

*Int. Zoo Yb.* (2012) **46**: 209–220  
DOI:10.1111/j.1748-1090.2011.00164.x

## Analysis of the European captive Southern white rhinoceros *Ceratotherium simum simum* population using the *International Studbook for the African White Rhinoceros* (2001–2004) and integrating reproductive health findings

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The goal of *ex situ* conservation is to maintain genetic diversity, avoid inbreeding and maximize equal representation of founder individuals. Analysis of a well-maintained studbook yields important data concerning fertility and mortality that is invaluable to *ex situ* conservation. To evaluate the reproductive status of the European captive Southern white rhinoceros *Ceratotherium simum simum* population, basic demographics and population parameters were calculated using the *International Studbook for the African White Rhinoceros Ceratotherium simum* (2001–2004) data with the integration of recent scientific findings regarding reproductive health of individuals within the 'reproductive age'. Kinship analysis of the 2001–2004 population was also performed to evaluate genetic diversity. Results indicated the population is declining 1.19 times faster than it is growing. To realize a 1% population increase at the 2001–2004 death rate, reproduction would have to increase by 214%. It is necessary to increase the genetically contributing subpopulation and to achieve a reproduction capacity that surpasses the rate currently possible with natural mating.

*Key-words:* genetic diversity; population analysis; relationship coefficients; reproduction; white rhinoceros.

### INTRODUCTION

All five rhinoceros species are highly threatened and are listed on *The IUCN Red List of Threatened Species* (Baillie *et al.*, 2004;

IUCN, 2010). Declining natural habitats resulting from human encroachment and the ensuing human–animal conflicts, as well as political unrest and corruption, civil wars, failed conservation efforts and poaching of rhinoceros species and sub-species, have already led to the extinction of several sub-species, such as the Sumatran rhinoceros subspecies *Dicerorhinus sumatrensis lasiotis*, the Javan rhinoceros subspecies *Rhinoceros sondaicus inermis* and the 'western' black rhinoceros subspecies *Diceros bicornis longipes* (IUCN, 2010; see also IUCN, 2006). The Northern white rhinoceros *Ceratotherium simum cottoni* is the most threatened white rhinoceros species in the Africa with a remaining wild population of only three or four animals and, therefore, is considered demographically extinct (De Merode *et al.*, 2005; Amin *et al.*, 2006; see also IUCN, 2008). It is highly likely that in the next few decades many of the rhinoceros species and subspecies will only exist in captivity. In the early 1900s, the Southern white rhinoceros *Ceratotherium simum simum* experienced a severe bottleneck of c. 10–20 individuals and extensive *in situ*

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conservation efforts have lead to a substantial increase in the wild population (Merenlender *et al.*, 1989; Kingdon, 1997; Braude & Templeton, 2009). Although still considered highly threatened, it is consequently the largest wild population of any rhinoceros species and the most common rhinoceros species in captivity (IUCN, 2008).

Traditionally, species conservation efforts have been focused *in situ* and involve reducing mortality rates through habitat conservation and prevention of poaching. However, for several threatened species, including those in Africa, *in situ* conservation activities alone are insufficient to safeguard the future of the species owing to the extremely low numbers of individuals in wild populations and limited access to these populations because of civil unrest and war. This has lead to the inclusion of *ex situ* conservation with a focus that is more geared to increasing population numbers through captive propagation while maintaining genetic diversity, avoiding inbreeding and maximizing equal representation of founder individuals (Ballou & Lacy, 1995; Hedrick, 2005). Zoos in particular recognize their potential to contribute to *ex situ* conservation through the long-term propagation of threatened species in captivity; that is, inter-institutional breeding programmes (Ballou & Foose, 1996). Specifically for the Southern white rhinoceros, zoos attempt to establish breeding protocols that can be applied at least to the Northern white rhinoceros species, in addition to studying fertility and variables that affect fertility and reproduction. Unfortunately, this too is limited for the Southern and Northern white rhinoceros as current populations in captivity are as threatened as their wild counterparts mostly owing to a high rate of premature reproductive pathology and cycle disorders reducing the number of ♀ reproductive candidates (Hermes *et al.*, 2006). As a result of this low number of reproducing individuals in captivity, the genetic diversity potential of captive populations is similarly threatened. Consequently, the use of artificial reproductive techniques (ART) have become increasingly significant

for the success of *ex situ* conservation, the management of genetic diversity and, in some cases, the establishment of self-sustaining captive populations, all of which are paramount for the survival of the white rhinoceros species.

The most important component of captive-breeding programmes involved in *ex situ* conservation is reliable and accurate basic population data. The best source of compiled data is a studbook, which is a chronology of a captive population listing vital information on animal identities, sexes, parentage, and birth and death dates, as well as information on animal movements between institutions and between *in situ* and *ex situ* populations (Glatston, 1986; Hutchins & Wiese, 1991; Ballou & Foose, 1996). A well-managed studbook is imperative for the establishment and long-term management of captive populations so they can fulfil their specific conservation goals. Analysis of the studbook provides an insight into the genetic diversity and demographic stability of a population. It also yields invaluable data on patterns of fertility and mortality occurring under the prevalent management conditions. This information is equally relevant to conservation research and to captive management (Glatston, 2001).

Using studbook data combined with current scientific findings to perform a comprehensive analysis could provide valuable data for *ex situ* conservation and, in turn, species conservation. To evaluate clearly the reproductive status of the Southern white rhinoceros population in captivity in Europe, a basic evaluation of the *International Studbook for the African White Rhinoceros* *Ceratotherium simum* (2001–2004) (Ochs, 2005) was performed with the integration of recent scientific findings regarding reproductive health of individuals within the reproductive age. In addition, kinship analysis of the European Endangered Species Programme (EEP) white rhinoceros population (2001–2004) (Versteeg, 2007) was evaluated in order to determine genetic diversity, which is extremely important for *ex situ* species conservation.

## METHODS AND MATERIALS

### Studbook analysis

*International Studbook for the African White Rhinoceros* *Ceratotherium simum* (2001–2004) (Ochs, 2005) was used as a pedigree and data source to calculate population demographics and several population parameters. The 2001–2004 studbook was chosen because the time period coincides with the reproductive health assessment performed by Hermes *et al.* (2006). With the information available, age standardized ‘net reproductive rates’ [defined as:  $R_0 = \sum l_x f_x$ ; where ( $l_x$ ), the proportion of ♀♀ surviving to each age ( $x$ ), is multiplied by ( $f_x$ ), the average number of offspring produced at each age ( $x$ ), and then adding the products from all the age groups] and simplified age-standardized ‘death rates’ [defined as:  $M_0 = (\sum m_x/P_x) \times 1000$ ; where  $m_x$  is the total number of deaths for age ( $x$ ) and ( $P_x$ ) is the proportion of the population at age ( $x$ ), and then adding the results from all age groups and multiplying by 1000] could not be calculated because of the large percentage of wild-caught individuals whose age is unknown (Siegel *et al.*, 1976). Therefore, crude birth rates and crude death rates were calculated (defined below) for the EEP white rhinoceros population 2001–2004.

### Calculations

*Crude death rate:* [total number of deaths ( $n = 34$ )/total living population ( $n = 240$ )]

*Crude birth rate:* [total number of births ( $n = 17$ )/total living population ( $n = 240$ )]

*Calculated reproductive productivity for ♀♀ and ♂♂:* [total number of successful ♀ breeders ( $n = 22$ ) or ♂ breeders ( $n = 21$ )/total number of individuals within the breeding age ( $n = 70$  ♀♀;  $n = 93$  ♂♂)]

*Per cent of nulliparous ♀♀:* [total number of post-pubescent non-reproducing ♀♀ ( $n = 79$ )/total number of post-pubescent ♀♀ ( $n = 115$ )]

### Genetic analysis

Genetic diversity calculations, such as effective population size ( $N_e$ ) [using the method of Falconer (1982)], effective number of ancestors ( $f_a$ ) [using the method of Boichard *et al.* (1997)] and founder genome equivalents ( $N_g$ ; aka effective number of founder genomes) [using the method of Hagger (2005)], were not mathematically possible to perform for several reasons; the first, because of the low percentage of known ancestors for the current reference population (1.22%). This means that 98.4% of the founder generation (F0) have no known ancestry, unknown age and/or unknown parents. Second and consequently, it is because of the low quality of the studbook data as a pedigree [generation coefficient =  $1.71 \times 10^{105}$ , practically 0; calculated with the method of Hagger (2005)]. Therefore, the genetic analysis of the EEP white rhinoceros population was performed by employing Sewall Wright’s ‘Coefficients of Inbreeding and Relationship’ (Wright 1922) ( $r = 0$  for unknown relations,  $r = 0.5$  parent–offspring and full siblings;  $r = 0.25$  grandparent–grandchild and half siblings;  $r = 0.125$  great grandparent–great grandchild) (Figs 1–3). The individual coefficients were summed up for different groups. This sum represents the genetic diversity score of the particular group or individual. Using the sum of coefficients allows for the mathematical inclusion of 0 values for unknowns, which is not possible with the previously mentioned equations.

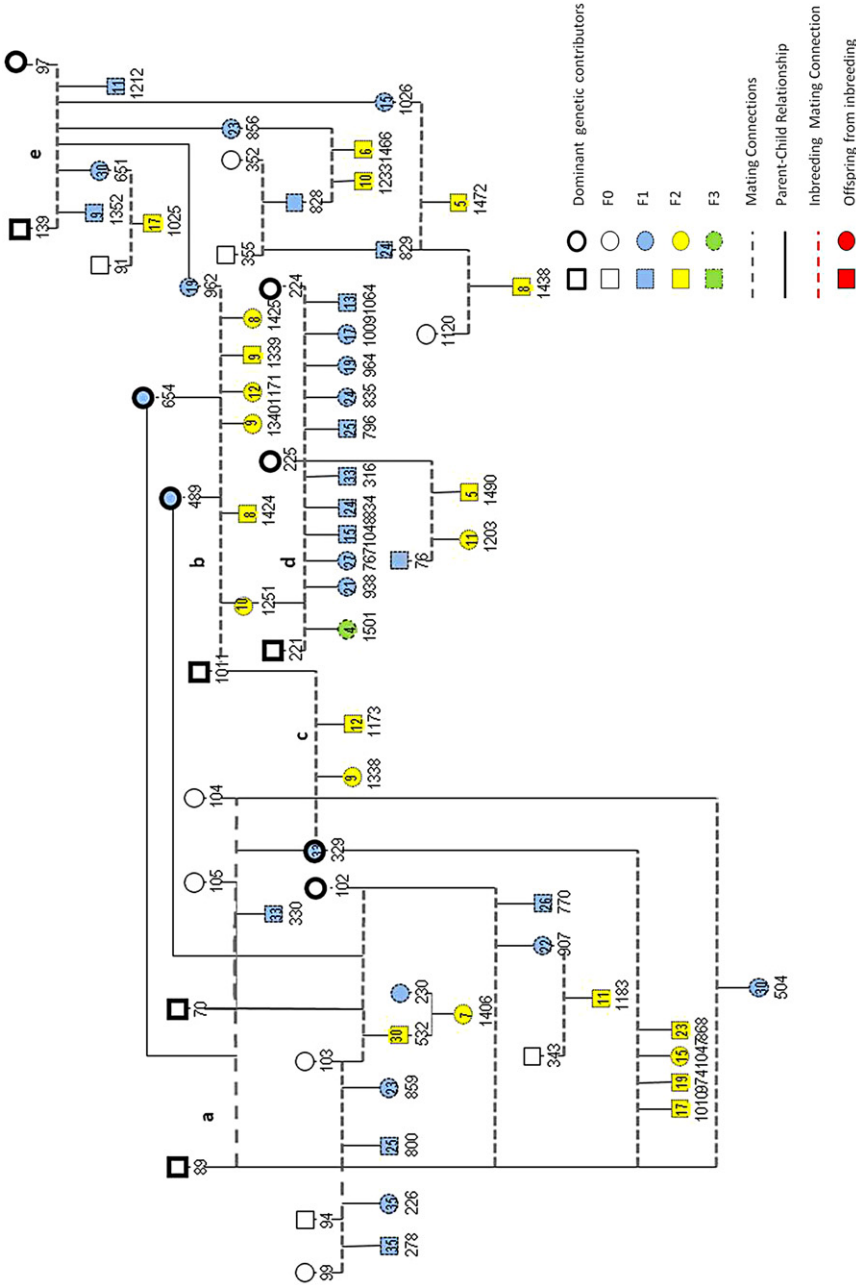
### Calculation of $r$

*Genetic score:*  $r = \sum [\text{relationship coefficient}^{(\sum \text{of respective relationships})}]$

## RESULTS

### Demographics

The total EEP Southern white rhinoceros population for the 2001–2004 time period consists of 240 (105.135: ♂♂.♀♀) of which 119 (59.60) were captive born and 121 (46.75)



**Fig. 1.** Family tree of the largest rhinoceros family represented in the European Endangered Species Programme Southern white rhinoceros *Ceratotherium simum simum* population. The dominant ♂ genetic contributors are 89, 1011, 221, 70, 491 (see Fig. 3) and 139. Dominant ♀ genetic contributors are 225, 224, 102, 329, 489, 654, 494 (see Fig. 3), 496 (see Fig. 3) and 97. Grey lines indicate mating connections. Black lines indicate parent-child relationships. Squares represent ♂ and circles represent ♀. Known ages of individuals are with indicated within and individual identification numbers are listed under the respective square or circle. Letters a, b, c, d, e indicate major connecting links between family lines. White fill-in colour indicates F0 generation, blue fill-in colour represents the F1 generation, yellow fill-in colour represents the F2 generation.

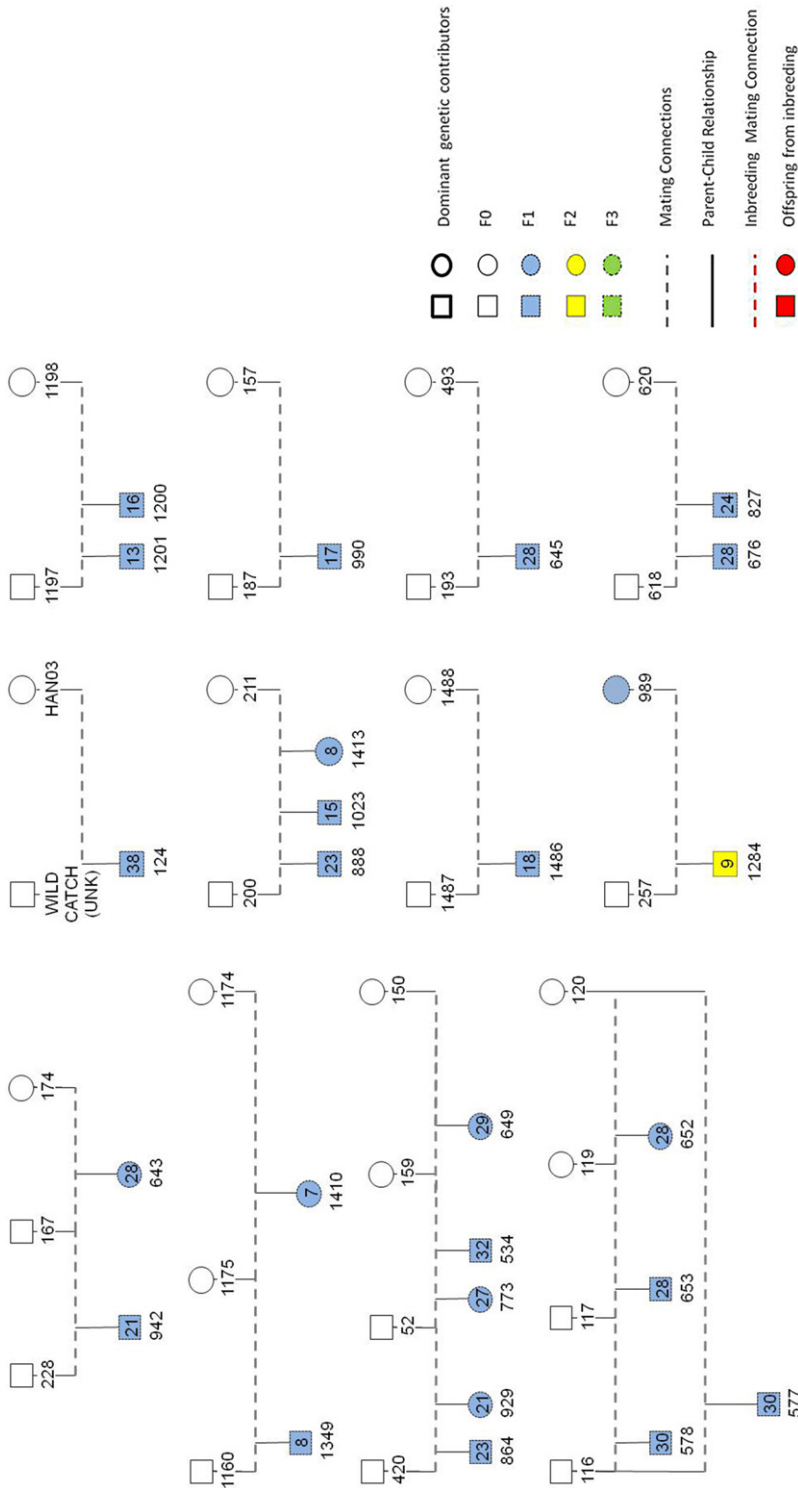
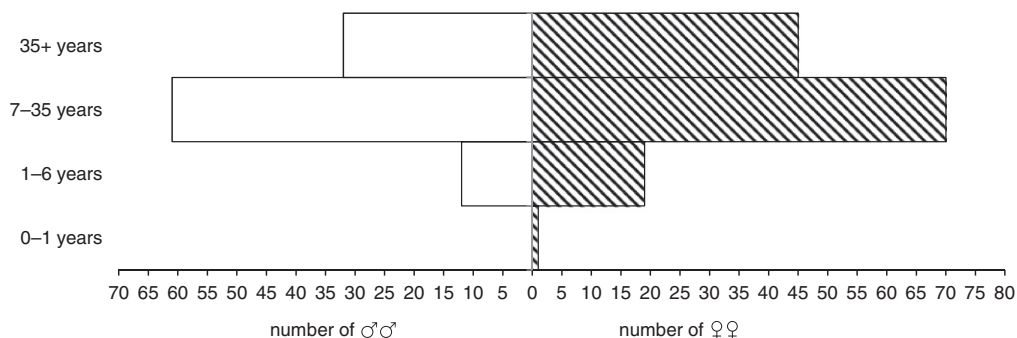


Fig. 2. Single-branch family trees represented in the European Endangered Species Programme Southern white rhinoceros *Ceratotherium simum simum* population. Grey lines indicate mating connections. Black lines indicate parent-child relationship. Squares represent ♂♂ and circles represent ♀♀. Known ages of individuals are with indicated within and individual identification numbers are listed under the respective square or circle. White fill-in colour indicates F0 generation, blue fill-in colour represents F1 generation, and yellow fill-in colour represents F2 generation. 989's parents are unknown although she was born in captivity.





**Fig. 4.** Population pyramid illustrating the skewed age distribution of the European Endangered Species Programme 2001–2004 Southern white rhinoceros *Ceratotherium simum simum* population and highlighting the dramatically under-represented juvenile and infant population, and the large portion of the population that is aging and soon to be exiting the breeding population.

were imported from wild populations. The average age is 23.7 years. The crude death rate for the 4 year period is 14% and crude birth rate is 7% for this period. The average age of the ♂ population is 24.2 years. The average age of the ♀ population is 23.4 years with an age distribution of one infant ( $\leq 1$  years), 19 prepubescent juveniles (1–6 years), 70 within reproductive age (7–35 years) and 45 post-reproductive ( $>35$  years) (Fig. 4). Only 57 (21.36) of the 2001–2004 post-pubescent living population ( $n = 208$ ; 93.115) have successfully bred at least once. This figure theoretically represents the genetic effective population ( $N_e = 57$ ) of the total population based solely on age and reproductive success data. It also includes 14 ♀♀ that were previously but are no longer within the reproductive age. The 2001–2004 reproductive-age subpopulation, as defined by age (♀♀  $\geq 7$ –35 years old, ♂♂  $\geq 5$  years old), includes 163 (93.70) out of 240 with an average age of 17.5 years, 43 of which have bred at least once (21.22) resulting in  $N_e = 43$  for this breeding subpopulation; again, this is a theoretical figure and not a calculated value with statistical relevance.

### Calculated parameters

The calculated reproductive productivity score of 31.4% for the 2001–2004 reproductive-aged ♀ subpopulation and 22.5% for

the reproductive-aged ♂ subpopulation. This figure only includes births entered in the stud-book. The average age at first pregnancy is 8.6 years and there is an intra-calving interval of 2.35 years (this figure is based on only the few multiparous ♀♀ in the 2001–2004 EEP Southern white rhinoceros population).

### Inclusions of reproductive health data

In addition, Hermes *et al.* (2006) examined *c.* 35.7% ( $n = 25$ ) of the total EEP Southern white rhinoceros reproductive-aged ♀ subpopulation ( $n = 70$ ) and thereby discovered that 76% ( $n = 19$ ) had reproductive pathology and 84% ( $n = 21$ ) had oestrous acyclicity, thus potentially requiring reproductive assistance to reproduce successfully; and six ♀♀ within the breeding age (*c.* 24%) were confirmed with ultrasound as being incapable of reproducing owing to the severity of reproductive pathology.

### Diversity analysis

The 121 individuals (46.75) defined as the 2001–2004 founder population (F0) are wild-caught individuals, most with no known ancestry or genetic relationship to one another. However, only 35 (14.21) of these individuals have reproduced (i.e. contributed genetically to the 2001–2004 population).

	NUMBER OF EVENTS	<i>r</i>
Parent–offspring	154	4.379E-47
Full siblings	7	7.813E-03
Grandparent–child	39	3.309E-24
Half siblings	7	6.104E-05
Great-grandparent–child	6	3.815E-06
		0.0078773499

**Table 1.** Relationship coefficients (*r*) calculated for the 2001–2004 European captive Southern white rhinoceros *Ceratotherium simum simum*.

	NUMBER OF EVENTS	<i>r</i>
Parent	207	4.86E-63
Children	212	1.52E-64
Grandparent	64	5.42101E-20
Grandchild	64	5.42101E-20
Great grandparent	4	2.44E-04
Great grandchildren	2	1.56E-02
Full siblings	166	1.07E-50
Half siblings	388	2.52E-234
		0.015869141

**Table 2.** Relationship coefficients (*r*) calculated for the 2001–2004 European captive Southern white rhinoceros *Ceratotherium simum simum*. Pedigree includes all genetically contributing individuals of the current living European populations 2001–2004 (deceased and post-reproductive individuals are included in this figure).

Furthermore, 62% of the entire captive-born offspring (74 out of 119 individuals) originate from the same 15 (6.9) individuals. The analysis demonstrates that only a few diverse familiar genes are represented in the F1 ( $n = 89$ ), F2 ( $n = 28$ ) and F3 ( $n = 2$ ) generations. The reproductive-age subpopulation had a genetic score of  $r = 0.688$ . The entire EEP Southern white rhinoceros population had a genetic score of  $r = 0.0078$  (Table 1). The genetic score for the pedigree ( $n = 173$ ; eliminating 55 genetically non-contributing wild-caught individuals and 12 captive-born with unknown parents, but still includes deceased or no longer reproductive individuals) is  $r = 0.0158$  (Tables 2 and 3).

## CONCLUSIONS

The analysis of the *International Studbook for the African White Rhinoceros* *Ceratotherium simum* (2001–2004) (Ochs, 2005) reveals very disturbing details. Applying the findings of Hermes *et al.* (2006), using the large study group as a representative study population for the 2001–2004 EEP Southern white rhinoceros population, to the analysis of the studbook, it is determined that only 53 of the 70 reproductive-aged ♀♀ are available for reproduction owing to the predicted loss of 24% of the population because of premature reproductive senescence. Of the 53 remaining predicted reproductively available ♀♀, 28–31 individuals may still require some reproductive assistance because of the high rate of reproductive pathology present in nulliparous ♀♀ over 15 years of age. This figure is based on the number of nulliparous ♀♀ in the representative study population ( $n = 17$ ), 76% and 84% of which have severe pathology and cycle disorders, respectively, interfering with natural mating success and reproductive productivity (pathology  $n = 13$ , 52% of total study population; cycle disorders  $n = 14$ , 57% of total study population). The resulting percentages for the total study population (52%, 57%) were then applied to the number of ♀♀ calculate above to be reproductively available ( $n = 53$ ). The accuracy of these estimates is supported by the fact that the percentage of nulliparous ♀♀ in the study population is 68% (Hermes *et al.*, 2006), which is similar to that calculated for the 2001–2004 EEP Southern white rhinoceros population, 68.6% ( $n = 79$  out of 115; prepubescent individuals were removed) and for the reproductive-aged subpopulation, 69% ( $n = 49$  out of 71).

After applying the calculated reproductive ♀ productivity of 31.4% and inter-calving interval of 2.35 years to the predicted 53 reproductively available ♀♀, it is predicted that 16.64 births per 2.35 years (or 7.08 births per year) for the next 4 year period. After applying the previously calculated crude death rate (8.4 deaths per year), it is easy to see that the population is declining almost



	FEMALES	MALES	TOTALS
	≥7–<36 YEARS	>5 YEARS	
Full sibling	3.125E-02	1.250E-01	1.563E-01
Grandparent	2.500E-01	5.960E-08	2.500E-01
Parent	1.776E-15	1.084E-19	1.776E-15
Half sibling	2.441E-04	2.500E-01	2.502E-01
Great grandparent	1.000E+00	1.953E-03	1.002E+00

**Table 3.** Relationship coefficients ( $r$ ) calculated for the 2001–2004 European captive Southern white rhinoceros *Ceratotherium simum simum*. Reproductive-aged population is defined as ♀♀ ≥7 years and <36 years of age; ♂♂ >5 years of age.

1.19 times faster than it is growing. To maintain the 2001–2004 population size, it is necessary to at least have a crude birth rate equal to the crude death rate. To even realize a 1% population increase over a 4 year period at the 2001–2004 crude death rate, the crude birth rate would have to be increased by 214%. However, in order to achieve self-sustainability, it has been demonstrated in studies with wild horses, the evolutionary relative of the rhinoceros, that a reproducing subpopulation (i.e. the genetically contributing portion of the population theoretically defined as  $N_e$ ) of 30–35% of the total population is necessary. In other words, a total population size of 240 would require a minimum ‘genetic effective population size ( $N_e$ )’ of 72 (Coates-Markle, 2000). The 2001–2004 EEP Southern white rhinoceros population has a theoretical  $N_e$  of only 43. Over the next 4 years, ten ♀♀ will age out of the ‘reproductive-age’ subpopulation of which three are proven breeders (genetically contributing members), thus reducing the  $N_e$  to 40. On the other side, 27 individuals (9.18) will age into the reproductive-age subpopulation potentially contributing to the  $N_e$ , although even if all new entering members contributed genetically, the population would still be shy of the minimum required  $N_e$  for self-sustainability. In the end, it is not only necessary to increase the genetically contributing subpopulation but also to achieve a crude reproductive rate that surpasses the rate currently possible with natural mating. ART could be used to satisfy one of the goals of *ex*

*situ* conservation efforts, namely establishing a self-sustaining captive population.

The Northern white rhinoceros *C. s. cottoni* captive population is as demographically extinct as the wild population, with only eight (3.5) animals remaining (J. Christman, International Studbook Keeper, pers. comm.). Since the publication of the 2001–2004 white rhinoceros studbook, four (1.3) individuals have died. Hermes *et al.* (2006) examined six of the seven ♀♀ from the global captive *C. s. cottoni* population, and all but two had severe pathology and are considered unavailable for reproduction. The tragic situation in the Northern white rhinoceros population is evident without analysis. It is obvious that the captive population is on the brink of extinction and there is no possibility of replenishing with wild-caught animals because the wild population is made up of only four animals at best estimate (a mother with calf, a suspected breeding ♂ and a single ♂ sighted during aerial surveillance: Amin *et al.*, 2006). The future for the Northern white rhinoceros is grim.

Maintaining genetic diversity is a primary population-management goal for long-term *ex situ* conservation. Management approaches for genetic diversity aim to minimize changes in the genetic constitution of the population while in captivity so that if and when the opportunity arises for animals to be reintroduced into the wild, they will represent, as closely as possible, the genetic characteristics of their wild counterparts (Hedrick *et al.*, 1986; Lacy *et al.*, 1995). Genetic variation is

also the basis for adaptive evolution and must be retained to maintain the population's potential to adapt to the ever-changing environment (Ballou & Foose, 1996). The low number of available and successfully reproducing individuals brings the genetic diversity of the EEP Southern white rhinoceros population into question. It is generally accepted that a higher rate of genetic heterogeneity is directly associated with, and even necessary, for individual fitness (Jimenez *et al.*, 1994; Frankham & Ralls, 1998; Keller, 1998). The genetic score of  $r = 0.688$  for the breeding subpopulation indicates a dangerously higher rate of genetic similarity ( $r = 0.5$  indicates immediate family relationship, such as full siblings and parent-child) compared with the entire captive population, which has a genetic score of  $r = 0.0078$ ; however, this figure is skewed owing to the large number of unknowns that were scored as no relationship, and because non-contributing wild-caught individuals were also scored as 0, which more than likely grossly underestimates the genetic similarity of wild-caught individuals. The true genetic relationship of wild-caught individuals is not well known and the bottleneck of the 1900s suggests that there is a high rate of genetic similarity. Microsatellite studies are needed to determine more accurately the genetic heterogeneity of the wild-caught subpopulation within the EEP Southern white rhinoceros population. Even so, this could indicate that there is a genetic component to consider when examining reproductive success in the captive rhinoceros. The need to expand the genetic diversity by incorporating under- and non-represented individuals or novel familiar gene lines in breeding programmes is clear.

The analysis itself, as well as the predictions made through the analysis, are supported by 1995–2007 EEP *Ceratotherium simum* population analysis report in Part 4 of the *European White Rhinoceros Studbook* (Versteegen, 2007). In this report, the stability of the absolute numbers of EEP Southern white rhinoceros population is attributed solely to importing wild animals to combat deaths and lack of births. With the exception

of 1998, 2000 and 2005, year after year, there is an unfortunate trend of more deaths than births; and the high crude death rate is expected at least to continue if not increase because of the large percentage (30%) of elderly individuals (>35 years of age) in the EEP Southern white rhinoceros population. Furthermore, Versteegen (2007) also highlights the low reproductive productivity and crude birth rate of the EEP Southern white rhinoceros population, especially within the F1 generation. Out of 274 F1 generation members, only 13% ( $n = 35$ , 14.21) have successfully bred the majority of which were ♀. Similarly, only 26% ( $n = 70$ , 27.43) of the total 269 wild imports have bred. It must be stated that these figures are skewed by the inclusion of historic data, which does not reflect the recent increase in captive-breeding success as a result of the advancements made by zoos in the area of reproduction and husbandry; although, removing the dated data and limiting the data pool to the last 12 years does not improve the situation. From 1995 to 2007, Versteegen (2007) reports that eight out of 36 breeding wild-caught individuals are responsible for a reproductive productivity of 22%. Versteegen (2007) further reports that the 12 imports from 2000 have not bred.

Continually, Versteegen (2007) lists the 12 highest ♂ and ♀ reproducers, seven of the ♀♀ and six of the ♂♂ on the list are also the highest genetic contributors to the 2001–2004 EEP Southern white rhinoceros population illustrating the risk of endangering the genetic diversity. Fortunately, according to this report, the majority of births from 1995 to 2007 ( $n = 80$ ) are occurring as a result of wild-caught–F1 generation unions ( $n = 38$ ) or wild-caught–wild-caught unions ( $n = 27$ ) rather than F1–F1 unions ( $n = 15$ ), which has attributed to maintaining the low genetic score ( $r = 0.0078$ ) of the entire population.

It is apparent that the goal of self-sustainability is far from reach. However, zoological institutions are major contributors to the conservation of threatened species through *ex situ* conservation programmes. Their commitment is seen in the cooperative captive-breeding programmes based on

sound genetic principles. The essence of any *ex situ* conservation programme is the identification of genetically valuable animals to be bred, how often and with whom they are to breed with. Therefore, cooperation regarding reporting among zoos, maintenance of reliable, accurate studbooks and analysis of the data are imperative for reaching conservation goals. Ultimately, regular updating of the international studbook (Frese, 2009), and combining *in situ* and *ex situ* conservation strategies should be considered for implementing a comprehensive conservation plan for all the rhinoceros species globally.

Lastly, the reproductive technology and genetic management is expanding rapidly. Considering the current threatened status of all rhinoceros species and the low reproductive success specifically of captive white rhinoceros species, some type of intervention is needed to preserve this species while maintaining the highest possible genetic diversity. These species have a long gestational period that makes population recovery more difficult. In captivity, it is important to overcome additional obstacles, such as distance between genetically valuable reproductive pairs and reproductive pathology of genetically valuable individuals. For these reasons, the use of ART has become increasingly more important for *ex situ* species conservation. ART, and specifically the use of cryopreserved semen, allows for the use of genetic material without the need for mating encounters, which can be dangerous owing to high risk of transportation and communicable disease, and which are often ultimately unsuccessful because of pairing incompatibility. The importation of new genes from free-ranging individuals without the need to import individuals is also possible, thus accommodating the need for incorporating novel familiar gene lines. In addition, the use of genetic material after the death of non- or under-represented individuals is also possible with ART; thus facilitating population recovery, maintaining genetic diversity and, ultimately, sustainability. However, the cost of ART is often a limiting factor and the success of ART is greatly

reduced by the same reproductive pathology that it is used to overcome. The biggest disadvantage of ART is the lack of understanding of how these techniques will work in wildlife species, especially as natural reproduction is not always completely understood.

#### ACKNOWLEDGEMENTS

We would like to thank the Stipendium des Abgeordnetenshaus Berlins for the financial support, and Dr Andreas Ochs and the Berlin Zoo for the preparation and maintenance of the White Rhinoceros Studbook.

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Manuscript submitted 7 October 2010;  
revised 2 August 2011; accepted 1 November 2011