

# Low birth rates and reproductive skew limit the viability of Europe's captive eastern black rhinoceros, *Diceros bicornis michaeli*

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Received: 9 June 2014 / Revised: 18 June 2015 / Accepted: 24 July 2015  
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**Abstract** Ex situ populations play a critical role for the conservation of endangered species, especially where in situ populations face imminent threats. For such populations to act as vital reserves, they must be viable and sustainable. Eastern black rhinoceros (*Diceros bicornis michaeli*) epitomise the delicate nature of conservation, as a steady increase in the in situ population over the last two decades is threatened to reverse due to intense poaching pressures on rhinoceros across sub-Saharan Africa. This study utilized population viability analysis to evaluate the demographic and genetic viability of the European captive population of eastern black rhinoceros, and compared demographic parameters to in situ reference populations. Although self-sustaining, the ex situ population performs poorly relative to in situ counterparts, growing at a rate of only 1–2 % per annum compared to 6–8 % for managed wild populations. Captive females start reproducing later, have longer inter-calving intervals, and a lower proportion breed each year. Furthermore, over 40 % of reproductive-age animals have yet to reproduce, with additional implications for the maintenance of genetic diversity. Pedigree analysis highlights the unequal contribution of wild-caught founders to the current population; 69 % of which have no living descendants, and more than a third of the current population are related to five founders. This results in a current genome equivalent of just 13.39 equally reproducing founders. Although

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Communicated by Simon Ingram.

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reproductive skew is not unusual in wild populations, it severely undermines efforts to maintain genetic and phenotypic diversity in captive breeding programmes. We suggest that understanding and alleviating the causes of reproductive skew must be an important consideration for small population management to maintain the genetic and demographic viability of ex situ populations.

**Keywords** Ex situ · Genetic viability · Pedigree analysis · PVA · Reproductive skew · Sustainability

## Introduction

Currently one-fifth of the world's vertebrate species are classified as threatened with extinction, and current conservation efforts remain insufficient to overcome drivers of biodiversity loss including overexploitation, habitat loss and degradation, and the introduction of invasive species (Hoffmann et al. 2010). Ex situ populations are thus playing an increasingly important role in global conservation strategies (IUCN 2002); acting as vital reserves to safeguard endangered species against extinction, as resources to expand our knowledge of species in need of conservation, and raising awareness and support for global conservation issues. To fulfil these goals, captive populations should be self-sustaining without supplementation from the wild (Lees and Wilcken 2009, 2011), and populations should be managed scientifically and cooperatively to ensure their long-term viability (Leus et al. 2011b). A population is generally judged to be sustainable in the long-term if reproduction at least equals mortality, it is demographically stable, and 90 % of genetic diversity is maintained (Foose et al. 1995). This level of genetic diversity is considered to be the minimum required for a species to retain the natural characteristics representative of their wild counterparts (McPhee and Carlstead 2010), giving them the potential to adapt to future changes in the environment without becoming adapted to captivity (Williams and Hoffman 2009).

To achieve these important goals it is often necessary to manage ex situ populations regionally or globally, taking a metapopulation approach (Leus et al. 2011b). Even so, captive populations often suffer from low founder-number and small population size, and many cooperative breeding programmes fail to reach some or all of these targets (Leus et al. 2011a; Long et al. 2011). An important aspect of captive management is therefore not only to ensure the growth of captive populations, but also to incorporate genetic management to ensure that all founders are well represented within the population to maintain the adaptive potential of the species in the future.

Population viability analysis (PVA) is an important tool to ensure populations are genetically and demographically sustainable, and is useful for both in situ (Armbruster and Lande 1993; Bakker et al. 2009; Daleszczyk and Bunevich 2009) and ex situ populations (Faust et al. 2006; Leimgruber et al. 2008; Zeoli et al. 2008). PVA can be used to estimate the likely future growth rate of a population (Wittmer et al. 2010), the risk of extinction over a given time period (Lee et al. 2011), or the time required to reach a target population size (Earnhardt et al. 2001). Although longer-term predictions should be used with caution (Beissinger and Westphal 1998), PVA techniques can also be used to investigate which factors may primarily be limiting growth rates, and to quantify the relative contribution of particular groups of individuals to overall population growth (Dunham et al. 2008). Application of these techniques can be beneficial to identify factors that influence the viability of a population, allowing targeted

management to achieve the goals of the population and the metapopulation as a whole. In this paper we apply these analyses to the European Endangered Species Programme (EEP) population of eastern black rhinoceros (*Diceros bicornis michaeli*).

The black rhinoceros (*Diceros bicornis*) has been listed as critically endangered on the IUCN Red List of Endangered Species since 1996, following an estimated 97.6 % decline in the wild population, reaching a low of just 2410 individuals in 1995 (Emslie 2012). Poaching for their horn was the main cause of this precipitous decline, and remains an ever increasing threat to species survival (Milliken and Shaw 2012). Despite increases in the wild population over the last two decades due to concerted conservation efforts, just 5055 individuals were estimated to remain across Africa at the end of 2012 (Emslie 2013). The western black rhinoceros (*D. b. longipes*) was declared extinct in 2011 (Emslie 2011), leaving the eastern black rhinoceros the rarest of the three remaining subspecies, with 799 individuals left in the wild (Emslie 2013). In situ populations that are well-protected against poaching are growing relatively well; for example, in Kenya between 2007 and 2011, populations of eastern black rhinoceros in well-established sanctuaries achieved annual growth rates exceeding 6 % per annum (KWS 2012). However, the recent increase in poaching pressure on all wild rhinoceros populations (Emslie 2013) means there is an increasing importance of captive breeding programmes to ensure the survival of this taxa. Ex situ populations act as a safeguard against further decline, and as a potential source of surplus individuals for reintroduction where safe and practical to do so (Fyumagwa and Nyahongo 2010). Accordingly, a target growth rate of 5 % per annum has been proposed for captive populations, similar to that set for managed wild populations (Knight et al. 2013; KWS 2012).

However, captive populations of eastern black rhinoceros have typically not been self-sustaining; with the growth rate of the North American population limited by high mortality, susceptibility to various health problems and inconsistent rates of reproduction (Foose and Wiese 2006). Although approximately 10 % of the global population of eastern black rhinoceros are held by European zoological institutions, the demographic sustainability and genetic health of this population has not been formally assessed. Here we evaluate the current performance and sustainability of the European captive population of eastern black rhinoceros. Specifically, pedigree analysis and PVA were used to investigate the genetic and demographic viability of this population and to identify factors that may be limiting population performance compared to their in situ counterparts in Kenya. As in situ rhinoceros populations are intensively managed and can achieve high natural growth rates, they provide a useful benchmark for demographic parameters to assess the relative performance of captive breeding programmes against realistic biological targets. Demographic parameters were compared within the captive population over time and with in situ populations to identify whether differences in fecundity or mortality could explain differences in growth rates. Furthermore, the impact these parameters may have upon the long-term growth and genetic health of the population were explored, as these have important implications for the management of captive breeding programmes in general.

## Methods

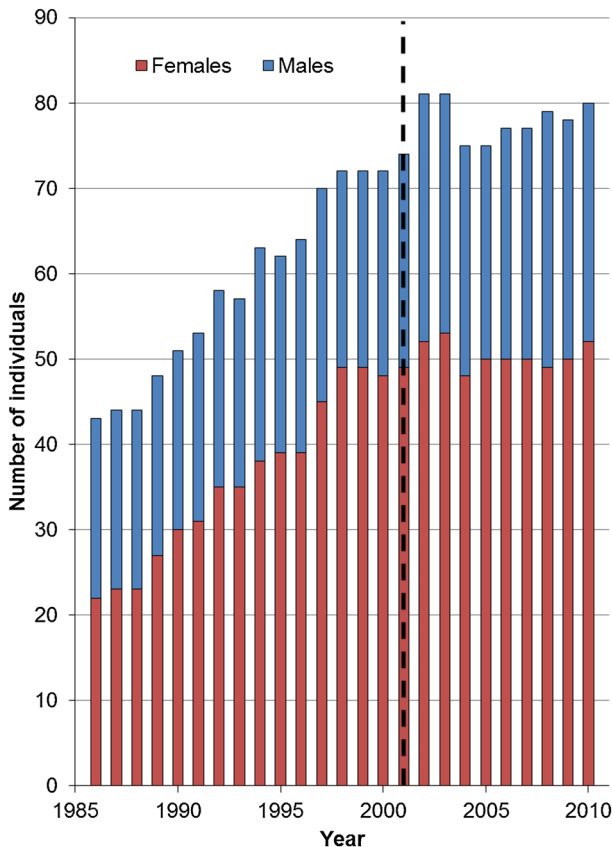
### Study population and demographic information

The EEP population of eastern black rhinoceros as of 31st December 2010 consisted of 78 individuals (27 males and 51 females), situated at 15 zoological institutions across Europe

(Biddle and Pilgrim 2011; Pilgrim 2009). A target growth rate of 5 % has been set for this population, and breeding is recommended for all non-related individuals (Biddle and Pilgrim 2013). Breeding management in this population varies according to both individual behaviour and the facilities available at each institution; compatible pairs or one male plus two females may be housed together continuously until conception occurs, or alternatively, pairs may only be introduced during oestrus (Pilgrim and Biddle 2014).

Demographic data were compiled from the European Association of Zoos and Aquariums (EAZA) studbook for the Eastern black rhinoceros (*D. b. michaeli*), contained within the Single Population Animal Record Keeping System (SPARKS; (ISIS 2004)) from 1st January 1986 to 31st December 2010. Population growth appears to have slowed in this population over the last decade compared to the preceding 15 years (Fig. 1); therefore, demographic data from two time periods; (1) 1st January 1986 to 31st December 2010, and (2) 1st January 2001 to 31st December 2010, were used in all analyses.

The age and full pedigree of all individuals in the population was determined from the studbook, and data on all births and deaths in the EEP population during the two time-periods used to calculate vital rates (Table 1) for use in population modelling, and



**Fig. 1** European captive population of eastern black rhinoceros (*Diceros bicornis michaeli*), from 1986 to 2010. Column height represents the total population size, composed of males and females. Dashed lines reflect the two time periods for data collection; (1) 1st January 1986 to 31st December 2010 and (2) 1st January 2001 to 31st December 2010

**Table 1** Vital rates (mean, variance and total number of females used in each calculation) calculated from the EAZA studbook for female eastern black rhinoceros (*Diceros bicornis michaeli*), based on two time periods for data collection (1) 1st January 1986 to 31st December 2010 and (2) 1st January 2001 to 31st December 2010. Vital rates include survival ( $s_{1-6}$ ), transition ( $g_{1-5}$ ) and fecundity ( $f_{3-5}$ )

Age class	Vital rate	1986–2010				2001–2010			
		Mean	Variance	Total females <sup>a</sup>	VSS	Mean	Variance	Total females <sup>a</sup>	VSS
0–1	$s_1$	0.8718	0.0447	63.1	0.0194	0.9054	0.0261	22.6	0.0122
1–5	$s_2$	0.9921	0.0009	202.4	0.0060	1.0000	0.0000	90.5	0.0000
5–9	$s_3$	0.9832	0.0053	172.3	0.0147	0.9941	0.0004	86.4	0.0038
9–17	$s_4$	0.9879	0.0007	249.0	0.0079	0.9769	0.0011	157.8	0.0130
17–33	$s_5$	0.9748	0.0019	292.3	0.0102	0.9775	0.0018	118.4	0.0085
33+	$s_6$	0.9465	0.0249	50.2	0.0000	0.9704	0.0024	39.6	0.0000
0–1	$g_1$	1.0000	0.0000	57.0	0.0000	1.0000	0.0000	21.0	0.0000
1–5	$g_2$	0.2486	0.0197	202.0	0.0032	0.2815	0.0084	88.0	0.0001
5–9	$g_3$	0.2337	0.0231	175.0	−0.0012	0.2311	0.0098	88.0	−0.0017
9–17	$g_4$	0.1142	0.0119	245.0	−0.0123	0.0800	0.0056	155.0	−0.0088
17–33	$g_5$	0.0455	0.0047	270.0	−0.0156	0.0815	0.0081	96.0	−0.0182
5–9	$f_3$	0.0664	0.0076	170.2	0.0123	0.0322	0.0009	85.7	0.0049
9–17	$f_4$	0.1029	0.0141	244.5	0.0264	0.0518	0.0026	153.9	0.0186
17–33	$f_5$	0.0768	0.0048	284.0	0.0190	0.0772	0.0048	114.9	0.0192

Individuals in age class 33 + cannot transition to a higher age class, and based on historical studbook data, only individuals age 5–32 have reproduced. Variance stabilised sensitivity (VSS) values reflect the potential impact of the different vital rates on overall population growth; the larger the VSS value, the greater impact a change in that vital rate would have on population growth rate

<sup>a</sup> The total number of females used to calculate each vital rate for the two time-frames. For fecundity ( $f_3$ – $f_5$ ), number of females was calculated as the sum of the proportion of the census interval (1st January to 31st December each year) that each female spent at a given age within an age class; survival ( $s_1$ – $s_6$ ) was also pro-rated in this way unless a female died, when she was counted as that age for the entire inter-census interval. Females that left the population during an inter-census interval were only counted for the proportion of time that they were present; the total number of females for transition probability ( $g_1$ – $g_5$ ) was calculated as the number of females within an age class at each census that either progressed to the next age class by the following census, or remained in the current age-class

demographic parameters (Table 2) for comparison between the two time-periods. During these two time-periods there were a total of 64 males and 107 females, and 39 males and 71 females present, respectively. Between 1986 and 2010, there were a total of 104 calves (38 males, 63 females, and 3 of unknown sex) born to 41 dams and 28 sires; 68 deaths (31 males, 34 females, and 3 of unknown sex); 11 imports from outside the EEP; and 14 exports. Of these, 38 births (14 males and 24 females), 25 deaths (9 males and 16 females), 2 imports and 7 exports occurred between 2001 and 2010.

As a comparison between the ex situ population and their in situ counterparts, data from eight managed populations of *D. b. michaeli* in Kenya, supplied by Kenya Wildlife Service (KWS), were compiled to act as a reference population. These data covered a time-period of between 7 and 27 years, depending on population history and completeness of the records available. Recorded data included estimated or known dates of birth and death, translocation history, and any calves produced (date of birth and dam and sire identity). The identity of the dam was recorded in 91 % of births, but the sire only in 37 %. A set of

**Table 2** Average demographic parameters calculated from the EEP population of eastern black rhinoceros (*D. b. michaeli*) over the two time periods 1st January 1986 to 31st December 2010 and 1st January 2001 to 31st December 2010, compared to data from managed populations in Kenya, and against minimum targets to achieve 5 % growth (du Toit et al. 2001)

Demographic parameter	EEP 2001–2010			EEP 1986–2010			KWS		
	Target	Average	Achieving target	Average	Achieving target	Average	Achieving target		
<i>Females</i>									
Age at first reproduction	<7 years	9 years 10 months 25 days	X	9 years 7 months 21 days	X	8 years 2 months 1 day	X		
Inter-calving interval	<3 years	3 years 10 months 17 days	X	3 years 5 months 4 days	X	3 years 2 months 14 days	X		
Adult females <sup>a</sup> breeding per year	>30 %	11.30 %	X	15.70 %	X	23.74 %	X		
Annual population mortality rate <sup>b</sup>	<4 %	2.22 %	✓	2.49 %	✓	1.19 %	✓		
Annual infant <sup>c</sup> mortality rate	<10 %	9.57 %	✓	12.87 %	X	2.84 %	✓		
Annual sub-adult <sup>d</sup> mortality rate	<5 %	0.00 %	✓	0.79 %	✓	0.66 %	✓		
<i>Males</i>									
Age at first reproduction	–	11 years 1 month 7 days	–	10 years 10 months 17 days	–	11 years 0 months 9 days	–		
Adult males <sup>a</sup> siring per year	–	22.00 %	–	29.20 %	–	31.20 %	–		
Annual population mortality rate <sup>b</sup>	<4 %	2.80 %	✓	3.56 %	✓	1.61 %	✓		
Annual infant <sup>c</sup> mortality rate	<10 %	5.75 %	✓	22.59 %	X	4.37 %	✓		
Annual sub-adult <sup>d</sup> mortality rate	<5 %	1.76 %	✓	0.71 %	✓	1.38 %	✓		
Adult sex ratio (#F:1 M)	>1	1.92	✓	1.81	✓	1.50	✓		
Proportion of calves (age 0–4)	>28 %	17.63 %	X	20.35 %	X	25.4 %	X		
Proportion of calves (age 0–1)	>8 %	4.60 %	X	5.60 %	X	7.42 %	X		

**Table 2** continued

Demographic parameter	EEP 2001–2010		EEP 1986–2010		KWS	
	Target	Average	Achieving target	Average	Achieving target	Average
Average annual growth rate <sup>e</sup>	>5 %	1.15 %	✗	2.19 %	✗	8.38 %
						✓

<sup>a</sup> Adult females age 5–32, adult males age 7–32

<sup>b</sup> Average mortality of population as a whole, not separated by age class or category

<sup>c</sup> Infant refers to calves age 0–1

<sup>d</sup> Sub-adult females are age 1–5; sub-adult males are 1–7

<sup>e</sup> The average annual growth rate is that calculated from the defined time frame, and includes growth due to natural increase (births and deaths) and net migration (imports and exports)

performance indicators for black rhinoceros previously established to evaluate the success of different populations relative to the target of 5 % growth (du Toit et al. 2001) were also used to compare the performance of in situ and ex situ populations (Table 2).

## Population modelling

To assess the demographic sustainability of the EEP population, a PVA was carried out using a single-sex, female-based stochastic transition matrix model constructed in MATLAB (The MathWorks Inc 2008). Demographic information on all births and deaths between 1986 and 2010 were used to calculate age-specific fecundity and mortality for each year. The number of births or deaths that occurred to females at a particular age were divided by the total number of females of that age within a given census interval. A census date of 31st December was used each year, so for each census interval (1st January to 31st December inclusive), the total number of females at each age was calculated by summing the proportion of the year that each female spent at that age (i.e. pro-rated). This method prevents over-inflation of the sample size, since depending on their birth date, individuals could be counted at two ages for part of each census year. Any individuals that left the population during a census interval were included only as the proportion of the year that they were present. For calculating mortality, females that died within a given census interval were counted at that age for the whole of that year.

Due to the small population size and long-lived nature of this species, females were divided into six age-classes (infant, 0–1; sub-adult, 1–5; three reproductive age-classes, 5–9, 9–17 and 17–33; and post-reproductive, 33+) based on similarities in observed fecundity and mortality. The transition probability of females in one age-class at time  $t$  progressing to the next age-class by time  $t + 1$  was calculated as the number of females that moved to the next age-class by the following census, divided by the total number of females that started in that age class. The vital rates of fecundity ( $f_{1-6}$ ), survival (1-mortality;  $s_{1-6}$ ) and transition probability ( $g_{1-6}$ ) were calculated for each age-class, for each year (1986–2010), and the mean and variance in each rate calculated across years (Table 1). In this population, no females have ever produced a calf before age 5 or after age 32, so  $f_1$ ,  $f_2$  and  $f_6$  were calculated as zero. The observed variance in each vital rate likely consists of that due to demographic and environmental factors, so an attempt was made to partition the total variance according to the method of Akçakaya (2002). However, after subtracting an estimate of variance due to demographic stochasticity, remaining environmental variance was negligible; therefore, the total observed variance was used in the simulations described below. The population at the start of the simulation included the 51 females present on the census date of 31st December 2010 ( $n = 2, 8, 7, 16, 14$  and 4 per age-class).

Separate stochastic simulations were conducted using mean vital rates and variance calculated from each of the two time-periods. Code from Morris and Doak (2002) was adapted to include the six age-classes and matrix elements which reflect the potential contributions an individual in each class would contribute to all other classes by the following census (Fig. 2). Births within this population are distributed throughout the year, so the contribution by each class  $j$  individual to the population at the next census consists of (1) surviving and progressing to the next age class,  $s_j g_j$ , (2) surviving and staying in the same age class,  $s_j (1-g_j)$ , and (3) reproduction,  $f_j \sqrt{s_j} \sqrt{s_j}$ , (Fig. 2).

For each stochastic model, vital rates were drawn from the beta distribution specified by the observed mean and variance for each rate, and used to determine matrix elements as described above for each year of the simulation. The transition matrix was multiplied by



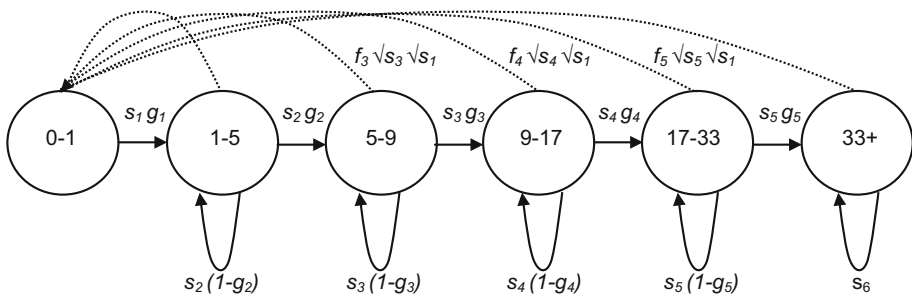
the population vector,  $n$ , to give the population size the following year. This was repeated as single-year time steps for 100 years, with 1000 runs of the model. If the quasi-extinction threshold of 20 individuals was met within a given simulation, the model moved to the next run and the overall probability of extinction was calculated across all 1000 runs. In addition to this stochastic simulation, a model using Monte-Carlo simulations to estimate the impact of demographic stochasticity alone was run, where the fate of individuals within each age-class was determined by selecting a random number and comparing its value to the probabilities for survival and fecundity (Morris and Doak 2002). However, as results were very similar and the observed variance was found to be predominantly due to demographic stochasticity, only the results from the full stochastic simulation are shown. In addition to running simulations with a starting population as of 31st December 2010, two further scenarios were modelled. The stable age-distribution, to which a population is predicted to converge over time (Morris and Doak 2002), was determined from the two sets of vital rates, adjusted to the same total population size ( $N = 51$ ) and used as the starting population. This was used to investigate the potential effect of changing age-structure on population growth when the vital rates used in the simulation remained the same.

To investigate the potential impact of each vital rate on overall population growth, a variance stabilised sensitivity analysis (VSS) was also performed, based on an arcsine square-root transformation (Link and Doherty 2002). When applied to vital rates that are probabilities, this transformation does not scale the variance in a vital rate to the size of the mean, so the absolute magnitude of a change has meaning independent of the value of the vital rate (Dunham et al. 2008). Sensitivity analysis code from Morris and Doak (2002) was modified to incorporate VSS according to Eq. 1, where  $\theta$  is the vital rate under analysis (Link and Doherty 2002):

$$VSS = \frac{\partial \log \lambda}{\partial [2 \sin^{-1}(\sqrt{\theta})]} = \left( \frac{\sqrt{\theta(1-\theta)}}{\lambda} \right) \frac{\partial \lambda}{\partial \theta} \tag{1}$$

### Genetic analysis of the EEP population

Small populations tend to lose genetic diversity at a greater rate, and the finite size of captive breeding programmes can lead to the loss of genetic diversity over time due to



**Fig. 2** Schematic diagram of the potential contribution by female black rhinoceros in six age-classes at time  $t$  to the population at time  $t + 1$ ;  $s_j$  is the survival rate for individuals in class  $j$ ,  $g_j$  is the probability that an individual in class  $j$  transfers to class  $j + 1$  by the following census, and  $f_j$  is the rate of fecundity of individuals in class  $j$ . *Dashed lines* represent the recruitment of new individuals into the population through reproduction ( $f_j \sqrt{s_j} \sqrt{s_1}$ ); *solid lines* represent individuals moving between, or remaining within age classes

**Fig. 3** Population size projection (females only) from MATLAB model showing results from simulations using **a** 25- and **b** 10-year demographic data for vital rate calculation. The average projected population size based on stochastic simulations is represented by the *solid line*; *error bars* represent one standard deviation in population size across 1000 runs; *open markers* represent the minimum and maximum population size estimates obtained from simulations for each year of projection. *Note* the difference in scale on the y-axis between the two scenarios, representing the difference in final projected population size by 100 years

pronounced random drift and inbreeding effects (Lacy 1989). The effective population size ( $N_e$ ) can be used to predict the rate of loss of genetic diversity,  $1/N_e$  (Wright 1969). For any given population, the effective population size is often smaller than the census population size ( $N_T$ ) or total number of adults ( $N_A$ ), due to factors such as fluctuating population size across generations, high variance in family sizes, and an unequal sex ratio (Frankham et al. 2010). The effective population size was calculated for the current EEP population, based on the number of living males ( $N_m$ ) and females ( $N_f$ ) that have produced offspring ( $N_e = 4N_mN_f/(N_m + N_f)$ ), (Wright 1969) and according to Nunney (1996). This second approach used demographic data over the last 25 years to incorporate the generation time, average life expectancy, sex ratio of adults and variation in survivorship and fecundity of the two sexes between years.

Population management software, pm2000 (Lacy and Ballou 2002; Pollak et al. 2002), was used alongside SPARKS to extract population demography and pedigree information from the eastern black rhinoceros studbook. Using this software, the genetic sustainability of the current population was evaluated using population statistics obtained from a 1000-run gene drop simulation; each founder was assigned two unique alleles and Monte-Carlo simulations used to estimate the probability of allele transmission from the founders to the living descendants via the known pedigree. First, the level of genetic diversity in the current population was estimated relative to the wild founder population. Second, the theoretical population size and population growth rate required to achieve the target of retaining at least 90 % genetic diversity was estimated in pm2000, keeping all other parameters constant and solving for genetic diversity at the end of 100 years.

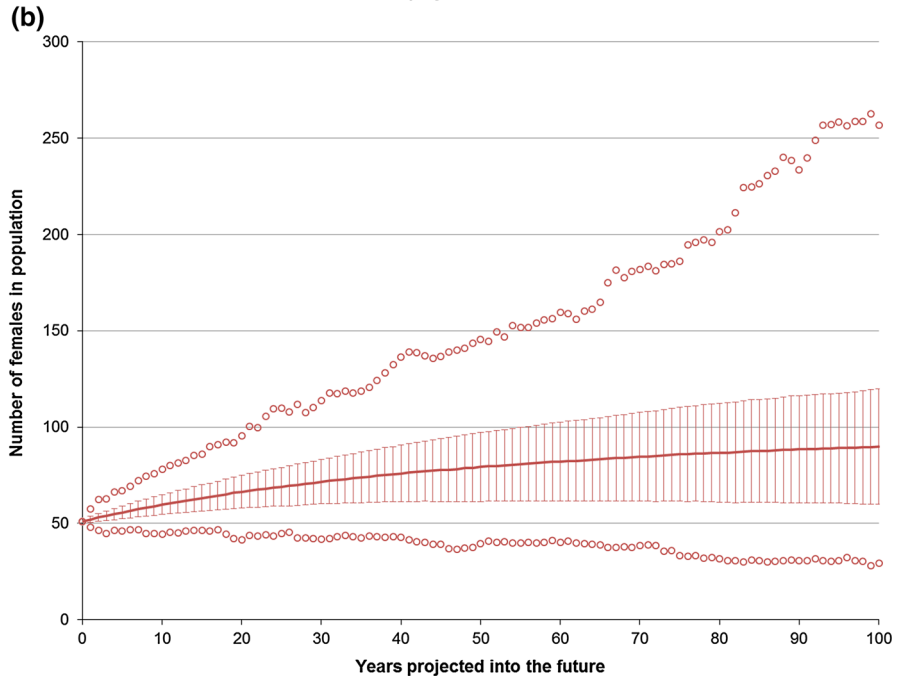
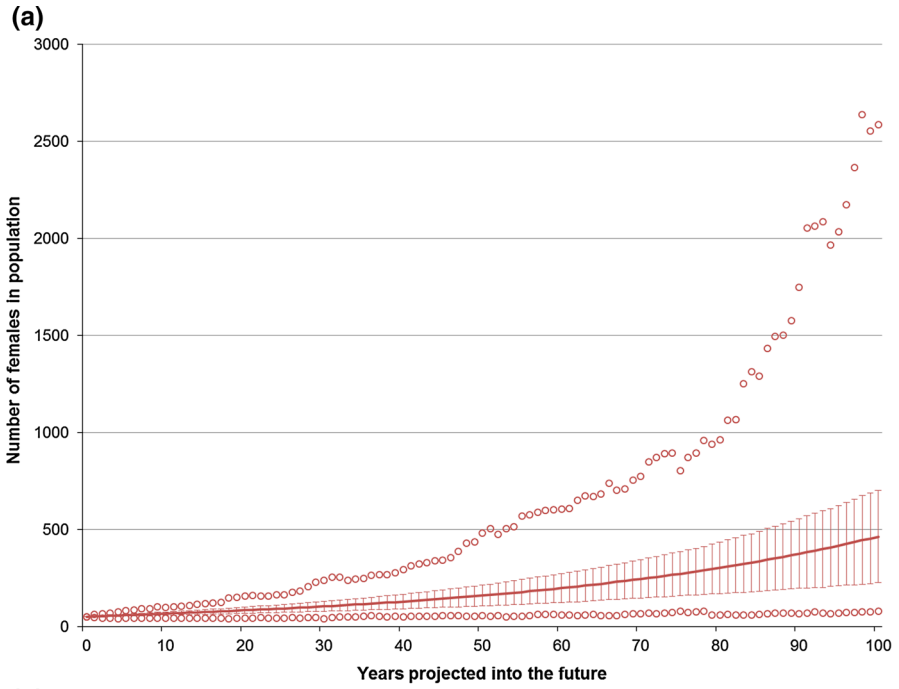
The founder genome equivalent (FGE) (Lacy 1989) was also calculated using the outcome of the gene-drop simulation in pm2000. FGE indicates how many founders would have resulted in the same genetic diversity as present in the current population, had they all reproduced equally and no alleles were lost due to random drift. Here,  $N_f$  is the number of founders,  $p_i$  is the proportion of genes in the current descendant population that were contributed by founder  $i$ , and  $r_i$  is the proportion of founder  $i$ 's alleles that have been retained within the current descendant population (Eq. 2).

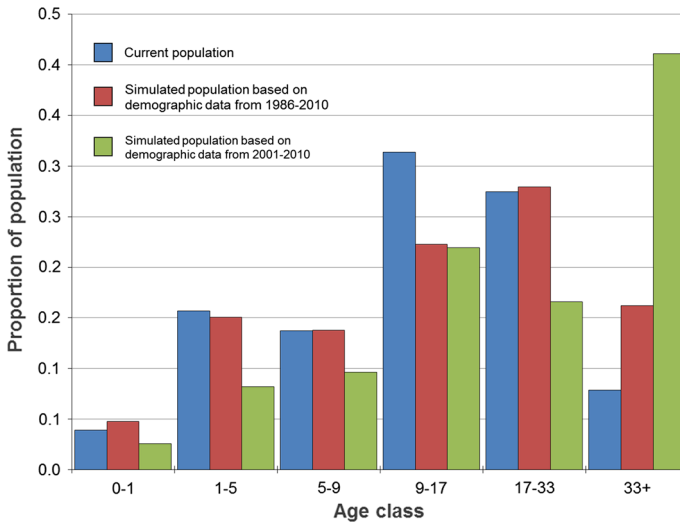
$$FGE = \frac{1}{\sum_{i=1}^{N_f} (p_i^2/r_i)} \quad (2)$$

## Results

### Population modelling

The projected stochastic growth rate of the EEP population according to the simulations based on demographic data from the last 25- and 10-year time-periods ( $\pm$  SD) were 1.0212





**Fig. 4** Proportional age structure of females in the EEP population as of 31st December 2010 (current population) and the stable age-distributions based on vital rates calculated from 1986–2010 or 2001–2010 demographic data

(0.0048) and 1.0052 (0.0033), respectively. These represent projected growth per annum of 2.12 % and 0.52 % (Fig. 3).

The prediction resulting from the last 25-year data is consistent with the average annual change in population size between 1986 and 2010 of 2.19 % (SD 5.07 %). However, the simulation resulting from the last 10-year data predicts a slower rate of growth in the future than that observed between 2001 and 2010 of 1.15 % (SD 4.24 %). This may in part be related to potential changes in the age-structure of the population over time. Figure 4 illustrates the female age-structure of the current population (31st December 2010) compared to the stable age-distribution based on the vital rates calculated from the two time-periods. Although the stable age-distribution predicted from the last 25-year vital rates is largely similar to the current age-structure; that based on the last 10-year data is skewed towards the oldest age class. When the starting population was adjusted to these stable age-distributions, the effect on growth was quite apparent, with projected stochastic growth rates ( $\pm$  SD) of 1.0200 (0.0048) and 1.0008 (0.0033), respectively. In the projections based on the last 10-year data, this indicates that once the population converges towards a stable distribution with over 40 % of females in the post-reproductive age class, this could have a major impact on future population growth, with projected annual growth reduced from around 0.5 to 0.08 %. In comparison, the projected growth based on the stable age-distribution from the last 25 years remains at around 2 % per annum.

The predictions made using sensitivity analyses indicate that reproduction appears to be limiting the growth of the EEP population (Table 1). Variance-stabilised sensitivity analysis using data from the last 25 years indicates that there is most potential for increasing the growth rate of the population through increasing reproduction of females aged 9–17, followed by increasing neonatal survival, and reproduction of females aged 17–33. Using data from the last 10 years, population growth could be most influenced by increasing reproduction in both 17–33 and 9–17 year old females, respectively, followed by increasing the survival of 9–17 year old females. Under both of these scenarios, the projected growth rate was most sensitive to changes in fecundity, therefore increasing

reproduction of females aged 9–33 years would have the greatest impact on overall population performance.

## Comparisons of population performance

### *EEP population over the last 25 years*

Performance indicators (du Toit et al. 2001) for the EEP population calculated from the two time-periods are given in Table 2. These illustrate that during the 10-year period from 2001 to 2010, females started to breed later, with longer inter-calving intervals, and a lower proportion of females breed each year as compared to the 25-year time-period. Additionally, individual females also produced a higher average number of calves in the period between 1986 and 1995 (40 calves born to 19 dams 1986–1995 (mean 2.11), than females between 2001 and 2010 (38 calves born to 25 dams 2001–2010 (mean 1.52); (Mann–Whitney U  $P = 0.03$ ).

However, the difference in fecundity between the two periods may not just be due to individual females reproducing at a slower rate; but also due to a high degree of reproductive skew. Unequal reproduction has been an issue historically in this population; of the 144 *D. b. michaeli* females in the EEP studbook, 52 (36.1 %) produced at least one calf, whereas 64 (44.4 %) either died or left the population without reproducing, and 28 (19.4 %) have not reproduced, but are still alive and have the potential to do so. Furthermore, this reproductive skew continues to be an issue; the current EEP population on the 31st December 2010 consisted of 51 females, 37 of which were in the reproductive age-class (age 5–32), but 49 % had yet to produce offspring.

This reproductive skew amongst females could also contribute towards the differences in growth rate between the two time-periods. During the 10-year period from 1986 to 1995, when growth was relatively high, there were 34 females of reproductive age (5–32 years), of which 56 % gave birth during that 10-year period. In comparison, during the 10-year period from 2001 to 2010, when population growth was slowest, there were 56 females of reproductive age; of which only 45 % successfully gave birth. Although there tended to be a higher proportion of non-breeding females age 5–32 in latter 10-year period, this difference was not significant across the two time periods (Mann–Whitney U;  $P = 0.298$ ). However, the average age of first reproduction for this population is around 9 years old (Table 2), so when only prime-aged females (9–17 years) were considered, a significantly higher proportion of females produced a calf during the earlier time-period (Mann–Whitney U;  $P = 0.01$ ). Out of 17 females that were in this age class between 1986 and 1995, 15 (88 %) produced at least one calf. In comparison, 34 females were in this age class between 2001 and 2010, but only 17 (50 %) reproduced during this time.

Similarly for males, unequal reproduction appears to have been an issue both historically and in the current population. Out of a total of 124 *D. b. michaeli* males in the EEP studbook, 46 (37.1 %) sired calves, 63 (50.8 %) either died or left the population without reproducing, and 15 (12.1 %) have not reproduced, but are still alive and may still contribute. Of the 27 males in the current population, 19 are in the reproductive age class (age 7–32), and 42 % of these have yet to sire offspring.

### *Comparison of wild and captive populations*

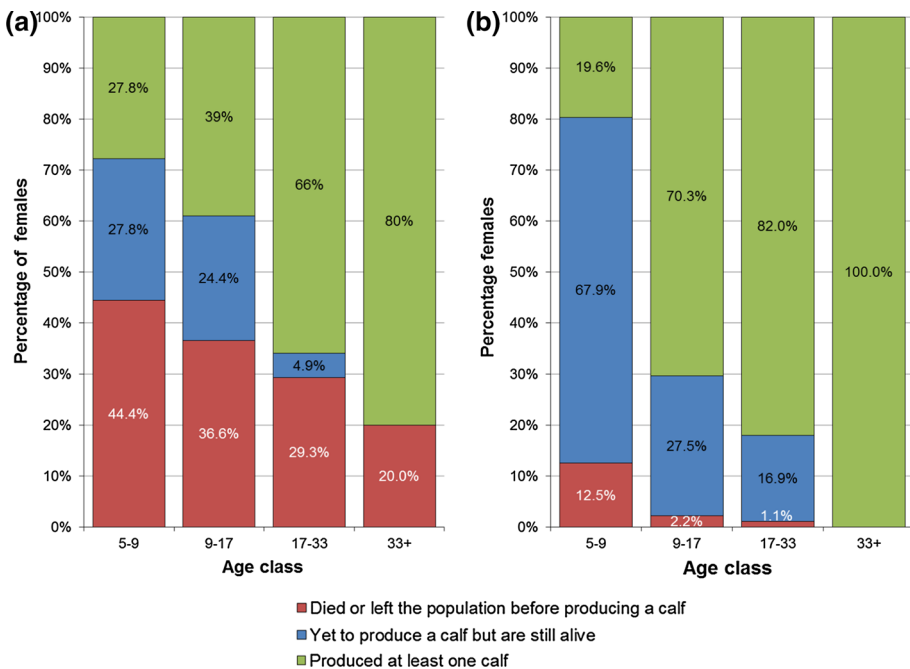
Compared to the wild reference populations, the European captive population under-performs on all measures of reproduction; females start to reproduce later, have longer inter-

calving intervals, and a lower proportion of females breed each year (Table 2). As a result, reproductive output is lower in captivity; wild breeding females produce a higher number of calves per year than those in the EEP population (mean in situ: 0.232 calves per year ( $N = 168$  females); mean ex situ: 0.195 calves per year ( $N = 55$  females); Mann–Whitney  $U$   $P = 0.02$ ).

The proportion of females that contributed offspring to the next generation was also reduced in captivity. The percentage of females that had never reproduced (including both current members yet to breed and those that have since died or left the population) was significantly higher across three age classes in the captive population compared to the wild population (Cross-tabulation with Pearson's Chi square test: 9–17:  $\chi^2 = 11.602$ ,  $df = 1$ ,  $P = 0.001$ ; 17–33:  $\chi^2 = 4.134$ ,  $df = 1$ ,  $P = 0.042$ ; 33 + :  $\chi^2 = 4.286$ ,  $df = 1$ ,  $P = 0.038$ ; Fig. 5). Furthermore, reproductive skew tended to be higher in the current captive population, with 43 % of females aged 9–32 yet to reproduce, compared to only 27 % of the wild population ( $\chi^2 = 3.003$ ,  $df = 1$ ,  $P = 0.083$ ).

Although there are no published benchmarks for male reproduction, the age at first conception was very similar across wild and captive populations, and in captivity was fairly consistent across the two time-periods (Table 2). The percentage of wild adult males siring each year was slightly higher compared to the captive population, particularly between 2001 and 2010. However, these indicators should be treated with caution, as the sire identity records from the wild population were less complete because paternity was not always known.

Overall mortality in the EEP population was below the target of 4 % across both time-periods, but still higher than their wild counterparts (Table 2). Sub-adult mortality in the



**Fig. 5** Percentage of females in each age class in **a** the EEP ex situ population and **b** the in situ reference population that produced at least one calf, died or left the population before producing a calf, or have yet to produce a calf but are still alive and have the potential to contribute

captive population was more variable across the two time-periods, but the higher estimate for males (2001–2010) and females (1986–2010) was similar to in situ populations. Infant mortality in captivity was above the 10 % target in both females and particularly in males over the last 25 years; however it was reduced in both sexes over the last 10 years. Despite this improvement, captive infant mortality was much higher than estimates from wild populations. However, neonatal deaths may be underestimated in the wild, as stillborn calves or those that die within the first few days of life may not be recorded. Of the 19 captive deaths in the 0–1 age class between 1986 and 2010, 10 were recorded as premature/stillbirths, a further four died on day 0, and two within the first week of life; all of which could potentially be unrecorded under wild conditions. If neonatal deaths were underestimated in situ due to these cases not being observed, and assuming that the stillbirth rate may be similar between the two populations, in situ neonatal mortality could potentially be as much as 10 % higher, making it more comparable to the ex situ population.

Over the last 25 years there was a significant birth sex ratio skew in the EEP population, with 62 % female and 38 % male calves born (One sample binomial test:  $P = 0.017$ ). In contrast, the offspring recorded across the eight in situ reserves were 51 % male and 49 % female (One sample binomial test:  $P = 0.544$ ). In addition to the higher mortality rates for males aged 0–1 over the last 25 years, this birth sex ratio has resulted in a strong skew towards adult females, with almost 2 females to every male (Table 2).

### Genetic analysis of the EEP population

Of the 135 wild-caught founders, 69 % are no longer represented in the ex situ population. Moreover, the contribution of the remaining 41 founders has been unequal, resulting in 33 % of the current population being related to five highly-represented founders (percentage representation of founders range 0.3–10.2 %). Analysis of founder allele retention indicates that this has resulted in a current founder genome equivalent (FGE) of just 13.39 wild-caught founders, had they all reproduced equally. However, with the genetic diversity still present in the population, the potential exists to increase the FGE to 22.69, if non-breeding individuals were to contribute and founder representation were equalised.

The effective population size ( $N_e$ ) of the current population was estimated to be 31.54 based on 12 male and 23 female breeders. Based on a census population size ( $N_T$ ) of 78, this gives a  $N_e/N_T$  ratio of 0.4044, indicating that only around 40 % of the population are effectively contributing to the next generation. However, using the total number of adults in the population as opposed to  $N_T$  (Frankham 1995) gives a  $N_e/N_A$  ratio of 0.5632 based on the number of breeders in the current population (Wright 1969), and a  $N_e/N_A$  ratio of 0.6095 based on the variance in fecundity over the last 25 years (Nunney 1996). Which-ever estimate is used, an effective population size 40–60 % below that of the total population size means there is increased potential for genetic diversity to be lost due to genetic drift and the effects of small population size (Nunney and Elam 1994).

Despite the reduced effective population size, computer simulation of the EEP pedigree indicates that the current population has retained an estimated 96.3 % of the genetic diversity (GD) of the founder population, with a potential upper limit of 97.8 % if all non-breeding individuals were to contribute optimally. However, slow rates of growth and continued unequal representation could mean that this diversity may not be retained over the next 100 years. With projected stochastic growth rates of 1.005 and 1.021 respectively, and a theoretical maximum carrying capacity of 100 individuals, simulations suggest that 90 % GD can only be retained for between 88 and 93 years. Even with an unlimited population size, it is unlikely that 90 % genetic diversity can be retained with average

growth rates limited to 0.5 % per year. However, if the target growth rate of 5 % can be achieved, and an increased carrying capacity of 106 individuals, this would be sufficient to maintain the target of 90 % GD for at least the next 100 years.

## Discussion

In this study we used population viability analysis to predict the likely future growth of the EEP population of eastern black rhinoceros, using parameters calculated from demographic data from the last 10- and 25-year time-periods. Although currently self-sustaining, sub-optimal reproductive output and high reproductive skew are currently undermining the growth and genetic viability of this important captive population. The ex situ population under-performs on all reproductive parameters compared to their in situ counterparts, particularly over the last decade when growth rates were reduced. The final models reported here represent the most robust use of the studbook data available, incorporating observed variance in vital rates to give reliable predictions about future population performance, while still allowing a direct comparison to parameters calculated from in situ demographic data. These models suggest that this captive population is projected to grow at a rate of between 0.5 and 2 % per annum, which is well below the target of 5 % and growth rates achieved in managed populations in situ. At present the EEP population is estimated to have retained more than 90 % of founder genetic diversity; however unequal founder representation and continued reproductive skew is limiting longer-term genetic viability. For this captive population to act as a safeguard against further decline of the wild population, it is essential that the growth rate is increased while maximising genetic diversity by reducing the reproductive skew across individuals.

Comparison of demographic data from the ex situ population with eight Kenyan reserves indicates that sub-optimal performance is likely due to three contributing factors. Firstly, the average age at first calving for female black rhinoceros was higher in captivity than observed in situ. Although females in captivity show signs of sexual maturity as early as 3–4 years of age (Edwards 2013; Smith and Read 1992), they often conceive much later, with the average first birth for the historical EEP population occurring around 9–10 years of age. Secondly, captive females have longer average inter-calving intervals than in situ populations, often exceeding 3½ years and resulting in a lower proportion of females breeding each year. Thirdly, both historically and in the current population, a large proportion of both males and females are failing to contribute offspring, resulting in high reproductive skew. The goal of the EEP is to breed all individuals in the population (Biddle and Pilgrim 2013); however, the constraints of captivity could contribute to differences in reproductive success. With a finite number of breeding bulls available (Edwards et al. 2015b), and a maximum of two females introduced at a time to each bull, this will often limit breeding opportunities for other females within the population. This can result in young females not being introduced to a bull for breeding immediately that they reach sexual maturity. Similarly, females will often not be re-introduced to a bull until her previous calf has been weaned at between 18–24 months of age (Pilgrim and Biddle 2014), meaning inter-calving intervals of less than three years are relatively uncommon in captivity. These factors may contribute to a later age at first birth, increased inter-calving intervals and reduced lifetime reproductive success compared to females in managed, free-ranging populations in situ.



Of additional concern within this captive population is the change in demographic parameters over the last decade compared to the preceding 15 years. Age-specific fecundity over the last decade was approximately half that from the last 25 years; a lower proportion of females, particularly prime-aged females, bred successfully, and those that did produced calves at a lower rate. This had a clear impact on the projected growth rate of the population, and even more so when the theoretical stable age-distributions were used as the starting population in stochastic simulations. Under the 10-year stable age-distribution scenario, the already reduced fecundity declines further over time as females age and an increasing proportion of the population become post-reproductive. Reduced individual reproductive success could be associated with differences in physiology or behaviour that impact breeding management (Edwards et al. 2015a, b) or to underlying genetic differences (Cain et al. 2014). Nonetheless, low rates of reproduction not only have the potential to impact the overall growth rate of the population, but also exacerbates the impact of reproductive skew on the maintenance of genetic diversity in the future.

Captive populations of endangered species are often small, fragmented and closed to importation (Ballou et al. 2010), making them particularly vulnerable to the loss of genetic diversity due to genetic drift and inbreeding. Due to space limitations in captivity, populations large enough to counteract the effect of drift (Lande and Barrowclough 1987) are rarely achievable for many endangered species, particularly mega-vertebrates. Therefore, an important aspect of captive population management is to maximise the effective population size and to carefully manage genetic diversity through pedigree-driven breeding recommendations. Estimates from wild populations suggest that effective population sizes are often only around 10 % of the total population (Frankham et al. 2010); whereas captive or managed populations typically have higher ratios between 0.2–0.5 (Earnhardt et al. 2004; Foose and Ballou 1988), with values as high as 0.7 previously reported (Willis and Wiese 1993). Although this suggests that the variance in reproductive success between individuals means that only around 40–60 % of the genetic diversity present in the population may be carried forward to future generations, increasing the potential for alleles to be lost through genetic drift.

Variance in lifetime reproductive success is not uncommon (Clutton-Brock 1988), and the loss of lineages may occur in wild populations as a result of natural catastrophes or differences in competitive ability (Gompper et al. 1997). Indeed, in situ populations of black rhinoceros show high levels of male reproductive skew (Cain et al. 2014; Garnier et al. 2001); not surprising as this species naturally exhibits a polygynous or polygynandrous mating system (Christensen et al. 2009; Hutchins and Kreger 2006), and dominant males tend to monopolise a high proportion of matings. Although reproductive skew may therefore not be unusual in wild populations, particularly in males, in small captive populations it severely undermines efforts to maintain the genetic and phenotypic diversity present in the founder population. Although there have been no benchmarks established for male reproductive parameters, a lower proportion of captive males breed each year compared to the in situ reference population, suggesting the skew could in fact be higher in captivity. In contrast, reproductive skew is less common in females, often associated with cooperative breeders (Cant 1998) where variance in lifetime reproductive success can be high. In non-cooperative group-living species, variance in reproductive success may occur within years based on age or competitive ability (Rubenstein and Nunez 2009), but differences in lifetime reproductive success are often lower. In a species such as the black rhinoceros, where adult females are generally considered to be relatively solitary (Goddard 1967), the occurrence of a strong reproductive skew over time seems unusual. Moreover,

the high variance in female reproductive success observed in the ex situ population is not reflected to the same degree in the wild reference population, suggesting that this may be a consequence of captivity that warrants further investigation.

Management is also an important factor to consider when attempting to equalise reproductive success across individuals. Breeding recommendations are generally based on maximising genetic diversity, however, in the black rhinoceros introductions are not always successful. Nulliparous females in this population exhibit a high proportion of irregular oestrous cyclicity, potentially coming into oestrus less often, and may not exhibit overt behavioural signs of receptivity (Edwards et al. 2015a). When introductions occur, they may be characterized by a lack of sexual interest, sexual interest but failure to mate, or by aggression (Edwards 2013). Together, these factors can make timing introductions difficult, and may result in the premature separation of potential breeding pairs. This could contribute to reproductive skew as individuals that are easier to manage may inadvertently be provided with better opportunities to breed.

In addition to high levels of reproductive skew within both sexes, an additional concern with the EEP population is a consistent female-biased birth sex-ratio. This is contrary to the SSP population of black rhinos, with a male biased birth sex ratio (Dennis et al. 2007; Foose and Wiese 2006; Roth 2006), and poses an interesting management dilemma. Although a sex ratio that is skewed towards females can be beneficial for maximising population growth (Lenz et al. 2007), by the end of this study there were only nine males housed at five institutions that had bred in the last five years, whereas 14 institutions held breeding-age females. The current adult sex-ratio skew in combination with unequal reproductive success across individuals potentially limits breeding opportunities and contributes to the reduced reproductive output of this population. Although the cause of this birth sex ratio skew is currently unknown, the lack of any birth sex-ratio skew in situ, and the presence of a skew in the opposite direction in the North American population suggests that some aspect of captive management could be involved in this interesting phenomenon. Indeed, comparing management factors between the two ex situ populations may provide a useful insight into the observed differences in birth sex ratio.

In contrast to clear differences between in situ and ex situ populations in several reproductive parameters, mortality rates were more similar. One parameter where the in situ and ex situ populations differed was mortality within the 0–1 age-class. Differences between the two populations could be in part related to the possibility of under-reported stillbirths and neonatal mortality in situ. However, the captive population exceeds the benchmark established to achieve 5 % growth, particularly in males over the last 25 years. Indeed, 0–1 survival was the second most important vital rate in sensitivity analysis from the last 25-year time-period, indicating that reducing mortality rates would have a strong influence on overall population growth. Mortality in this age-class has reduced over the last decade, but still represents between 5 and 10 % of males and females, respectively. It is therefore important to understand underlying causes of stillbirths and neonatal mortality so that potential risk factors can be reduced.

## Conclusion

Incorporating PVA into population management can provide useful information, not only on projected future growth and the impact of changing age-structure on future population performance, but also through sensitivity analyses to determine which age classes and

demographic parameters have the most potential to influence population growth. The additional comparison to in situ reference populations as reported here also provides a biological benchmark, outlining what improvement may be feasible for this species. Together, these analyses indicate that sub-optimal reproductive output and reproductive skew are currently undermining the growth and genetic viability of this population of eastern black rhinoceros. For the EEP population to achieve its goal of 5 % growth, reproduction must be increased closer to the parameters described for the in situ reference population. We must understand factors underlying differences in reproductive success, so that individual fecundity can be increased to at least that observed between 1986 and 1995. Perhaps more importantly, however, the proportion of individuals contributing to the next generation must also be increased, which will not only benefit overall growth rates, but will also improve the potential for retaining genetic diversity in this important ex situ population.

**Acknowledgments** The authors would like to thank the Kenya Wildlife Service rhino programme for providing demographic information on in situ reference populations, and anonymous reviewers for constructive feedback on improving the manuscript. This work was funded by a NERC CASE studentship, and the North of England Zoological Society, with contribution from The Thriplow Charitable trust and the Association of British and Irish Wild Animal Keepers (ABWAK). S. Shultz is supported by a Royal Society University Research Fellowship.

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