Note: Sensitivity and elasticity of asymptotic population growth $\lambda_{(a)}$ to adult survival were the highest (dark gray) and were the lowest to primiparous fertility (light gray).

The model illustrated an immediate change in elephant numbers and reduced population growth ($p < 0.0001$; Table S4) after the removal of elephants in 2003 ($p < 0.0001$). The model further confirmed a delay in population growth from 2004 to 2007 ($p < 0.0001$; Table S4), possibly in direct response to the removal of 11 elephants during 2005. Based on model coefficients, population growth decreased from 0.066 ± 0.002 (95% CL: 0.063–0.070) for the period before the management intervention to 0.003 ± 0.009 (95% CL: -0.017–0.025) during 2004–2007, and then increased to 0.042 ± 0.004 (95% CL: 0.033–0.055) after the time lag period (Figure 2b). The Chi-squared goodness-of-fit test confirmed model fit ($\chi^2 = 11.8$, $p = 0.89$).

6.4 | Demography

The age structure before (2003) and after (2020) the removal of elephants was similar (Pearson's Chi-square, $\chi^2_{16} = 7.46$, $p = 0.96$). Heterogeneity of the stage-specific proportional abundances was lower in 2003 (Pielou's $J' = 0.892$) than in 2020 (Pielou's $J' = 0.851$). Stage-specific survival of infants (0–3 years) and juveniles (4–7 years) were higher in 2003 than in 2020 and the mean ($\pm$ SE years) age at first calving (2003: 13.8 ± 0.85 and
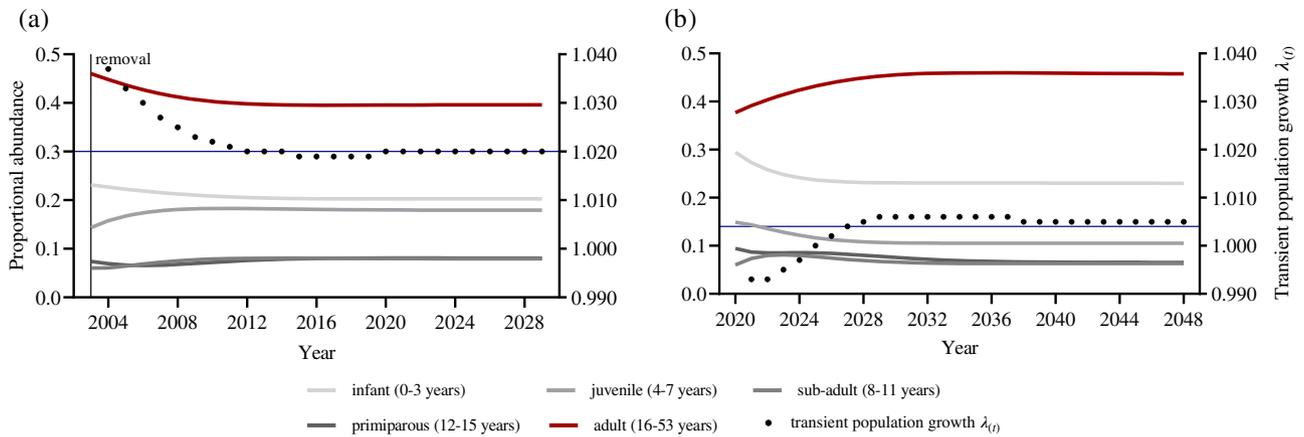
FIGURE 3 Projected stage-specific proportional abundance and transient population growth ($\lambda_{(t)}$) (dotted curve) as a function of year based on the stage structures and vital rates recorded for the population in (a) 2003 and (b) 2020. Projected transient and asymptotic (blue line) population growth in 2020 was lower than in 2003. The modelled stage-specific proportional abundances of all stages changed for the initial 8 to 12 years of projection and converged to a stable stage structure after 26 years in 2003 and 28 years in 2020.
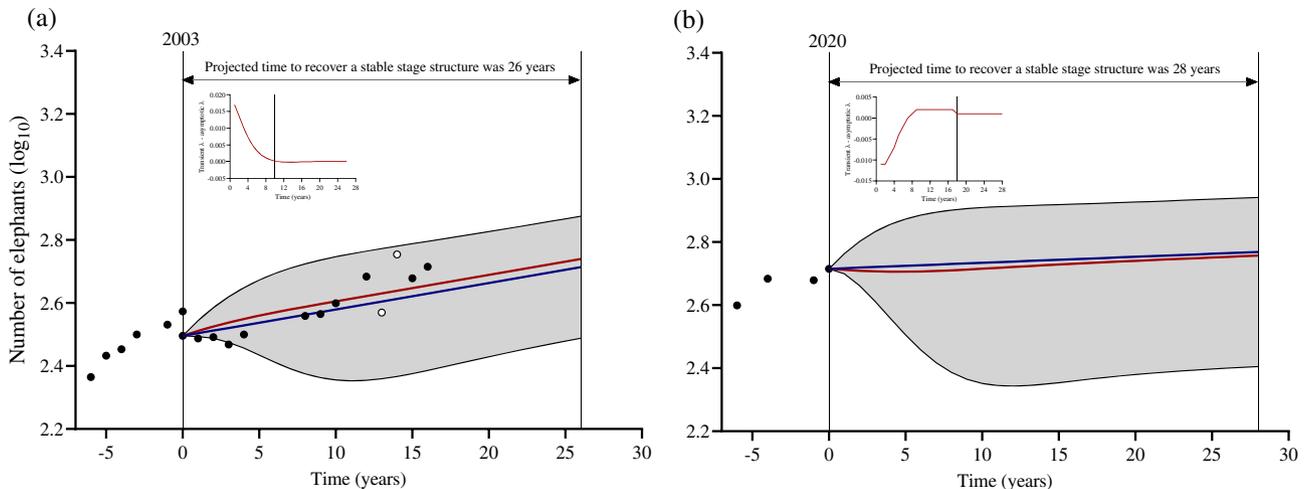

FIGURE 4 Resilience frameworks (see Capdevila et al. 2020) to illustrate the projected path to recovery (stability in stage structure and lambda) for (a) 2003 and (b) 2020. The lines show the projected elephant numbers ($\log_{10}$) based on asymptotic (blue line) and transient (red line) population growth rates. The inset graphs show the convergence as the difference between yearly transient and asymptotic growth rates over time. After 10 years for 2003 and 18 years for 2020 the difference between transient and asymptotic rates was zero. The projected time to recover a stable stage structure was 26 years in 2003 and 28 years in 2020 (transient period based on the damping ratio). The transient envelope (in gray) for 2020 was larger than for 2003 (refer to Table S7 for the transient envelope metrics). After the intervention, the yearly counts (black dots and the two identified as outliers [white circles]; see Figure 2a) fell inside the 2003 envelope and tracked the population sizes predicted by modelled asymptotic and transient growth on a logarithmic scale.

2020: 14.0 ± 0.40) and calving interval (2003: 3.96 ± 0.34 and 2020: 4.05 ± 0.22) were similar (Table 2). In 2020, 41% of the elephant population consisted of adult females, whereas in 2003, it was 49%.

6.5 | Population projections

The modelled asymptotic population growth was 1.020 in 2003 and 1.004 in 2020. Growth was most sensitive to adult survival (Table 3). For asymptotic growth, elasticity

was the highest for adult survival, and the lowest for primiparous fertility (Table 3).

The stage structure in 2003 was closer to a projected stable stage structure at the time of convergence (Keyfitz's $\Delta = 0.093$) than in 2020 (Keyfitz's $\Delta = 0.137$) (Figure S5). The modelled stage-specific proportional abundances of all stages changed for the initial 8–12 years of projection (Figure 3). Transients prevailed in 2003 and 2020 (Figures 3 & 4). The projected time to recover a stable stage structure (i.e., the transient period based on the damping ratio) before the

TABLE 4 Elasticity of the modelled transient population growth to stage-specific survival and fertility and the contribution of these vital rates to a change in the modelled geometric mean transient population growth ($\log\lambda_g$)

Stage-specific vital rate	Elasticity	Contribution
Infant survival	0.17	0.005
Juvenile survival	0.28	0.065
Subadult survival	0.04	−0.003
Primiparous survival	0.30	0.000
Adult survival	0.32	0.000
Primiparous fertility	0.004	−0.00001
Adult fertility	0.04	0.0003

Note: The contribution of juvenile survival was the highest (dark gray).

interventions was 26 years (2003) and 28 years thereafter (2020) (Figure 4).

The transient envelope for 2020 was larger (reactivity and inertia higher) than for 2003 (Figure 4; Table S7). Attenuation (first-step, maximum, and long-term attenuation) were lower in 2020 than in 2003. The modelled transient growth for the population in 2003 predicted a population that was 5.8% larger in size at the time of convergence than that predicted by asymptotic growth, and 1.7% smaller following the removal of elephants and extended droughts. After the first removal of elephants, the yearly counts tracked the population sizes predicted by modelled asymptotic and transient growth on a logarithmic scale (Figure 4a).

6.6 | Life table response experiment

Our simulation of changes in stage-specific vital rates explained 6.8% of the difference in the projected geometric mean transient population growth between the two time periods ($\log\lambda_g = 1.023$ from 2003 to 2019 and $\log\lambda_g = 1.002$ from 2020 to 2036). The modelled elasticity of transient growth to stage-specific vital rates mirrored those we calculated for asymptotic growth. Elasticity was the highest for adult survival and lowest for primiparous fertility (Table 4). However, juvenile survival made the greatest contribution to the change in the modelled mean transient population growth, and was lower in 2020 (0.964) than in 2003 (0.995) (Table 4).

7 | DISCUSSION

Our assessment showed the prevalence of transient dynamics in a small elephant population confined to

Addo Elephant National Park. Modelled transients lasted 12 years, but full recovery of stability of the age structures took at least 24 years. In addition, a time-lag model illustrated a four-year delay in population growth. However, the population started to increase again thereafter, rendering the management intervention ineffective in the long-term. Elephant population management plans therefore should consider the duration of transients and how environmental disturbances, such as droughts, might amplify transient dynamics.

Valid assessments of the numerical and demographic responses of populations to disturbances depend on credible approaches to the analyses and interpretation of information, preferably presented in a format that policymakers and conservation managers can apply (i.e., Hone et al., 2017, 2018). We used established survey and modelling approaches (e.g., Fujiwara & Diaz-Lopez, 2017; Wauchope et al., 2021) to extract and analyze information within a framework of demographic resilience. This approach considers transient dynamics in response to disturbances of the age structure and/or vital rates of a population (Stott et al., 2011; Capdevila et al., 2020). Our assessment should enrich evidence-based conservation plans and actions (Salafsky et al., 2019; Sutherland et al., 2019). This is essential when considering the high costs of conservation interventions, especially in these days of a shortage of funding for conservation management (Lindsey et al., 2020; Dobson et al., 2020).

Savanna elephant populations do respond to exploitation, droughts and management interventions such as culling and the provisioning of water. For instance, severe poaching reduces elephant numbers and densities (Booth & Dunham, 2016; Robson et al., 2017; Schlossberg et al., 2019), and shifts their age structure, sex ratio, and age of maturity (Owens & Owens, 2009), whereas droughts cause an increase in age-specific mortalities (Corfield, 1973; Walker et al., 1987; Dudley et al., 2001; Moss, 2001) and change elephant distribution when populations are not fenced (Robson & van Aarde, 2018; Smit et al., 2020) or where water is provided (Purdon & van Aarde, 2017). Elephants also respond to culling by emigrating from the regions where culling took place (van Aarde et al., 1999). The demographic responses of elephants to management interventions have been modelled occasionally (e.g., Woodd, 1999; Woolley et al., 2008; but see Morrison et al., 2018), but the consequences of disturbances for demographic resilience have not been assessed before.

Elephants in relatively small parks often are managed intensely (Young & van Aarde, 2011; Smit et al., 2016). At present, contraception and translocations are used to keep elephants from becoming overpopulated in some places, while supplementation of resources, demographic

enrichment and control of illegal hunting aim to maintain or increase population sizes elsewhere (summarized in van Aarde et al., 2008; Hayward & Slotow, 2016). Measures of the effectiveness of interventions (usually only based on population growth from counts) unwittingly assume asymptotic dynamics that imply stability in population growth, structure and vital rates (e.g., Wood, 1999; Knight et al., 2001; Woolley et al., 2008; Booth & Dunham, 2016; Kuiper et al., 2018). Stability seldom, if ever, occurs in nature (Hastings et al., 2018). Therefore, management interventions that alter population size, structure or demography may be better assessed in a framework of demographic resilience that rests on transient dynamics induced by disturbances (see Capdevila et al., 2020).

Support for transient dynamics to describe the response of species to disturbances increased over the last two decades (e.g., Heppell et al., 2000; Ezard et al., 2010; Stott et al., 2011; Gamelon et al., 2014; Koons et al., 2016; Jackson et al., 2020). Transient dynamics are particularly relevant for savanna elephants. They are large, live long (Lee et al., 2016), have extended and overlapping generations (Wittemyer et al., 2013), have high adult survival rates (e.g., van Aarde et al., 2008; Lee et al., 2011), and low fecundity (late maturity and few offspring) (Lee et al., 2016). These life-history characteristics should buffer populations against disturbances in the highly variable savannas where elephants live. However, intense anthropogenic disturbances, such as poaching, culling, and large-scale translocations, may destabilize their age structures (Jones et al., 2018; Parker et al., 2021). These disturbances will generate transient dynamics that last considerably longer than the period typically considered by most management interventions.

Our case study examines the possible causes of reduced population growth following the removal of elephants from MC in AENP, as the removals should not have changed their age structure. Elephants here could not disperse. Population growth could only result from the difference between birth and death rates or the removals of elephants by management. These removals reduced population size and density, but co-occurring periods of drought during these removals may have reduced the per capita population growth. Droughts diminish the quality and quantity of food, as implied by the rainfall related reduction in EVI (Walker et al., 1987; Loarie et al., 2009; Young & van Aarde, 2010; Tsalyuk et al., 2019). The relatively small size of MC also does not allow elephants to move to areas less affected by drought, as is the case in larger protected areas (i.e., in Kruger National Park, Abraham et al., 2019). Conception rates are typically lower in dry years (Gough & Kerley, 2006; Rasmussen et al., 2006; Trimble et al., 2009), and an

extended drought might also have reduced survival among the younger elephants (Foley et al., 2001, 2008; Young & van Aarde, 2010; Lee et al., 2011; Boult et al., 2018). The harsh conditions during the droughts reduced age-specific survival which also coincided with a lowered number of adult females relative to the non-breeding cohort in 2020, and collectively destabilized the age structure.

Our modelled elasticity confirmed the high sensitivity of asymptotic (long-term) and transient (short-term) population growth to adult survival for a long-lived species and less so for the survival of their young (Heppell et al., 2000; Gamelon et al., 2015; Parker et al., 2021). However, juvenile survival contributed most to a change in annual population growth, in line with the demographic buffering hypothesis (Gaillard et al., 1998, 2000; Hilde et al., 2020). In elephants, juvenile survival is labile while that of adults is robust. In the long term this should buffer populations from disturbances, but as showed by our assessment, not in the short term. The relatively high contribution of juvenile survival to the modelled transient population growth showed that juvenile survival drives transient dynamics.

Lower than average rainfall that lowered food quality and availability may have reduced juvenile survival (also see Young & van Aarde, 2010) and destabilized the population's age structure. The removal of elephants may have rendered this population more sensitive (i.e., a larger transient envelope for 2020) to drought. To summarize, the combined effects of removing elephants from the population during periods of prolonged droughts compromised demographic resilience (i.e., the ability to resist and recover from a disturbance).

The modelled regaining of a stable age structure and recovery from the disruptions lasted about 28 years, irrespective of the disturbances induced by removing elephants. Therefore, the response of the population to disturbances in MC was in line with species with long generation intervals and extended transient dynamics (Ezard et al., 2010). For instance, the continuous attenuated state illustrated resistance to disturbances as expected for a long-lived species (e.g., North Atlantic right whales [Fujiwara & Caswell, 2001]; conifer trees [Kwit et al., 2004]; and cranes [Gerber & Kendall, 2016]). Considering the generation length (~24 years) of elephants, the time needed for demographic recovery in response to disturbances exceeded most conservation directed management plans.

Trends deduced from time series of counts (Garaï et al., 2004; Slotow et al., 2005; Chase et al., 2016) that informed the management of elephant populations assume stability in age structures and vital rates. This is not the case in our approach. Measures of the

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effectiveness of interventions to stifle population growth should preferably be based on transient dynamics along with that of asymptotic dynamics (e.g., Gamelon et al., 2014; Koons et al., 2016; Capdevila et al., 2020).

AUTHOR CONTRIBUTIONS

Rudi van Aarde conceived the idea. Rudi van Aarde and Robert Guldemond jointly designed the study and with Celesté Maré collected the data. Cornelius Louw, Celesté Maré and Camilla Nørgaard analyzed the data. Rudi van Aarde, Robert Guldemond and Celesté Maré designed the tables and figures and wrote the first draft of the manuscript. All authors reviewed, edited and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All the data pertaining to this paper can be found in the on-line version of the Supporting Information.

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