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Group composition impacts reproductive output and population viability in captive white rhinoceros

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Abstract

Captive breeding programmes can play an important role in the conservation of species threatened with extinction in the wild. White rhinoceros, *Ceratotherium simum*, have suffered drastic declines due to illegal poaching across their range, and captive populations have the potential to safeguard this species from extinction. However, white rhinoceros birth rates in captivity have been extremely low, and there is substantial variation in breeding success between different institutions. A better understanding of the factors limiting their reproduction in captivity could improve their breeding management and conservation potential. This study used studbook data ($n = 467$) and comparisons with wild populations in Kenya ($n = 236$) to assess the breeding performance and viability of the European captive southern white rhinoceros, *Ceratotherium simum simum*, population. Our results show that the European population is declining 2% annually under current demographic parameters. On average, just 10% of females calved annually, in comparison to almost 40% across wild populations. To become self-sustaining, this must increase to a minimum of 17%, though reaching this target may lead to additional management challenges. Further analyses using studbook ($n = 134$ individuals) and multi-institutional questionnaire data ($n = 20$ institutions) suggest that modifying the social structure of captive groups could improve female breeding success. Institutions housing larger groups had proportionally greater breeding success, and females were more likely to copulate if housed with another breeding female, and more receptive to bulls if housed in a group with a lower mean age. These findings highlight the importance of considering social conditions in captive breeding programmes, particularly for species with complex social systems and low reproductive rates.

Introduction

One of the key goals of zoos worldwide is to support global conservation (WAZA, 2018). However, careful management is required to maintain reproductively viable populations in captivity. Captive breeding programmes aim to increase population size while minimizing inbreeding, retaining genetic diversity and maintaining a stable age-sex structure, thus ensuring population viability for possible reintroduction efforts (Lacy, 1997; Ballou *et al*., 2010). Establishing self-sustaining captive populations is often challenging (Snyder *et al*., 1996), partly due to the difficulty of replicating natural social conditions; the captive environment may prevent the formation of social bonds and group structures that are important for reproduction (Price & Stoinski, 2007; Rose & Croft, 2015). Identifying the factors that inhibit reproduction and developing effective captive management techniques is therefore a priority for many endangered species (Snyder *et al*., 1996).

Captive populations have the potential to play an important role in the conservation of the southern white rhinoceros, *Ceratotherium simum simum*. This subspecies has recovered from near extinction in the late 1800's, to a current population of around 18 000 individuals (International Rhino Foundation, 2019). However, due to the sharp increase in demand for rhino horn from 2007, illegal poaching has caused the rapid decline of rhinoceros species worldwide (Di Minin *et al*., 2015). The northern white rhinoceros, *Ceratotherium simum cottoni*, has already been driven to extinction in the wild due to extensive poaching and civil war in its range countries (Tunstall *et al*., 2018). Birth rates in southern white rhinoceros are no longer exceeding death rates in many populations (International Rhino Foundation, 2019), and this subspecies could be subject to another population crash if the rate of poaching continues to escalate.

Maintaining captive populations of southern white rhinoceros is crucial, not only to provide a safeguard for this subspecies until the threat from poaching is reduced, but also to retain genetically viable populations for any future reintroduction attempts. However, white rhinoceros reproduction in captivity has been relatively unsuccessful due to low fertility in captive-born females (Swaisgood, Dickman, & White, 2006). Non-reproductive females have been shown to exhibit irregularities in oestrous cycles (Brown *et al*., 2001; Hermes *et al*., 2006, 2007) and reproductive-organ pathologies (Hermes *et al*., 2014). The latter are significantly more common in nulliparous than parous females and may be minimized by at least one pregnancy (Hermes *et al*., 2006). While these factors may explain reproductive failure in some instances, they do not explain why many females, including those without pathologies or irregular oestrous cycles, fail to mate upon reaching sexual maturity.

One factor that may influence female breeding success is their captive management. Diet has been linked to a loss of fertility in captive female white rhinoceros (Tubbs *et al*., 2012, 2016), and this has been attributed to the gut microbiota's transformation of dietary phytoestrogens (Williams *et al*., 2019). However, the same relationship was not apparent in females born in the wild (Tubbs *et al*., 2016), and this does not explain why so many females fail to engage in mating events to begin with.

Social conditions have previously been posited as influencing reproduction in captive female white rhinoceros (Swaisgood *et al*., 2006; Metrione, 2010). White rhinoceros have the most complex social system of all the rhinoceros species, with adult females and sub-adults forming groups of up to 18 individuals in the wild (du Toit *et al*., 2006). However, in captivity, group size is largely dependent on available housing conditions, with group sizes in European institutions ranging between 2 and 11 individuals (Versteege, 2018). Research across 16 North American institutions housing white rhinoceros suggests those housing more than two individuals have greater reproductive output (Metrione, 2010). Moreover, females housed together from adolescence have lower faecal corticosterone metabolite levels than those introduced later in life (Metrione & Harder, 2011), suggesting familiarity may reduce stress, and social bonds may be important for female wellbeing.

Failure to breed in captivity has repeatedly been linked to stress resulting from prolonged confinement in sub-optimal conditions (Peng *et al*., 2007; Marshall *et al*., 2016), and limited opportunity for social interaction (Mallapur *et al*., 2009; Swaisgood & Shulte, 2010), in a range of different species. For example, mating group compositions (red pandas, *Ailurus fulgens*, Wei *et al*., 2005), group size (penguins, *Spheniscidae*, Blay & Côté, 2001) and group age (Scimitar-horned oryx, *Oryx dammah*, Little *et al*., 2016), have been linked to reproductive success in captivity. It is therefore possible that inadequate social conditions contribute to stress, and subsequently reproductive performance, in female white rhinoceros, or conversely, that social factors facilitate female reproduction.

Most studies on the factors driving female white rhinoceros breeding success focus on a small number of institutions (Brown *et al*., 2001, $n = 6$; Carlstead & Brown, 2005, $n = 6$; Patton *et al*., 1999, $n = 6$; Metrione, 2010, $n = 16$; Metrione & Harder, 2011, $n = 12$; Tubbs *et al*., 2016, $n = 9$; Williams *et al*., 2019, $n = 1$), making it difficult to capture variance in group sizes and reproductive performance. Using an entire meta-population to evaluate breeding performance and population viability will help to identify the factors limiting reproduction, providing guidance to improve the breeding management and conservation potential of captive white rhinoceros.

The European Association of Zoos and Aquaria Ex-Situ Programme (EEP) population of southern white rhinoceros provides an ideal model to evaluate the factors driving breeding performance in captive white rhinoceros; the EEP studbook holds long-term data on all births, deaths, group compositions and transfers within the population since the 1950's (Versteege, 2018). The EEP breeding programme was set up in 1992 under the EAZA Rhinoceros Taxon Advisory Group (TAG; Versteege, 2018). The goal of the Rhinoceros TAG is to ensure all captive populations are healthy, self-sustaining, genetically viable and capable of being an effective tool in support of rhinoceros conservation in the wild (Pilgrim & Biddle, 2020). Understanding the factors limiting population growth in the white rhinoceros EEP is thus a crucial first step towards developing a self-sustaining population for potential reintroduction efforts.

Population viability analysis (PVA) provides a framework to evaluate population persistence and the potential factors limiting population growth. PVA uses stochastic simulations to project the fate of a population based on specified demographic and life history parameters (Keedwell, 2004). Sensitivity analysis can then be used to identify which parameters are limiting population growth, such as female fecundity (Edwards *et al*., 2015) or infant mortality (Mortensen & Reed, 2016). To develop effective breeding management strategies, performance parameters should also be assessed in relation to realistic benchmarks. For captive populations, the performance parameters of in-situ counterparts provide a good target (Edwards *et al*., 2015), and can be used to assess the potential for improvement of ex-situ populations.

In this study, we use a combination of long-term demographic studbook data, PVA and a multi-institutional questionnaire to investigate the sustainability and breeding success of the EEP population of southern white rhinoceros. Firstly, we evaluate current reproductive performance, using comparisons with two in-situ populations in Kenya to assess the potential for improvement. Next, we investigate the future viability of the population, identify the key factors mediating population growth and determine where improvements are required to obtain a self-sustaining population. Lastly, we investigate how husbandry and social conditions relate to female reproductive behaviour and breeding success and provide guidance on the development of targeted breeding management strategies.

Materials and methods

Population performance

We used demographic data from the European Association of Zoos and Aquariums (EAZA) studbook for southern white rhinoceros to determine eight population performance parameters: growth rate, mortality rate, birth rate, infant mortality rate, female fecundity, inter-calving interval length, and both male and female age at first reproduction (see Supporting Information Table S1 for full descriptions of how parameters were derived). Data from 83 captive institutions were extracted from 01 January 1997–31 December 2016 (n = 467), and 01 January 2007–31 December 2016 (n = 330), to investigate both long- and short-term population performance (the length of approximately six and three inter-calving intervals, respectively), capturing any recent improvements in husbandry, while also coinciding with the period covered by our questionnaire. For all measures, we defined adult females as >8 years old, and adult males as >13 years old, on the 1st of July, for each year during the specified timeframes. These sex-specific age-limits are based on female mean age at first calving (6.5–7.5 years) and the age at which males reach sexual maturity (10–12 years) (Metrione & Eyres, 2014). The age-sex structure and proportion of (1) breeding individuals (2) potential breeders and (3) post-reproductive age females (defined as >34 years old; Versteege, 2018) present on the 31/12/2016 were also determined.

We assessed demographic performance parameters against benchmarks established by the Southern African Development Community rhino management group (Supporting Information Table S1; du Toit *et al*., 2006), as well as performance parameters for two Kenyan wild populations, Lewa Wildlife Conservancy (n = 140) and Meru National Park (n = 96), using data supplied by the Kenya Wildlife Service. These data encompassed the time period 01/01/2007 to 31/12/2018.

Long-term population viability

Population viability analysis

We conducted a PVA of the EEP population using Vortex v10.2.5 (Lacy & Pollak, 2017). Mean age-sex-specific mortality rates during the study timeframe were used until mean sex-specific age of first reproduction, after which they were divided into age-sex classes based on reproductive life history and mortality parameters derived from the population (Supporting Information Table S2).

As there are no estimates of inbreeding load (B) in white rhinoceros, the lethal equivalent value in black rhinoceros, *Diceros bicornis* – a species with a similar demographic history, population size and taxonomy – was set as the baseline in the PVA model: B = 16.00 in relation to offspring production (Cain *et al*., 2013). Inbreeding load is the decline in fitness associated with inbreeding and can be represented by the number of lethal equivalents per gamete; inbreeding load is twice the number of lethal equivalents for a diploid individual (Keller & Waller, 2002; Cain *et al*., 2013). The inbreeding coefficient (F) was set at F = 0.0079, based on half the average coefficient of relationship, r (Wright, 1922), estimated to be r = 0.0158 for the EEP population between 2008 and 2012 (Reid *et al*., 2012). An additional model was also employed to examine population viability in relation to those individuals actively contributing to the gene pool, using F = 0.344 based on the estimate of r = 0.688 for the EEP breeding population (Reid *et al*., 2012). Breeding was limited to pairs of individuals with F < 0.25 in the baseline model (Ballou *et al*., 2010), but no limit was applied to the breeding population model, as inbreeding levels were F > 0.25.

We determined all other baseline scenario parameters using the EEP demographic studbook data (see Supporting Information Table S2) and ran each model with 1000 iterations over a 100-year timeframe. The number of individuals in the population at the end of 2016 (n = 301) was used as the starting population size and carrying capacity was set at 1000 to allow for unrestricted population growth. As female fecundity was the main parameter under investigation, the baseline model was re-run, sequentially increasing the percentage of females calving annually by 1% to determine the minimum level required to obtain a positive mean growth rate, and thus a self-sustaining population.

Sensitivity analyses

We used sensitivity analyses to determine how population growth rate is impacted by seven vital parameters: the percentage of females calving annually, standard deviation in the percentage of females calving annually, infant mortality rate, sub-adult mortality rate, adult mortality rate, starting inbreeding coefficient and lethal equivalents (see Supporting Information Table S3 for full details).

To assess the impact of small changes in vital parameters on population growth rate, we used a relative sensitivity analysis (Mortensen & Reed, 2016), sequentially varying each vital parameter ±10% of its baseline value (Supporting Information Table S3). Each scenario was projected over 100 years with 1000 iterations. The relative sensitivity of the model to changes in each parameter was calculated using the equation: $(\lambda+ - \lambda-)/(0.2 \times \lambda0)$, where $\lambda+$ and $\lambda-$ are the output from adjusted parameter values, $\lambda0$ is the output of the baseline model, and 0.2 is the total perturbation of the parameter values (±10%) (Mortensen & Reed, 2016).

To determine which parameters explained the most variability in whether the population was self-sustaining after

100 simulated years (approximately seven generations), we used a logistic regression analysis (McCarthy, Burgman, & Ferson, 1995; Mortensen & Reed, 2016). Latin hypercube sampling in Vortex was used to create 1000 parameter sets with input values selected from a range of biologically realistic parameter values (Supporting Information Table S3). Each parameter set had 10 iterations, resulting in a dataset of 10 000 populations, each with a mean population growth rate, λ, after 100 years. Growth rate was collapsed to a binary value, based on whether each simulation resulted in a mean positive (1) or negative (0) growth rate. We ran all scenarios under the specified baseline conditions (Supporting Information Table S2), except for the parameters under investigation. Population carrying capacity was set to 10 000 to allow for unrestricted population growth. We analysed Vortex simulation results using a logistic regression, and the importance of each parameter was determined from their standardized regression coefficient (McCarthy *et al.*, 1995). As variable inflation factors (VIF) indicated multi-collinearity between model parameters, two separate models were employed so that all potentially important variables could be examined, including only those with VIF's <2 in the same model (Zuur, Ieno, & Elphick, 2010). Independent variables were plotted against the logit of the probability of a positive population growth rate, and visual inspection of plots revealed no non-linearity. Standardized residuals were used to check there were no influential outliers (standardized residuals >3).

Husbandry factors and social conditions

We used data from the EEP studbook and a questionnaire survey to assess whether husbandry factors and social conditions related to female breeding success and reproductive behaviour between 01 January 2012 and 31 December 2016. We chose this timeframe to incorporate current breeding performance at the time of data collection, and to ensure questionnaire respondents were familiar with individual's behaviour and husbandry conditions. Ethical approval for the research was obtained from the Academic Ethics Committee at Manchester Metropolitan University.

Studbook dataset

To assess institution breeding success, we used the proportion of reproductive-age (>8 years old) females that calved at each institution (*n* = 57) during the specified timeframe from the studbook. Females <8 years old that had already calved were also included as reproductive-age females to fully capture breeding success. Institutions without reproductive-age females, or those only housing single-sex or family groups (i.e., mother and offspring), were omitted. To investigate individual female breeding success, we determined whether each reproductive-age female (*n* = 134) calved during the study timeframe. Females >34 years old on 31 December 2016 were excluded to account for the potential impact of old age on female fecundity (Versteege, 2018).

We extracted the following seven variables from the studbook related to husbandry and individual life history that may affect female breeding success: age, birth origin, mean group size, mean group age, mean adult female group size, number of zoo transfers and the presence of a breeding female (see Supporting Information Table S4 for full variable descriptions). Institution latitude was also included to investigate the potential impact of climatic conditions on breeding success.

Questionnaire dataset

In November 2017, an online questionnaire on the husbandry and reproductive behaviour of captive white rhinoceros was sent to all EEP institutions housing both male and female white rhinoceros (*n* = 57). Twenty-four institutions completed the questionnaire (42%), from which 20 (35%) were suitable to include in the study.

The questionnaire (Supporting Information Appendix S2) consisted of 12 questions that addressed aspects of husbandry and reproductive behaviour. We collated questionnaire responses and used them to produce four additional predictor variables that may limit female reproductive behaviour and breeding success: enclosure size, whether the enclosure was a drive-through (i.e., a safari park), whether females were housed together at night, and whether females in oestrous were given access to breeding bulls at night (see Supporting Information Table S4 for full details). The questionnaire also resulted in three binary response variables: whether a cycling female (1) was observed exhibiting reproductive behaviour when paired with a bull, (2) was observed copulating with a bull, and (3) became pregnant after copulating with a bull, during the study timeframe. We defined reproductive behaviour as a female remaining still for >5 seconds while a bull attempted to chin-rest or mount (see also Swaisgood *et al.*, 2006). To ensure the viability of the statistical models, we excluded variables with very low variation or missing responses, except for the variable 'enclosure size', which had just two missing responses. Instead, we assigned missing values the mean to reduce the number of variables omitted from the analysis (Dodeen, 2003). Due to a modest sample size, all categorical variables were collapsed to binary to improve statistical power (see Supporting Information Table S4 for full details).

Statistical analyses

To determine the influence of predictor variables on the proportion of reproductive-age females that calved at each institution, we used logistic regression models, with a quasi-binomial distribution to account for over-dispersion in the response variable. To investigate which factors best predicted: (1) female calving success across the entire EEP population, and (2) whether females from the questionnaire sample (a) exhibited reproductive behaviour, (b) copulated or (c) became pregnant, following pairing with a bull, we used binomial generalized linear mixed effects models (GLMMs), including institution as a random effect. Variance inflation factors (VIFs) indicated multicollinearity between some model parameters. To avoid excluding potentially important variables, a set of models were run, including only variables with VIFs <2 in the same models (Zuur, Ieno, & Elphick, 2010). All regression assumptions were checked and met, as described in section "Sensitivity analyses". Transformations, including Log_{10}, square root and cube root, were used to adjust variables with uneven variances or skew, and improve their linear relationship with log odds. Model selection and model averaging based on Akaike information criterion (AIC) values were used to determine the relative importance and averaged estimates for the variables in each model set. The AICc (*Second-Order AIC*) correction for small sample size (Hurvich & Tsai, 1989) was used to prevent potential overfitting, and 2ΔAIC was set as the threshold for model averaging (Burnham & Anderson, 2002). Regular likelihood models were used to extract AICc values from the quasi-binomial *GLM* models (Bolker, 2017), and full models were reduced to minimum adequate models based on lowest *AICc*. All statistical analyses were carried out in R (R Core Team, 2016).

Results

Population performance

From 1997 to 2016, there were 467 white rhinoceros in the EEP population (268 females, 199 males), 200 calves were born and 206 individuals died or were stillborn (Table 1). The population was supplemented with 106 individuals from the wild (annual range: 0–18 individuals), 75% of which were female, and 49% of the total population was wild-derived. Out of the 222 reproductive-age females in the population, 38% (n = 85) calved (see Supporting Information Figure S1 for annual breakdown), compared to 98% (n = 48) of the 49 reproductive-age females in the two Kenyan populations. This has created a reproductive skew, with 5.4% (n = 12) of reproductive-age females producing 33% (n = 66) of all calves born during the study period. Of the females that did reproduce, 38% were born in captivity (Table 1). Of the 118 reproductive-age males (<13 years old), 37% sired offspring. Additionally, 10 males <13 years old sired offspring. Of the males that reproduced, 56% were captive-born (Table 1). Males also show a reproductive skew; 3.9% (n = 5) of reproductive-age and young reproducing males sired 32% (n = 62) of all calves born.

Table 1 The population size and breeding demographics for the EEP population between 1997 and 2016

Parameter	Males	Females	Total
Number recorded in the EEP	199	268	467
Number of calves born	104	88	200[a]
Number of individuals derived from the wild	26	80	106
Number of reproductive-age individuals	118	222	340
Number that calved/sired	54	85	139
Number that calved/sired and born in captivity	30	32	62
Number that calved/sired and born in the wild	78	117	195

EEP, European Association of Zoos and Aquaria Ex-Situ Programme.

[a] Note that sex was not recorded for eight calves and thus the number male and female calves born does not equate to the total number of calves born.

All demographic performance parameters for the wild populations were within the established benchmarks for white rhinoceros (Table 2). However, only mean annual mortality rate and female inter-calving interval length were within target for the EEP population over the short-term (2007–2016), and only annual mortality rate was within target over the long-term (1997–2016; Table 2). Only 8.6% of females in the EEP population calved annually between 1997 and 2016, in comparison to 39.7% across the wild populations. Consequently, annual birth rate (1.8%) and population growth rate (3.9%) were much lower in the EEP population compared to the wild populations (8.0% and 10.1%, respectively). Infant mortality rate was also high, at 22.5% over the long-term, in comparison to 8.4% for the wild populations. While there have been marginal improvements in most performance parameters (Table 2), most likely due to changes in husbandry practices over time, female age at first reproduction has increased from 9.9 years over the long-term, to 13.5 years over the short-term. Furthermore, 14% of adult females in the EEP population are >34 years old and thus unlikely to reproduce in the future.

Long-term population viability

Under the baseline scenario, the EEP population has a 0% probability of extinction within the next 100 years (approximately seven generations) due to the species' long generation time and low mortality rate. However, the population is in decline, with a deterministic (and stochastic) growth rate of −0.0196, representing a population decline of approximately 2% per annum (Fig. 1). The mean predicted population size after 100 years was estimated to be 46 individuals, 85% smaller than the population size in 2016 (n = 301 individuals). The baseline scenario predicts the population can maintain 96% of its current genetic diversity after 100 years when the starting inbreeding coefficient is F = 0.0079 (i.e., the genetic relatedness of the entire EEP population based on current estimates). However, when the starting inbreeding coefficient is increased to F = 0.344, (i.e., the genetic relatedness of the reproducing sub-population based on current estimates), maintenance of current genetic diversity reduces to 63% (Supporting Information Table S5).

Demographic factors mediating population growth

Relative sensitivity analysis indicated the percentage of females calving annually was the only parameter with a disproportionate effect on population growth rate (Table 3). Standardized regression coefficients also demonstrated that

Table 2 The mean demographic parameters calculated for the EEP population between 1997–2016 and 2007–2016, and for the in-situ reference populations in Kenya between 2007–2018

		EEP 1997–2016		EEP 2007–2016		*In-situ* 2007–2018	
Demographic parameter	Target	Mean	SD	Mean	SD	Mean	SD
Annual population growth rate	>5%	**1.80**	2.39	**2.06**	1.99	*8.00*	2.20
Annual birth rate	-	3.87	1.57	4.70	1.66	10.10	2.26
Annual mortality rate	<4%	*3.93*	1.20	*3.96*	1.24	*2.87*	2.58
Infant mortality rate (0–1 year)	<10%	**22.47**	12.49	**18.04**	10.08	*8.44*	8.51
Adult females calving annually	>30%	**8.61**	3.35	**10.49**	3.37	*39.72*	8.00
Female age at first reproduction	<7.5 years	**9.86**	5.64	**13.49**	6.58	*7.25*	1.65
Female inter-calving interval length	<3 years	**3.05**	1.79	*2.82*	1.45	*2.79*	0.62
Male age at first reproduction	-	14.51	6.05	13.73	6.36	13.41[a]	2.98

Previously established benchmarks for each demographic parameter were used as targets (du Toit *et al.*, 2006). Values in bold indicate below-target performance and values in italics indicate above-target performance. There are no established benchmarks for annual birth rate or male age at first reproduction.

EEP, European Association of Zoos and Aquaria Ex-Situ Programme; SD, standard deviation.

[a] Based on ranger mating observations in Lewa Wildlife Conservancy (n = 16 breeding males).

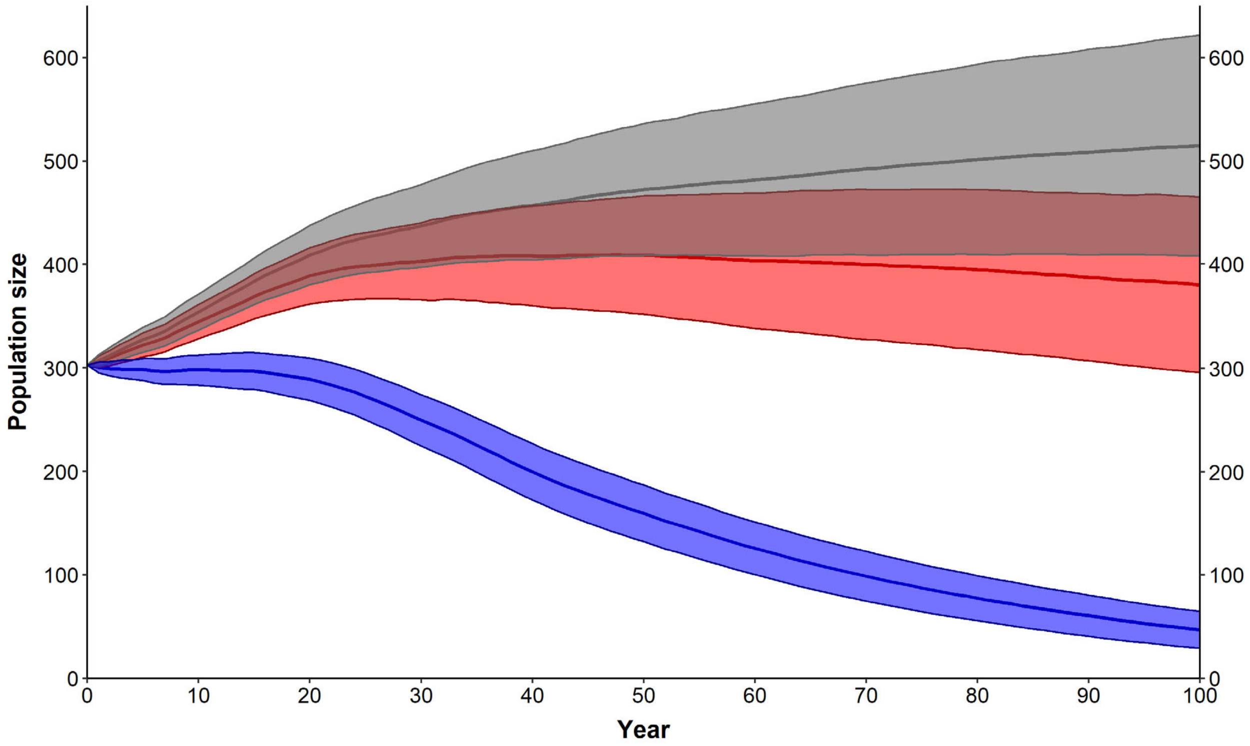

Figure 1 Average vortex population trajectories, with standard error, over the next 100 years for the EEP white rhinoceros population. Projections show the baseline scenario with current female fecundity (10%; blue), the baseline scenario plus 16% female fecundity (red), and the baseline scenario plus 17% female fecundity (grey). EEP, European Association of Zoos and Aquaria Ex-Situ Programme.

the percentage of females calving annually accounted for the most variation in self-sustainability of the population after 100 simulated years, followed by infant mortality rate (Table 3). Alternative models indicated that the mean growth rate switched from negative to positive under a scenario where 16% of females calve annually (0.2% average annual growth rate), though 17% were required to calve annually to maintain a positive population trajectory for 100 years (0.5% average annual growth rate; Fig. 1; Supporting Information Table S5).

Factors mediating reproductive success across the studbook

Between 2012 and 2016, 54 out of the 134 (40.3%) reproductive-age female white rhinoceros in the EEP population successfully calved at least once, and a total of 76 calves were born. However, 17 (22.4%) calves were either stillborn or died after 3 days. Of the 57 institutions from the EEP included in the analyses, 30 (52.6%) produced calves.

The proportion of females at an institution that calved increased as mean group size increased ($\beta = 2.35$, SE = 0.67, $P < 0.001$; range = 2.0–10.9; Supporting Information Table S6). Interpretation of the coefficient value suggests that for every 1% increase in group size, the proportion of females calving increases by 0.02 (i.e., 2.35/100 to account for the log transformation). Consequently, this suggests that increasing group size by 25% may increase the proportion of females calving by 23% (i.e., 2.35 × log(1.25)) and increasing group size by 50% may increase the proportion of females calving by 41% (i.e., 2.35 × log(1.50)). Individual females were more likely to have calved if they were born in the wild, of a younger age (range = 4.5–33.4 years old at the study mid-point), housed alongside a breeding female, or housed in a larger sized group (Fig. 2). Overall, the presence of a breeding female and birth origin were the two most important factors contributing to female calving success (see Supporting Information Table S7 for full GLMM results).

Factors mediating breeding behaviour, copulation and pregnancy across the questionnaire sample

Calving success across the questionnaire sample showed concordance with the studbook; of the 48 females in the questionnaire dataset, 21 (43.8%) successfully calved at least once. Additionally, 35 females (72.9%) were observed showing reproductive behaviour (remaining still for >5 seconds while a bull attempted to mount), 31 (64.6%) copulated and 23 (47.9%) became pregnant.

Mean group age (range = 8.13–1.2 years) was the most important factor contributing to female reproductive behaviour, while the presence of a breeding female was the main contributing factor to a female copulating or becoming pregnant (Fig. 2; see Supporting Information Table S8 for GLMM results). Females were more likely to exhibit reproductive behaviour, copulate and become pregnant if they were born in the wild or were housed with a breeding female (Fig. 2). Younger females (range = 4.5–32.9 years old at the study mid-point) were more likely to exhibit reproductive behaviour and copulate than older females, but were not more likely to become pregnant (Fig. 2). Females were also more likely to copulate and become pregnant if housed in a larger sized group (range = 2.0–8.4; Fig. 2).

Table 3 Sensitivity of EEP population growth to changes in parameter estimates

Parameter	Sensitivity to rate of increase[a]	Sensitivity to probability of a positive growth rate[b]	
		Model 1	Model 2
% of females calving annually	2.197 (1)	9.468 (1)	-
Infant mortality	−0.631 (2)	−2.376 (2)	−0.425 (3)
Adult mortality	−0.556 (3)	-	−0.600 (2)
Sub-adult mortality	−0.404 (4)	-	−0.624 (1)
Variation in % of females calving annually	0.102 (5)	−0.148 (4)	−0.090 (4)
Lethal equivalents	−0.025 (6)	−0.272 (3)	−0.056 (6)
Inbreeding coefficient (*F*)	−0.000 (7)	−0.022 (5)	0.086 (5)

Sensitivity ranks on absolute values are shown parenthetically. Negative values indicate a negative relationship between the parameter and response.

EEP, European Association of Zoos and Aquaria Ex-Situ Programme.

[a] Relative sensitivity to mean exponential rate of increase was determined by varying each parameter ±10% of its baseline value. Parameters with sensitivities >1 or <−1 have a disproportionate influence on population growth rate.

[b] Sensitivity to probability of a positive population growth rate was assessed using logistic regression models and standardized coefficients.

Discussion

Comparing data from 477 individuals across 83 captive institutions with 234 individuals across two wild populations, we demonstrate that the European captive population of southern white rhinoceros is performing far below its potential and is projected to decline at a rate of almost 2% per annum. On average, only 10% of females calve annually in the EEP population, compared to almost 40% across the two wild populations in Kenya. The low proportion of females calving annually is the key factor limiting population growth, though high infant mortality rates (22% for males and 23% for females) are also concerning. Recent improvements in the proportion of females calving annually (maximum 15% in 2020; Figure S1) are encouraging and, if that trend continues, the population may soon reach the level needed to achieve a self-sustaining population (17%). Our results suggest that several aspects of group composition are related to female reproductive success and breeding behaviour. In particular, institutions housing larger groups had proportionally greater breeding success, and females were more likely to copulate if housed with another breeding female, and more receptive to bulls if housed in a group with a lower mean age.

Only 38% of reproductive-age females in the EEP population have ever reproduced, in comparison to 98% across the wild populations, resulting in a severe reproductive skew. While the proportion of males siring offspring was also low (37%), male reproductive skew is more common in the wild (Guerier *et al*., 2012; Cain *et al*., 2013). This suggests that reproductive skew in females may be attributed to living in captivity, also identified as a key factor limiting reproduction in the EEP black rhinoceros population (Edwards *et al*., 2015).

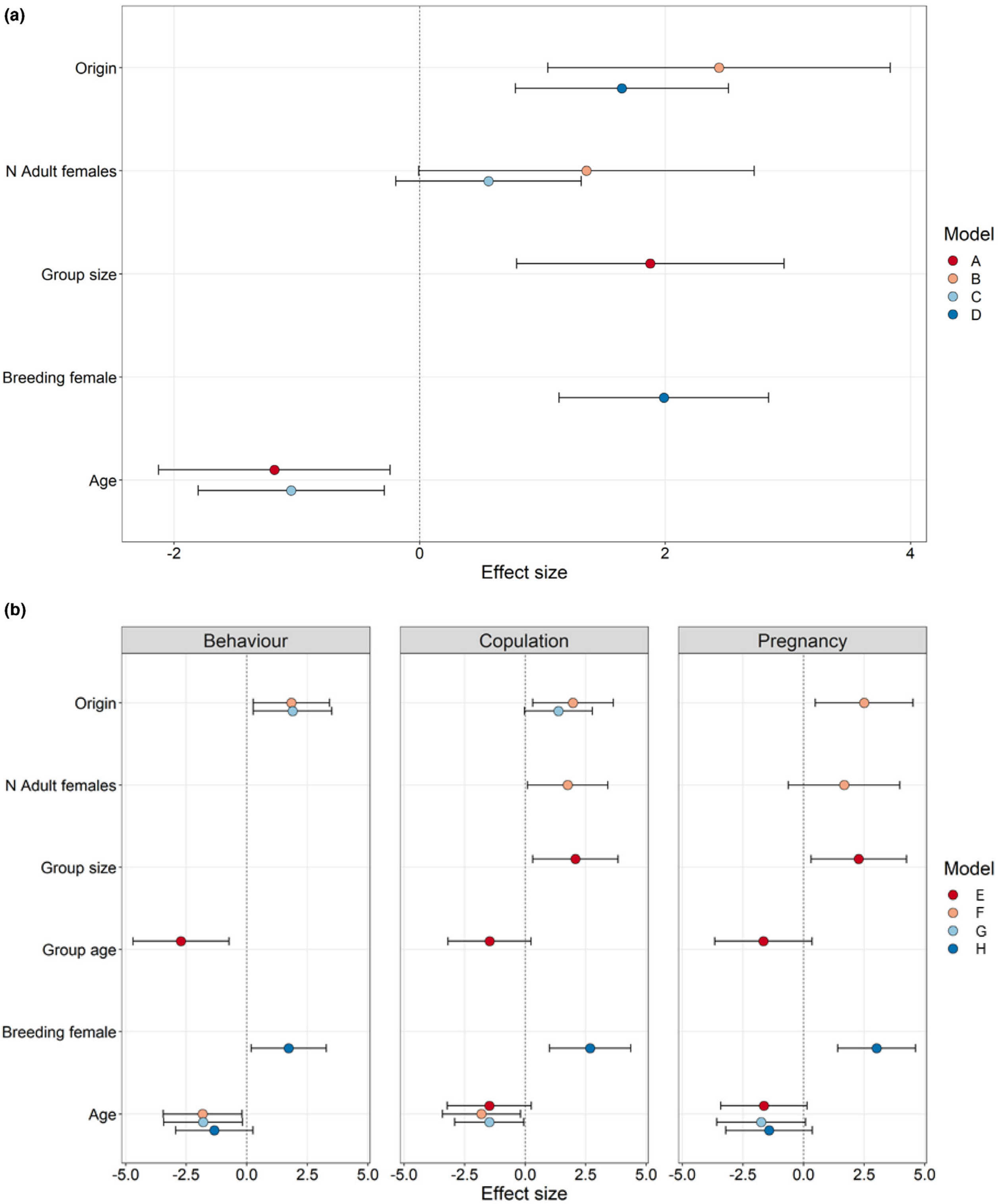

Figure 2 Average effect sizes (coefficient averages) and 95% confidence intervals for the averaged model predictors, with an RVI >0.5, used to explain (a) female calving success across the entire EEP, and (b) whether or not females exhibited reproductive behaviour, copulated, or became pregnant. Due to multicollinearity between predictor variables, a set of four models were run for each outcome variable, including only variables with VIFs <2 in the same model (predictors of the same colour). All predictors were standardized prior to analysis, making effect sizes comparable. See Tables S7 and S8 for model parameters. RIV, relative variable importance; VIF, variable inflation factor.

Management constraints in the captive environment may, to some extent, explain poor breeding success. Females are often housed separately from males, especially when they have a young calf (Metrione & Eyres, 2014), and therefore breeding opportunities may be missed. Additionally, introduction to a bull may be delayed if they are still in their natal herd, or an unrelated bull is not available. However, while these factors may explain why captive females have an older age at first reproduction (13.5 years old) compared to those in the wild (7.25 years old), they do not explain why so many females have never reproduced.

Our results suggest that differences in social conditions between institutions may account for the variation in white rhinoceros breeding success. Mean group size was the best predictor of institution breeding success, and the presence of another breeding female in the group significantly increased calving success, strongly suggesting female reproduction is socially facilitated. As most institutions currently house relatively small groups of white rhinoceros (mean = 4 across our sample), modifying groups to increase mean group size by 1–2 individuals would represent a substantial increase in group size (by 25% and 50% respectively) and could potentially increase the proportion of females calving at an institution by 23% and 41%, respectively, according to our results. However, enclosure size and density of individuals should first be carefully considered to ensure individuals have adequate space requirements.

In the wild, female white rhinoceros and dependent offspring often live in groups with several sub-adults (both male and female), occupying large home ranges that overlap with numerous other groups (Owen-Smith, 1975). While social relationships can last for over 5 months (Owen-Smith, 1975; Shrader & Owen-Smith, 2002), grouping patterns change periodically (Shrader & Owen-Smith, 2002; Metrione, Penfold, & Waring, 2007). In captivity, companionships regularly persist for several years, and individuals are kept in close proximity with limited opportunity to change associates (Metrione *et al*., 2007). Consequently, females in captivity may gain less social experience and develop stronger social bonds with fewer individuals than their counterparts in the wild.

Long-lasting social relationships can have demonstrable fitness implications for female mammals. Social familiarity has been shown to positively influence reproductive success in several other taxa (Grabowska-Zhang, Wilkin, & Sheldon, 2012; Martin & Shepherdson, 2012), and familiarity with social partners has been linked to reduced corticosterone metabolite levels in captive female white rhinoceros (Metrione & Harder, 2011). As rhinoceros are often transferred between institutions for breeding management purposes (Versteege, 2018), this may break important social bonds and have potential consequences on individual wellbeing and fitness. On the other hand, it could allow young females to leave their mother and socialize with other individuals, as would naturally occur in the wild when females chase away older offspring on the birth of a new calf. However, we found no discernible effect of number of transfers on female breeding success, possibly because the number of female transfers was relatively low (mean transfers per female = 1.4).

It is possible that the presence of other breeding females may stimulate reproduction. In captive female squirrel monkeys, *Saimbi sciureus*, the presence of social companions has been linked to more regular ovarian cycles and increased conception rates (Schiml *et al*., 1996), and in feral horses, *Equus ferus*, social bonds between unrelated females increase reproductive success (Cameron, Setsaas, & Linklater, 2009). This could also apply to white rhinoceros, as females have been observed to synchronize their oestrous cycles when they are closely 'bonded' (Brown *et al*., 2001).

Mate choice is also an important component of breeding success in captive animals. For instance, stripe-faced dunnart, *Sminthopsis macroura*, pairings based on female mate choice resulted in more pregnancies per oestrous cycle than those based on pedigree alone (Parrott, Nation, & Selwood, 2019). While we were unable to examine mate choice in our study, as most institutions in the EEP house just one adult male, it is possible that mate choice also influences female white rhinoceros breeding success.

Our results show that females born in the wild were more likely to exhibit reproductive behaviour and copulate than females born in captivity. Swaisgood *et al*. (2006) also found that females born in the wild were more likely to reproduce than those born in captivity, and suggest post-copulatory complications are likely the main cause of reproductive failure in captive-born females. However, deficiencies in socio-sexual behaviours may also play a role in the poor breeding success of female white rhinoceros, as 27% of reproductive-age females failed to exhibit reproductive behaviour when paired with a bull, and 35% never engaged in a mating event. Consequently, pre-copulatory complications should not be overlooked.

Age was also an important predictor of female breeding success. Both younger females, and females that were part of a group with a lower mean age, were more likely to exhibit reproductive behaviour than older females, or females that were housed in groups with a greater mean age. Furthermore, younger females were more likely to copulate and become pregnant than older females. Prolonged periods of reproductive inactivity have been linked to an increased incidence of reproductive pathologies and oestrous cycle irregularities in female white rhinoceros (Hermes *et al*., 2006), and thus older females that have not bred previously may have had more time to develop reproductive issues. As the ageing process of the female reproductive tract can be prevented by pregnancy (Hermes *et al*., 2006), stimulating breeding as early on as possible should be a priority of white rhinoceros captive breeding programmes. Our results suggest that housing females reaching sexual maturity alongside already breeding young females may help to stimulate reproduction.

The low proportion of individuals contributing to the gene pool is concerning. If captive white rhinoceros are to be used to supplement depleting populations in the wild, genetic erosion must be minimized (Ballou *et al*., 2010). The maintenance of genetic diversity is crucial for fitness and adaptive potential, and its loss reduces the probability of population persistence (Frankham, 2005). Captive breeding programmes aim to maintain a minimum of 90% of founder genetic diversity (Foose & Wiese, 2006), yet our PVA predicts the EEP reproducing sub-population of white rhinoceros can maintain just 63% of its genetic diversity after 100 years. Furthermore, genetic relatedness is likely higher than current estimates, which assume EEP founders were unrelated (i.e., assigning $F = 0$ to founders; Reid *et al.*, 2012). Assuming founders are unrelated is an unrealistic assumption for endangered species (Ruiz-López *et al.*, 2009); wild white rhinoceros populations are typically characterized by very low genetic diversity due to a severe population bottleneck in the late 1800's (Coutts & Rachlow, 2009; Guerier *et al.*, 2012). Low genetic diversity and inbreeding could therefore explain the high infant mortality rate in the captive population in comparison to the wild populations (22% and 8%, respectively).

While establishing infant mortality rates in the wild is often difficult due to the number of stillbirths and neonatal deaths that go unrecorded, the two populations in Kenya used in this study are so intensively monitored (each rhino must be sighted at least every 4 days) that any calf mortality post-birth would very likely be recorded. Inbreeding depression has been documented in several other species in captivity, including increased infant mortality in cheetahs, *Acinonyx jubatus* (O'Brien *et al.*, 1985), and reduced infant growth in Indian rhinoceros, *Rhinoceros unicornis* (Zschokke & Baur, 2002).

Our study suggests the European captive white rhinoceros population is not currently self-sustaining and that their poor reproductive performance may be linked to the captive environment. The proportion of females calving annually must increase to a minimum of 17% to improve the future viability of the population, and our results suggest this may be achieved by modifying social conditions. In particular, group size and age structure should be carefully considered, and where possible, housing sexually mature females alongside those already breeding may help to stimulate socio-sexual behaviours and reproduction. However, meeting these social requirements will be difficult for many institutions, and our findings highlight the potential conflict between the biological requirements of large, social species and what is feasible for captive conservation management. Future studies should focus on understanding female socio-sexual behaviours and oestrous cycles in captivity, and how natural grouping patterns in the wild influence female reproduction, to provide further guidance on the breeding management of captive white rhinoceros. The results of this study demonstrate the importance of considering the social environment in captive breeding programmes, and are likely relevant to the management of other species with complex social systems and low reproductive rates.

Author contributions

SES, CMB, SRdK and BC conceived the ideas and designed methodology; SES collected and analysed the data; SES led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information

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

Appendix S1. Table S1. The demographic parameters and established benchmarks used to assess the reproductive performance of the EEP white rhinoceros population. Established benchmarks are based on those produced by the SADC rhino management group (du Toit *et al.*, 2006).

Table S2. The baseline parameters applied in Vortex to model the viability of the European captive white rhinoceros population over 100 simulated years.

Table S3. The baseline parameter values and range tested in the global sensitivity analyses.

Table S4. Summary of all variables included in the analyses. Reproductive-age females were defined as females >8 and <34 years old on 31/12/16, or females that calved during the study period (01/01/12–31/12/16).

Table S5. The mean population growth rate, final population size and remaining genetic diversity, for the EEP population after 100 simulated years. SD represents the standard deviation.

Table S6. The quasi-binomial GLM predictors and top model output used to explain variation in the proportion of females that calved at each EEP institution between 2012 and 2016. For all models Group Size was Log_{10} transformed, Group Age was $\sqrt{}$ transformed, and Adult Female Group Size was $\sqrt[3]{}$ transformed. R^2 denotes the pseudo-R^2 value. AICc values were obtained from models without the quasi-binomial distribution. Only variables in the final reduced models are reported in the top model outputs.

Table S7. Averaged model parameters explaining calving success in captive female white rhinoceros in the EEP studbook. For all GLMM models, Age and Group Size were Log_{10} transformed, Group Age was $\sqrt{}$ transformed, and Breeding Females was $\sqrt[3]{}$ transformed. Institution was included as a random effect in all models. The mean AICc and range, for models with a ΔAIC <2, coefficient estimate, standard error, lower and upper confidence intervals, and relative variable importance (RVI) for each variable, are provided for each averaged set of models. Model outputs are only reported for variables in the final averaged model.

Table S8. Averaged model parameters explaining reproductive behaviour, copulation and pregnancy success in the female white rhinoceros included in the questionnaire dataset. For all GLMM models, Age was Log_{10} transformed, Crash size was $\sqrt{}$ transformed, Enclosure size was $\sqrt[3]{}$ transformed, and institution was included as a random effect. The mean AICc and range, for the models with a ΔAIC <2, coefficient estimate, standard error, lower and upper confidence intervals, and relative variable importance (RVI) for each variable are provided for each averaged set of models. Model outputs are only reported for variables in the final averaged model.

Figure S1. Annual proportion of females calving (line) and number of calves born (bar) in the European captive white rhinoceros population.

Appendix S2. Questionnaire survey questions.