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Population management of rhinoceros in captivity

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Captive-breeding programmes are important components of conservation strategies for rhinoceros. Rhinoceros in zoos can serve as (1) genetic and demographic reservoirs to reinforce wild populations as the need and opportunity occur, and (2) ambassadors to increase public awareness and support, especially financial, for conservation of wild populations. However, for these functions, rhinoceros in captivity must be managed scientifically and co-operatively to produce viable populations. Population-management programmes for Black rhinoceros *Diceros bicornis,* White rhinoceros *Ceratotherium simum* and Indian rhinoceros *Rhinoceros unicornis* are operating in various regions of the zoo world, especially North America [Species Survival Plans (SSP)] and Europe [European Endangered Species Programmes (EEP)]. Analyses indicate that rhinoceros populations in captivity are achieving variable levels of viability. In SSP and EEP populations Black rhinoceros and White rhinoceros are genetically but not demographically satisfactory, while Indian rhinoceros is healthy demographically but limited genetically. Improvement is needed and could be achieved through better management.

Key-words: breeding, captive, co-operative, demographic, genetic, management, population, rhinoceros, viable

Captive-breeding or propagation programmes are considered an important and sometimes integral component of conservation strategies for threatened species (Foose, 1983; WAZA, 2005). Successful breeding programmes in captivity require that populations are scientifically and co-operatively managed. The Rhinocerotidae is one of the most threatened families of mammals and needs support from captive-breeding (Foose & van Strien, 1997; Emslie & Brooks, 1999). Hence, rhinoceros were among the first of the taxa selected for scientifically and co-operatively managed breeding programmes at both the regional and global level (Foose, 1983). Because of the difficulties and uncertainties of protecting rhinoceros in the wild (e.g. the increases in poaching in Nepal and parts of Africa in 2003–2005; see also Amin, Thomas *et al.,* this volume), captive-propagation programmes are perhaps more important than ever. The significance of captive-breeding programmes and, therefore, population management of rhinoceros, is reflected by the fact that the logo used to identify such programmes in zoos depicts rhinoceros (Fig. 1).

However, although captive propagation is important, the actual performance of captive populations of various rhinoceros taxa continues to be variable and in many cases problematic. Adequate husbandry and veterinary care are essential foundations upon which demographic and genetic management can achieve viability of captive populations (WAZA, 2005). The husbandry and veterinary care of rhinoceros in captivity need to improve.

Table 1 provides an overview of the latest data available on the numbers of rhinoceros in captivity worldwide and Table 2 indicates the number of institutions maintaining various taxa. Because many zoos maintain more than one taxon

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Regional Captive Propagation Programs

Fig. 1. Logo designating a formal regional captive-breeding programme; for example, European Endangered Species Programme (EEP) or Species Survival Plan (SSP).

of rhinoceros, it is still difficult to estimate the total number of zoos that maintain these species. A rough estimate is that *c.* 250 zoos worldwide have rhinoceros in their collections. In North America there are *c.* 85 zoos and in Europe *c.* 85 zoos with rhinoceros of at least one taxon.

Of the five extant species (comprising 11 or 12 subspecies), there are full and formal breeding programmes for three: Black rhinoceros *Diceros bicornis,* White rhinoceros *Ceratotherium simum* and Indian or Greater one-horned rhinoceros *Rhinoceros unicornis* in at least two regions of the zoo world (Table 3). Separate programmes exist for two subspecies of Black rhinoceros, namely the Eastern black rhinoceros *Diceros bicornis michaeli* and Southern black rhinoceros *Diceros bicornis minor.* The regional population programmes for the White rhinoceros are for the Southern white rhinoceros subspecies *Ceratotherium simum simum.* However, there are also efforts in progress to promote reproduction in the small and languishing captive population of the Northern white rhinoceros subspecies *Ceratotherium simum cottoni,* considering the Critically Endangered status in the wild (IUCN, 2004; Hermes *et al.,* 2005; Amin, Thomas *et al.,* this volume). Some recent studies have suggested that there may be merit in managing the Indian and the Nepal populations of *R. unicornis* separately until more is known about the genetic relationship between the two (Zschlokke & Baur, 2002; Hlavacek, 2005). Finally, there are also attempts in progress to develop viable captive-breeding capabilities for a fourth species, the Sumatran rhinoceros *Dicerorhinus sumatrensis* (Khan *et al.,* 1999; Roth, 2002a,b). The Javan rhinoceros *Rhinoceros sondaicus,* although Critically Endangered (Foose & van Strien, 1997; IUCN, 2004), has rarely (and almost entirely in the 19th century) been maintained in zoos (Rookmaaker, 1998). There seem to be no prospects for captive-breeding this species in the foreseeable future.

GOALS OF POPULATION BREEDING AND MANAGEMENT IN CAPTIVITY

There are a number of goals for population management and propagation programmes for rhinoceros in captivity.

1. Development of viable captive populations as: (a) reservoirs of genetic and demographic material for potential reinforcement and/or re-establishment of populations in the wild as the need and opportunity occur; (b) self-sustaining populations to ensure animals for public exhibition and scientific investigations to fulfil the additional roles of rhinoceros in captivity.

2. Improvement of husbandry and management in captivity, through research into health, nutrition, behaviour, reproduction and genetics/demography, to facilitate the development of viable populations *ex situ* and to transfer results, as appropriate, to intensively managed populations *in situ.*

3. Strategic co-ordination of space and resources for rhinoceros among institutions within a region, as well as at the global level, to provide maximum assistance to as many rhinoceros taxa as possible (i.e. the development of Regional and Global Collection Plans).

TAXON	WORLD	EUROPE	NORTH AMERICA	CENTRAL & SOUTH AMERICA	ASIA	AUSTRALASIA	AFRICA
Eastern black rhinoceros *Diceros bicornis michaeli*	77.94 (171)	27.48 (75)	39.31 (70)	0.0 (0)	11.15 (26)	0.0 (0)	0.0 (0)
Southern black rhinoceros *Diceros bicornis minor*	36.33 (69)	1.1 (2)	22.19 (41)	0.0 (0)	1.1 (2)	6.6 (12)	6.6 (12)
SUBTOTAL BLACK RHINOCEROS	113.127 (240)	28.49 (77)	61.50 (111)	0.0 (0)	12.16 (28)	6.6 (12)	6.6 (12)
Southern white rhinoceros *Ceratotherium simum simum*	334.410.3 (747)	105.135 (240)	99.118 (217)	27.27 (54)	72.90 (162)	19.20 (39)	12.20.3 (35)
Northern white rhinoceros *Ceratotherium simum cottoni*	4.6 (10)	3.4 (7)	1.2 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
SUBTOTAL WHITE RHINOCEROS	338.416.3 (757)	108.139 (247)	100.120 (220)	27.27 (54)	72.90 (162)	19.20 (39)	12.20.3 (35)
TOTAL AFRICAN RHINOCEROS	451.543.3 (997)	136.188 (324)	161.170 (331)	27.27 (54)	84.106 (190)	25.26 (51)	18.26.3 (47)
Indian/Nepal rhinoceros *Rhinoceros unicornis*	80.74 (154)	22.23 (45)	26.29 (55)	0.0 (0)	31.22 (53)	1.0 (0)	0.0 (0)
Sumatran rhinoceros *Dicerorhinus sumatrensis*	4.5 (9)	0.0 (0)	2.3 (5)	0.0 (0)	2.2 (4)	0.0 (0)	0.0 (0)
TOTAL ASIAN RHINOCEROS	84.79 (163)	22.23 (45)	28.32 (60)	0.0 (0)	33.24 (57)	1.0 (0)	0.0 (0)
TOTAL CAPTIVE RHINOCEROS	535.622.3 (1160)	158.211 (369)	189.202 (391)	27.27 (54)	117.130 (247)	26.26 (52)	18.26.3 (47)

Table 1. Total rhinoceros population in captivity as at 31 December 2004: ♂.♀.unknown (total). Sources of data: Foose (2005) (Sumatran rhinoceros), Hlavacek (2005) (Greater one-horned or Indian rhinoceros) and Ochs & Mercado (2005a,b) (Black rhinoceros and White rhinoceros).

TAXON	WORLD	EUROPE	NORTH AMERICA	CENTRAL & SOUTH AMERICA	ASIA	AUSTRALASIA	AFRICA
Eastern black rhinoceros *Diceros bicornis michaeli*	51	16	26	0	9	0	0
Southern black rhinoceros *Diceros bicornis minor*	16	1	10	0	0	2	3
Southern white rhinoceros *Ceratotherium simum simum*	231	82	57	24	50	8	10
Northern white rhinoceros *Ceratotherium simum cottoni*	2	1	1	0	0	0	0
Indian/Nepal rhinoceros *Rhinoceros unicornis*	59	17	21	0	20	1	0
Sumatran rhinoceros *Dicerorhinus sumatrensis*	5	0	3	0	2	0	0

Table 2. Number of institutions maintaining various taxa of rhinoceros.

TAXON	EUROPE	NORTH AMERICA	AUSTRALASIA	ASIA
Eastern black rhinoceros *Diceros bicornis michaeli*	EEP	SSP		SSCJ
Southern black rhinoceros *Diceros bicornis minor*		SSP	participate in N American SSP	
Southern white rhinoceros *Ceratotherium simum simum*	EEP	SSP	ASMP	SSCJ
Northern white rhinoceros *Ceratotherium simum cottoni*	in 1 institution, trying to breed	in 1 institution, co-operating with Europe		?
Indian/Nepal rhinoceros *Rhinoceros unicornis*	EEP	SSP	Participate in North American SSP	CZA, SSCJ
Sumatran rhinoceros *Dicerorhinus sumatrensis*		GMPB		GMPB

Table 3. Overview of regional captive-breeding programmes for rhinoceros: ASMP. Australasian Species Management Programme; CZA. Central Zoo Authority; EEP. European Endangered Species Programme; GMPB. Global Management & Propagation Board; SSCJ. Species Survival Plan Committee Japan; SSP. Species Survival Plan.

4. Use of individuals in captivity as ambassadors to stimulate public knowledge of, awareness about and support (especially financial) for rhinoceros and their conservation; for example, the European Association of Zoos and Aquaria 'EAZA Rhino Campaign' (Dean & Bos, this volume) and other longer-term programmes in North America through the International Rhino Foundation (IRF). Especially important will be selected *in situ* efforts for rhinoceros with emphasis on those projects that are significant, feasible and provide appropriate opportunities for application of particular expertise that the captive-conservation community can provide in terms of intensive-management technology.

Development of viable populations in captivity requires that population management achieves certain goals (Foose *et al.,* 1995; Ballou & Foose, 1996; WAZA, 2005).

1. Self-sustaining reproduction.
2. Demographic security and, ideally, stability. Basically, the goal is a 95–99% probability that the population will demographically survive for a desired period of time (e.g. 100 years) (Foose *et al.,* 1995).
3. Genetic diversity adequate for: (a) fitness (at the individual level), the ability to survive and reproduce well under current environmental conditions; (b) adaptability (at the population level), the capacity to adapt to changing environments in the future.

The population-management plans in Europe [European Endangered Species Programmes (EEPs)] and North America [Species Survival Plans (SSPs)] have adopted the commonly recommended goal of 90% gene diversity (GD) for 100 years (Foose *et al.,* 1995; WAZA, 2005; Wiese & Willis, 2005). This goal was also adopted in the early stages of development of a Global Captive Action

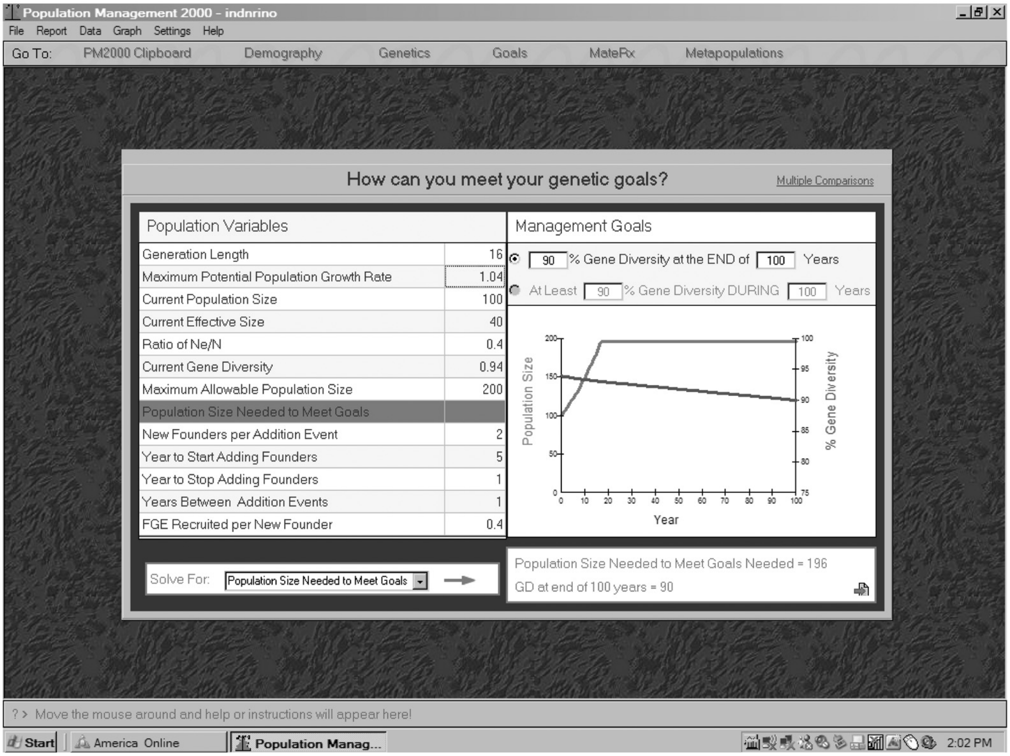

Fig. 2. Population Management 2000 (PM2000) screen for determining target population sizes.

Plan (GCAP) for rhinoceros (Foose, 1992).

4. Target population sizes sufficient to achieve these genetic and demographic goals. It is usually considered that the target size required for the genetic goals will also achieve the demographic ones. It is also important for a population to attain the target population size as rapidly as possible (Foose *et al.,* 1995).

A basic and simplistic scenario for development of a viable captive population includes these basic steps (Foose *et al.,* 1986, 1995; Ballou & Foose, 1996; Zschokke *et al.,* 1998).

1. Establish the captive population with sufficient individuals (the founders) from the wild population(s) to represent a high percentage of the gene pool. Usually, 20–30 individuals are considered necessary (Lacy, 1989).

2. Reproduce these founders as equally as possible to preserve as many of the founder genomes as possible; that is, to maximize preservation of Founder Genome Equivalents (FGE), a measure of the number and evenness of the founders represented in the population through time (Lacy, 1989).

3. Maximize the number of founders and the evenness of their representation by managing captive populations to maximize GD and minimize mean kinships (MK) (Ballou & Lacy, 1995). Inbreeding should also be minimized. Achieve these objectives by: (a) reproducing individuals with the lowest and most similar MKs; (b) reproducing individuals to minimize

RHINOCEROS TAXON	10/50/100 years (TARGET) WORLD	AFRICA	ASIA	AUSTRALASIA	EUROPE	NORTH AMERICA
AFRICAN RHINOCEROS						
Eastern black rhinoceros *D. b. michaeli*	200/240/240	10 ?	40/40/40	0	65*/100/100 + founders?	90/90/90
Southern black rhinoceros *D. b. minor*	80/160/400	50	0	20*/75/250 +6 founders	0	50/80/80
Southern white rhinoceros *C. s. simum*	515/525/500	0	150/?/?	45*/125/250 +30 founders	200/200?/200?	120*/120/120 +10 founders
ASIAN RHINOCEROS						
Indian/Nepal rhinoceros *R. unicornis*	145/250/250	0	55/80/80	0	40*/80/80 + founders?	50/90/90
Sumatran rhinoceros (Mainland) *D. sumatrensis*	12/40/100**	0	12/40/50	0	NA	0
Sumatran rhinoceros (Sumatran) *D. sumatrensis*	12/40/100**	0	12/40/50	0	0	10/20*/50 +10 founders
Sumatran rhinoceros (Borneo) *D. sumatrensis*	8/25/100**	0	8/25/50	(50)**	0	0

SUBTOTAL AFRICAN RHINOCEROS	795/925/1140	60	190/40?/40?	65/200/500	265/300?/300?	260/290/290
SUBTOTAL ASIAN RHINOCEROS	177/355/550	0	87/185/270	(50)**	40*/80/80	60/110/140
ALL RHINOCEROS TAXA	972/1280/1690	60	277/225?/310?	65/200/500	305/380?/380?	320/400/430

* The target indicated includes the acquisition of new founders (number given below). These are then included in the target population total.
** The target if (and when) husbandry of the species can be mastered and sufficient founders for *ex situ* populations can be produced by captive-propagation programmes within range states.

Table 4. Rhinoceros populations under intensive management *ex situ* **and** *in situ* **at both global and regional levels. Target numbers [established 1992–1995 by the Global Captive Action Plan (GCAP)]. No target population was proposed for the Northern white rhinoceros** *C. s. cottoni* **and no captive programmes were proposed for the Southwestern black rhinoceros** *D. b. bicornis,* **the Western black rhinoceros** *Diceros bicornis longipes* **and the Javan rhinoceros** *R. sondaicus.* **No input was available for Central and South America when the target populations and GCAP were formulated. NA. not applicable.**

inbreeding coefficients (Wiese & Willis, 2005).

4. Increase the population as rapidly as possible to the target size within the genetic guidelines.

It should be noted that rhinoceros populations will be more likely than many other taxa to sustain acceptably high levels (e.g. *c.* 90%) of GD for prescribed periods because of the comparatively long generation time, *c.* 15 years, with variation of 14–20 years, depending on the species and management programme. Gene diversity is lost per generation, not per year. However, while the long generation time is beneficial genetically, it reflects in part the long gestation and maturation periods for rhinoceros, which can be demographically problematic by limiting reproduction.

POPULATION MANAGEMENT METHODS AND TOOLS

Studbooks Studbooks are essential for proper genetic and demographic management of animal populations. Excellent international studbooks are maintained for Black and White rhinoceros (Ochs & Mercado, 2005a,b), Indian rhinoceros (Hlavacek, 2005) and Sumatran rhinoceros (Foose, 2005) in captivity. Regional studbooks are maintained for Black, White and Indian rhinoceros in North America, Black rhinoceros in Australasia, Black and Indian rhinoceros in Japan and Indian rhinoceros in India.

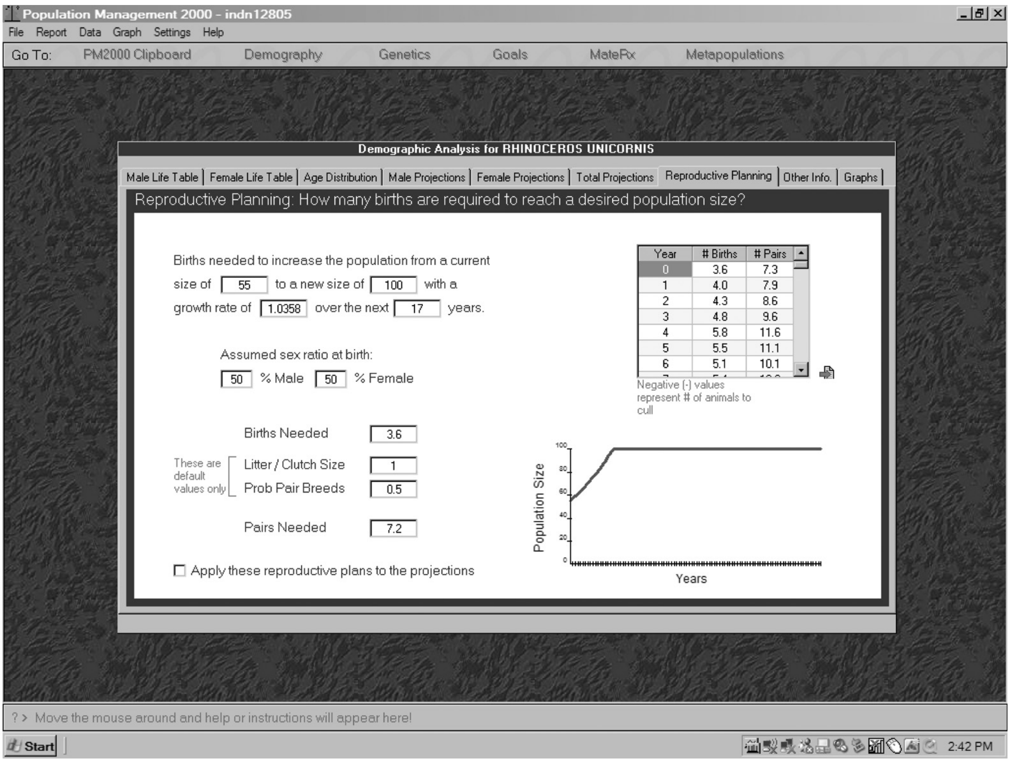

Fig. 3. PM2000 screen for reproduction planning; that is, prescribing how many births are needed to meet the population goals.

SPARKS and PM2000 The primary tools for analysing and managing small zoo populations have been the Single Population Animal Record Keeping System (SPARKS), compiled by the International Species Information System (ISIS) (ISIS, 2004), and Population Management 2000 (PM2000) (Lacy & Ballou, 2002; Pollack *et al.,* 2002). Alternative software is also in use (Zschokke *et al.,* 1998; Hvalacek, 2005). SPARKS is a record-keeping system that allows the relationships of all animals in the population to be compiled and used for population analysis. A SPARKS database is a studbook in a form that permits analyses for population management using various computer software tools. Using the vital statistics and pedigree data in a SPARKS database, the PM2000 software package is used to calculate genetic and demographic variables for the population. Demographic values for the population include age-specific fertility rates, age-specific survivorship and mortality rates, sex ratio, and rates of change in population size, especially the annual rate of change lambda (λ). Age pyramids are also available to reveal if the population is demographically stable. Genetic values for the population include the GD retained to date, FGEs, number and representation of founders, and N_e/N ratios (N_e is the genetically effective size of the population or how well the population is transmitting its alleles from one generation to the next; N_e is almost always lower than N but can be increased by good genetic management). Genetic values for each individual in the population include the inbreeding coefficient (F), MK value, genome uniqueness (GU) and the probability of loss of specific alleles. Combining the genetic and demographic analyses, managers use PM2000 to develop demographic and genetic goals for populations and, therefore, to establish target population sizes (Fig. 2) and prescribe the number of offspring that need to be produced to achieve desired rates of growth to or long-term maintenance of numbers at the target population size (Fig. 3). PM 2000 then permits managers to determine the best pairing options for the matings to produce the desired number of offspring based on minimizing MK values in the population while also avoiding high levels of inbreeding in individuals or loss of rare/unique alleles (Fig. 4).

ZooRisk While SPARKS and PM2000 use life tables and pedigrees to calculate deterministic population analyses and recommendations, ZooRisk (Earnhardt *et al.,* 2005; Faust & Earnhardt, 2005) uses a simulation modelling approach, similar to a gene-drop exercise, to predict the persistence of the population into the future. ZooRisk is a computer program designed to provide scientific assistance for management decisions based on a quantitative assessment of the risk of a population becoming extinct owing to demographic, genetic and management factors. ZooRisk is an individual-based model. Individual-based models are stochastic and can be used to predict the variability around an outcome, which is rarely the case with deterministic models. ZooRisk allows prediction of what is likely to occur based on the actual current living population, and historical birth and death rates. During a simulation the computer tracks each individual to determine if it lives or dies, and reproduces or not each year. These probabilities are based on the historical age-specific death and birth rates from the studbook. Each offspring produced throughout the simulation is also tracked throughout its simulated life. In this way, a population can be modelled into the future beyond the lifespan of a single animal. The power of the stochastic simulation is that the simulation is run multiple times so that a range of potential outcomes and probabilities of outcomes can be calculated. The ZooRisk program is also able to model various genetic-management strategies, such as management by MK, to predict the amount of GD that could be retained versus random breeding. However, it is important to recognize that the ZooRisk management scenarios are idealized, because reproduction by the best genetic pairs is more easily achieved in the simulation than in reality, where complications of, for example, logistics, health, behaviour and permits, can prevent optimal action.

Utilization of both deterministic and stochastic tools provides the most robust methods for viable population management. The various descriptions and assessments of the genetic and demographic status of rhinoceros populations in captivity in this paper have been performed using both SPARKS/PM2000 and ZooRisk.

The advent of ZIMS (Zoological Information Management System) will modify and improve the tools available for population analysis and management.

REGIONAL AND GLOBAL COLLECTION PLANS AND TARGET POPULATION SIZES

Target population sizes Target population (TP) sizes represent a compromise between the largest possible population for genetic and demographic goals and the competition for captive habitat (zoo space and resources) with other threatened taxa. Using preservation of 90% GD for 100 years as the primary goal, target population sizes (Table 4) for all regions of the zoo world at 10, 50 and 100 year intervals were formulated at the 1992 Rhinoceros GCAP Workshop in London (Foose, 1992), with subsequent adjust-

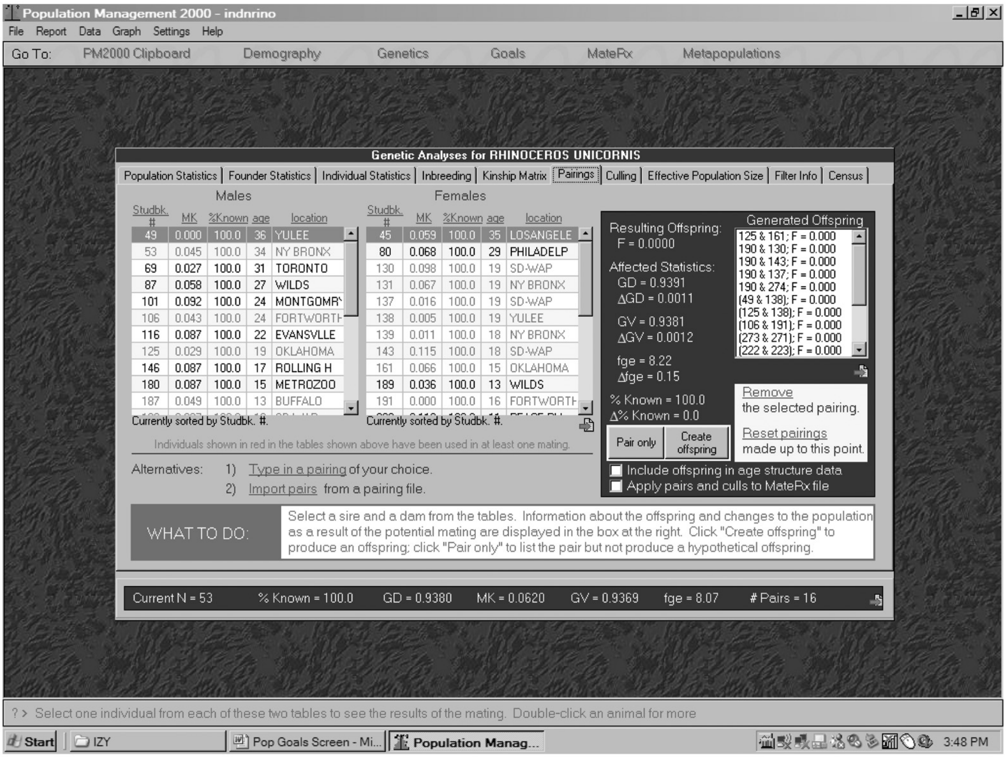

Fig. 4. PM2000 screen for selecting genetically optimal matings.

ments at the global level during various Conservation Breeding Specialist Group (CBSG) meetings and at the regional level through workshops of the regional rhinoceros Taxon Advisory Groups (TAG) (AZA RAG, 2002, 2005, in press; Lindsay, 2002). The 90% GD for 100 year goal will probably require population sizes greater than any one region can maintain. For example, a population of at least 200 Indian rhinoceros may be necessary to preserve 90% GD for 100 years, which is basically the combined sizes of the TPs for the SSP and EEP (Fig. 2). Hence, global co-operation between regional programmes (i.e. metapopulation management) will be necessary.

Regional Collection Plans Guided by the 1992 GCAP workshop and subsequently by criteria formulated by regional zoo associations [e.g. the American Zoo and Aquarium Association (AZA), which developed the SSPs in North America, the European EEPs, and the Australian Regional Association of Zoological Parks and Aquariums (ARAZPA), which developed REGASP (Regional Animal Species Collection Plan)], regional collection plans (RCPs) for rhinoceros have been evolving in different regions (AZA RAG, 2002, 2005, in press; EEP Rhinoceros Advisory Group, 2004; Lindsay, 2004). An RCP that has been functionally operating in North America since 1996 is nearly formalized. Basically, the RCP has confirmed which taxa will be managed as SSP populations and is co-ordinating allocation of captive-rhinoceros habitat to achieve the TP sizes; for example, by trying to reduce the population of White rhinoceros, especially when maintained in pairs, and converting this space for Black or Indian rhinoceros. Currently there are *c.* 350 rhinoceros spaces in the SSP and there is need and expectation for these to increase to 450 over the next decade. The EEP is at a slightly earlier stage in the development of a RCP. There is a need to review and refine the RCPs and TPs at the SSP and EEP regional levels and also to involve other regions so that satisfactory TPs can be confirmed at the global level.

It should be noted that operating separate population-management programmes for rhinoceros subspecies, rather than just species, may need to be revisited in the future in terms of habitat availability in captivity and TPs required to achieve goals. The current status of subspecies programmes described above (e.g. SSP programmes for two subspecies of Black rhinoceros) as well as the recommendations for even further subdivision in other species (e.g. Indian rhinoceros; Hvalacek, 2005), will particularly need to consider how much the genetic differences, however distinct, may have been caused quite recently by anthropomorphic reduction and fragmentation of wild populations.

SUMMARY OF STATUS OF CAPTIVE POPULATIONS AND MANAGEMENT

The most developed population management and propagation programmes for rhinoceros are in the North American (SSPs) and European (EEPs) regions. Hence, much of the remainder of this paper will emphasize these two regional programmes. It should also be noted that Western Plains Zoo, Dubbo, Australia, is the only institution in Australasia with Black and Indian rhinoceros, and participates in the SSP programmes for these taxa.

Table 5 presents the current population sizes, births and deaths since 2001, approximate λs, number of actual and potential founders, and GD retained for the SSP and EEP populations. It should be noted that a $\lambda > 1$ indicates population increase, a $\lambda = 1$ indicates a static or stationary population and a $\lambda < 1$ indicates a population decrease. The data in Table 5 suggest, simplistically and generally, that both the Black and White rhinoceros in captivity have the potential for viability with their genetic foundations excellent at the species level. However, demographically there are a number of health and husbandry problems with Black rhinoceros (Paglia & Dennis, 1999; Paglia *et al.,* 2002; Weber *et al.,* 2002; Miller, 2003; Dennis, 2005; P. M. Dennis, P. J. Rajala-Schultz, J. A. Funk, E. S. Blumer, R. E. Miller, T. E. Wittum & W. J. A. Saville, pers. comm.) and fertility issues with White rhinoceros (Patton *et al.,* 1999; Hermes *et al.,* 2002, 2004, 2005, 2006; Roth, this volume) that are limiting achievement of the potential viability. Captive populations of Indian rhinoceros are perhaps the most successful demographically but have a more restricted genetic foundation and would benefit from acquisition of additional founders for the SSP and EEP populations (Foose, 2000; Hlavacek, 2005).

Despite these problems, rhinoceros populations in captivity do appear to be demographically and genetically healthier than the elephant populations (Wiese & Willis, this volume), although managers of elephants in captivity have, in recent years, been more intensively attempting to resolve the problems preventing attainment of viability. An indication of the at least modest success of rhinoceros captive-breeding programmes is the comparatively high percentage of the current populations that is captive born (Table 6), especially for Eastern black rhinoceros and Indian rhinoceros.

DETAILS OF CAPTIVE POPULATIONS AND MANAGEMENT FOR RHINOCEROS TAXA

Black rhinoceros: demographic status The SSP populations of the Black rhinoceros are marginally self-sustaining with annual population growth rates (λ) of 1·017 and 0·996 for the eastern and southern subspecies, respectively, using demographic data for the last 10 years (1994–2004). The EEP population of Eastern black rhinoceros is performing similarly although full demographic analyses are not currently available for the EEP population. Problems that have limited development of self-sustaining populations are high mortality and sub-optimal reproduction (Smith & Read, 1992). The SSP populations are also below their TP size, with 70 (39.31) Eastern black rhinoceros and 50 (26.24) Southern black rhinoceros, although the southern SSP population seems on schedule for its 10 year TP goal. The same is true for the EEP population of Eastern black rhinoceros. More vigorous growth to TP sizes in the SSP has been limited by comparatively high mortality because of the various disease issues with Black rhinoceros in captivity and also some temporary limitations of space that have been caused in part by skews in the sex ratios. Although the SSP Eastern black rhinoceros population has a more balanced age structure, it also indicates a slight skew towards ♂♂. Indeed, a skew in the natal sex ratios of both subspecies of Black rhinoceros in North America has caused considerable management challenges, particularly locating space for excess ♂♂. This problem, in turn, inhibits the formation of pairs and the accommodation of offspring to enable reproduction to proceed at its full potential (AZA RAG, 2002, 2005). The problem has been particularly acute for the Southern black rhinoceros over the last 5 years, although the sex ratio in the SSP for this subspecies is still more even than for the Eastern black rhinoceros (AZA RAG, 2002, 2005). This phenomenon could simply be a result of the stochastic variation that can occur in small populations but the fact that it has occurred in three taxa of rhinoceros in the SSP and many other ungulates suggests that management factors may be involved. Various hypotheses have been put forward (S. J. Atkinson, 1997; P. M. Dennis, P. J. Rajala-Schultz, J. A. Funk, E. S. Blumer, R. E. Miller, T. E. Wittum & W. J. A. Saville, pers. comm.; T. Roth, pers. comm.) or will be tested about possible causes of this problem in Black (and White) rhinoceros population(s) in North America. Nutrition is a likely factor (Trivers & Willard,

TAXON	CURRENT POPULATION SIZE	BIRTHS 2000–2004	DEATHS 2000–2004	λ ANNUAL RATE OF CHANGE IN POPULATION SIZE	FOUNDERS		FOUNDER GENOME EQUIVALENTS		GENE DIVERSITY RETAINED	
					A	P	A	P	A	P
SSP POPULATION										
Eastern black rhinoceros *Diceros bicornis michaeli*	39.31 (70)	8.5 (13)	8.5 (13)	0·996	42	0	14·99	23·45	0·967	0·979
Southern black rhinoceros *Diceros bicornis minor*	26.25 (51)	8.5 (13)	6.6 (12)	1·017	25	3	11·96	23·23	0·958	0·979
Southern white rhinoceros *Ceratotherium simum simum*	82.89 (171)	19.8 (27)	7.12 (19)	1·001	55	47	26·09	93·90	0·981	0·995
Indian/Nepal rhinoceros *Rhinoceros unicornis*	26.29 (55)	12.11 (23)	9.7 (16)	1·041	22	2	7·39	16·33	0·932	0·969
EEP POPULATION										
Eastern black rhinoceros *Diceros bicornis michaeli*	27.48 (75)	4.10 (14)	4.10 (14)	*c.* 1·000	>30*	?	?	?	>0·950*	>0·950*
Southern black rhinoceros *Diceros bicornis minor*	1.1 (2)	0.2 (2)	0.0 (0)	>1·100†	2	0	2	2	NA‡	NA‡
Southern white rhinoceros *Ceratotherium simum simum*	84.112 (196)	12.10 (22)	15.20 (35)	*c.* 0·983	>40*	?	?	?	>0·970*	>0·970*
Indian/Nepal rhinoceros *Rhinoceros unicornis*	22.23 (45)	10.7 (17)	3.4 (7)	0·994 (10 year) 1·049 (5 year)	14	6	4·16	14·02	0·880	0·958

* Estimated value.
† Not sustainable because offspring exported.
‡ Because number so small and all offspring being exported.

Table 5. Comparison of management status of SSP and EEP populations of rhinoceros taxa: A. actual; P. potential (i.e. additional); NA. not applicable.

TAXON	%						
	WORLD	EUROPE	NORTH AMERICA	CENTRAL & SOUTH AMERICA	ASIA	AUSTRALASIA	AFRICA
Eastern black rhinoceros *Diceros bicornis michaeli*	90	85	93	NA	92	NA	NA
Southern black rhinoceros *Diceros bicornis minor*	60	NA	73	NA	NA	50	31
Southern white rhinoceros *Ceratotherium simum simum*	51	48	58	60	45	53	36
Northern white rhinoceros *Ceratotherium simum cottoni*	40	57	0	0	NA	NA	NA
Indian/Nepal rhinoceros *Rhinoceros unicornis*	77	86	87	0	51	100	NA
Sumatran rhinoceros *Dicerorhinus sumatrensis*	22	NA	40	NA	0	NA	NA

Table 6. Percentage of living rhinoceros that is captive born: NA. not applicable.

1973). From a stochastic perspective, the small sizes of the SSP populations for Black rhinoceros and a λ that is near 1·0 increase the possibility of extinction over the next 100 years. The current skew in sex ratio in the eastern subspecies places this population at even greater risk. ZooRisk simulations indicate a 10% probability of extinction for the eastern subspecies and 4% probability of extinction for the southern subspecies within 100 years. If reproduction rates can be increased in North America to increase the population and reduce risk of loss, there may still be space problems, as few new institutions seem interested in adding Black rhinoceros to their collections. A skew towards ♂♂ in sex ratios of calves does not seem to be occurring in the Black rhinoceros populations in the EEP or Japan.

Genetic status The SSP population of the eastern subspecies is currently healthy with 96·7% GD and 14·99 FGEs. The southern subspecies is slightly lower at 95·8% GD and 11·96 FGE. Both populations have been managed effectively in the past as indicated by the comparatively high effective-population size and N_e/N ratios of 0·6188 and 0·5346, for the eastern and southern populations, respectively. Comparable analyses are not currently available for the EEP population of Eastern black rhinoceros but estimates indicate that the situation is healthy. Stochastic simulations using ZooRisk, however, indicate that GD in the SSP Eastern black rhinoceros population may decline to 84·11% in North America in 100 years, even with good management by MK. The southern subspecies could decline to only 82·13% GD in 100 years if additional founders are not identified. This decline is a result of the inability of either population to grow rapidly enough and, therefore, to retain significant GD.

Southern white rhinoceros: demographic status The Southern white rhinoceros population in North America is also marginally self-sustaining with a λ of 1·001. This taxon is the largest SSP rhinoceros population with 171 (82.89) individuals. However, a large proportion of these animals are older and will be removed from the population in the next 10 years. Another major problem with this population is the extensive failure of F1 ♀♀ to reproduce (Swaisgood, 2003; AZA RAG, 2004; Swaisgood *et al.,* 2006). Many of these animals are already post-reproductive and genetically unavailable to the population. The large population size, however, provides this population with demographic stability over the next 100 years. A skew towards ♂♂ in natal sex ratios appears to be developing as a problem for this species in the SSP as well. Again, the same phenomenon does not appear to be occurring for White rhinoceros in Europe. ZooRisk simulations indicate a 0% chance of loss of the SSP population although the population does decline to a mean size of 72 animals over that time. Comparable analyses are not available at this time for the European population but inspection of the crude data on births and deaths suggests a similar situation.

Genetic status The Southern white rhinoceros population is also the most genetically secure SSP rhinoceros population, with retained GD of 98·1% or 26·09 FGE. Again, however, the genetic information of a number of potential founders may never be captured owing to reproductive problems. Nevertheless, ZooRisk simulations suggest that GD in this population will remain above 97% for the next 100 years with management by MK. As expected for a species that is more social than the Black or Indian/Nepalese rhinoceros, the effective population size for the White rhinoceros is lower ($N_e/N = 0·3266$). Although lower than the effective population size for other rhinoceros species, this value shows the positive effects of intensive management because this is much higher than N_e/N values typical of other herd/harem species. Again, comparable analyses are not available at this time for the European population but inspection of the crude data on births and deaths suggests a similar situation.

Northern white rhinoceros As noted earlier, this population is languishing with only ten individuals (4.6) in two zoos, Dvur Kralove, Czech Republic (3.4), and San Diego Wild Animal Park (SDWAP), CA, USA (1.2). Moreover, it is not clear if any of the animals are capable of natural reproduction. The ♀♀ at SDWAP are reproductively senescent. There may be two fertile ♀♀ at Dvur Kralove, including the calf born in 2000, but recent repeated matings of her parents have failed to produce another pregnancy (K. Tomasova, T. Hildebrandt & R. Hermes, pers. comm.). The only two potentially fertile ♂♂ at Dvur Kralove are related to the ♀ born in 2000 (one is her father, the other is her almost full brother). There will be an attempt at assisted reproduction in a desperate effort to prevent the total extinction of this subspecies. Part of this effort may entail using semen from an unrelated ♂ (at SDWAP) that produces sperm but does not manifest any reproductive behaviour.

Indian rhinoceros: demographic status Analysis of the life table of Indian rhinoceros in North America indicates that the deterministic annual population growth rate (λ) is 1·041. A similar situation appears to be occurring in the EEP population, at least over the last 5 years. There was a period 5–10 years ago when the EEP population of this species was not reproducing well but that situation has changed spectacularly in the last 5 years, with significant increased reproduction. The current SSP population is 55 (26.29) and moving well towards its TP size of 100. This population has the ability to grow vigorously and ZooRisk simulations indicate a 0% chance of extinction in the next 100 years, if zoo space can be identified to allow the population to grow to 100 individuals. This population has a good age structure, conducive to continued population growth. The age structure is slightly vertical rather than pyramidal but this is not a problem for a long-lived species, such as rhinoceros. The EEP population also seems to be on schedule for attainment of its TP goals.

Genetic status Although, demographically, both the SSP and EEP populations of Indian rhino are healthy, the genetic situation and foundations of both populations are unsatisfactory. A major problem is the over-representation of a few reproductively successful founders and their lineages (Zschokke *et al.,* 1998; Hvalacek, 2005). The SSP population has retained 93·2% GD and 7·39 FGE. These values are comparatively low compared to the African rhinoceros SSP populations because fewer animals have founded the Indian population in North America than is the case for Black and Southern white rhinoceros. The intensive management of this population has retained a significant amount of the original GD contained in the founders and has a robust N_e/N ratio of 0·4168. There is also significant potential GD (96·9%) in the population, which can be accessed with proper management by MK. If the SSP population could be allowed to grow to 100 over the next 15–20 years, ZooRisk simulations suggest the population managed by MK will be able to retain 93% GD. This goal is possible owing to the high potential GD in the SSP population but, again, only if management by MKs can be optimized. The EEP population has a more challenging genetic situation, which can be improved somewhat by very intensive management by MKs to achieve a broader and more balanced representation of founders. However, the addition of more founders will be beneficial, probably essential, for the long-term genetic viability of both the EEP and SSP populations. Efforts are in progress to acquire new blood, both from exchanges with zoos in range states and by rescue of orphans from the wild, such as the two new founders (a ♂ and a ♀) received at Tiergarten Schönbrunn, Vienna, Austria, in March 2006.

Sumatran rhinoceros: demographic status Although there are not enough animals or husbandry and breeding success for a full population-management programme for this species, its extreme endangerment in the wild does justify continued attempts to master the science and art of breeding the species in captivity.

Basic husbandry and especially reproductive biology have been challenging for the Sumatran rhinoceros. Mortality has been high, with only seven of 40 animals captured from 1984 to 1995 still surviving. Moreover, only one pair of this species has produced offspring to date (Khan *et al.,* 1999; Roth *et al.,* 2001, 2004; Roth, 2002a,b; Foose, 2005).

Genetic status There are few founders and, hence, limited GD owing to high mortality of rhinoceros moved into captivity since 1984 (Foose, 2005). However, the basic reproductive and, therefore, demographic imperative for this species supersedes genetic considerations. A Global Management and Propagation Board (GMPB) has recently been established to facilitate improvement in reproduction.

HUSBANDRY AND HEALTH ISSUES, MANUALS AND GUIDELINES

As indicated earlier and elsewhere (WAZA, 2005), genetic and demographic management must be founded on populations that are healthy and under good husbandry. This paper will not attempt to discuss in detail the various health and husbandry issues for the different species of rhinoceros in captivity but, generally and briefly, the most serious problems observed in each species are listed.

Black rhinoceros Disease and nutrition issues (Paglia & Dennis, 1999; Paglia *et al.,* 2002; Weber *et al.,* 2002; R. E. Miller, 2003; M. Miller, 2004; Dennis, 2005; P. M. Dennis, P. J. Rajala-Schultz, J. A. Funk, E. S. Blumer, R. E. Miller, T. E. Wittum & W. J. A. Saville, pers. comm.; Clauss & Hatt, this volume).

White rhinoceros Reproductive failures (Patton *et al.,* 1999; Hermes *et al.,* 2002, 2004, 2005, 2006; Swaisgood, 2003; AZA RAG, 2004; Swaisgood *et al.,* 2006; Roth, this volume).

Indian rhinoceros Acute pododermatitis (von Houwald, 2001; M. W. Atkinson *et al.,* 2002).

Sumatran rhinoceros Disease, nutrition and reproduction issues. (Khan *et al.,* 1999; Radcliffe *et al.,* 2002; Roth, 2002a,b; Roth *et al.,* 2004).

More details on these husbandry and health problems are available from the several husbandry manuals and guidelines now available, especially from the EEP and SSP (Fouraker & Wagener, 1996; Guldenschuh & von Houwald, 2002; AZA, 2005; Tomasova, 2005).

ORGANIZATIONAL STRUCTURES FOR POPULATION MANAGEMENT

At the global level, the international studbook for Indian rhinoceros (Hlavacek, 2005) provides some general recommendations for population management. Moreover, as mentioned earlier, there is now a GMPB for Sumatran rhinoceros in captivity. However, over the last decade, most population management of rhinoceros has been at the regional level. In North America, the SSP rhinoceros populations are managed by the Rhinoceros Taxon Advisory Group (Rhinoceros TAG) which includes all the Species Coordinators for the four species maintained. There are no longer separate SSP

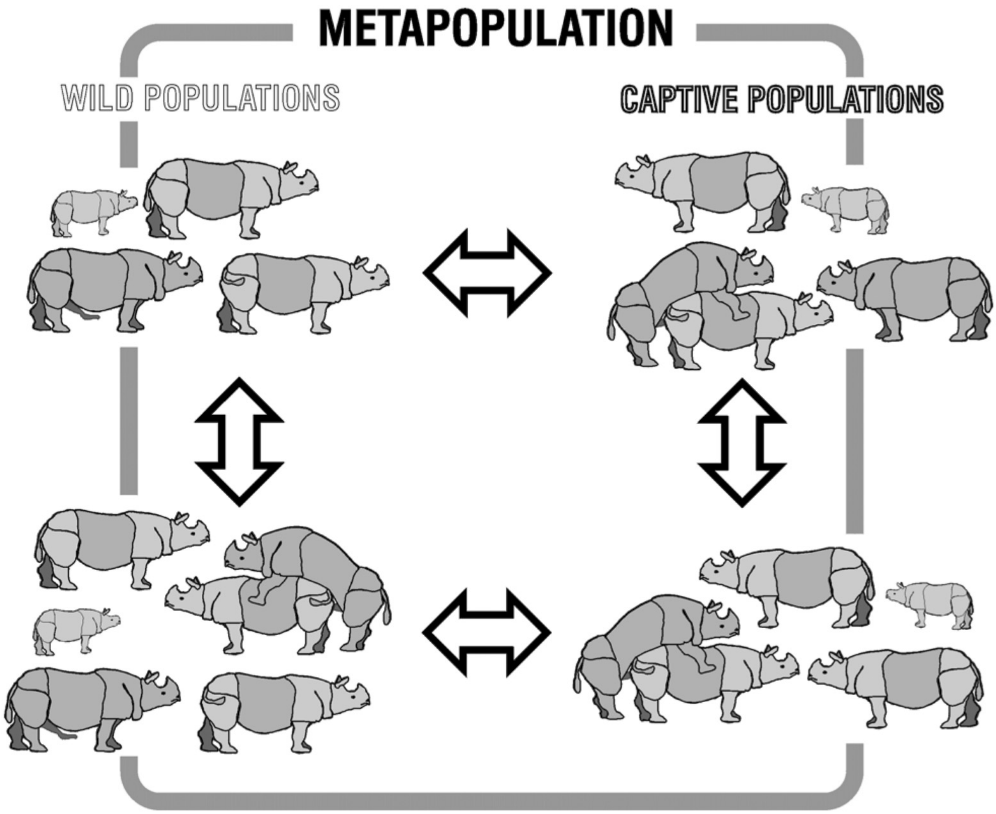

Fig. 5. Metapopulation management of regional captive populations and multiple wild populations of rhinoceros.

Management Committees for the different species. The EEP seems also to be moving in this direction but still has separate Management Committees for each species. In Japan, the Black rhinoceros, White rhinoceros and Indian rhinoceros are managed by a Species Survival Plan Committee Japan (SSCJ) and a National Studbook Co-ordinator. In Australasia, there is an Australasian Species Management Programme (ASMP) Co-ordinator and Committee for White rhinoceros but this region participates in the SSP programme for Southern black rhinoceros and Indian rhinoceros. In India, a regional plan is in progress under the auspices of the Central Zoo Authority (CZA). However, more co-operation and co-ordination is needed among the regional programmes. A good start occurred with the 1992 London Rhino Global Captive Action Plan Workshop but the effort has not been sufficiently sustained. Another Rhino Global Captive Action Plan Workshop, involving representatives from all regions with rhinoceros in captivity, will convene at Whipsnade Wild Animal Park, Dunstable, UK, in May 2006.

METAPOPULATION MANAGEMENT AND *IN SITU* MEGAZOOS

Achievement of the population viability goals for captive and other intensively managed populations of rhinoceros will almost certainly require metapopulation management among the various regional breeding programmes to achieve TP sizes and genetic/demographic goals. Metapopulation management may also be necessary, or desirable, between captivity and the 'wild' (Fig. 5). Moreover, as wild populations become smaller and more fragmented they require much the same kinds of intensive population management as more traditional populations in captivity (Foose *et al.,* 1995; WAZA, 2005). As an example, the Eastern black rhinoceros at the Lewa Wildlife Conservancy in Kenya, a free-ranging population that is, however, contained within fences, are listed in the international studbook for the Black rhinoceros (Ochs & Mercado, 2005a).

It is probably the case that interactive management, especially from captive to wild, is more of an option or safeguard for the future. Nevertheless, there have already been some successes, and failures, with reintroduction of Black rhinoceros (M. Hofmeyer, pers. comm.; http://www.rhinos-irf.org/news/african/marakele/brhino_reintro_at_marakele.htm). Explorations are in progress for more introductions of captive rhinoceros to the wild, both Black (to southern Africa) and White (to Uganda). These introductions will abide by the 'first do no harm' precautionary principle (Osofsky *et al.,* 2001). Perhaps movement of rhinoceros from captive to wild or at least free-ranging situations in native habitat, will be more of an option from regional captive programmes and populations in range states, for example India (B. R. Sharma, CZA, pers. comm.).

CONCLUSION

Captive-breeding programmes are important components of conservation strategies for rhinoceros but only if truly viable populations can be developed. Currently, there is good progress with the Indian rhinoceros, modest success with the Black and White rhinoceros, and a glimmer of hope for the Sumatran rhinoceros. However, problems in achieving the desired levels of viability persist. Husbandry, veterinary care and population management in captivity must improve if viable captive populations are to be achieved. The population-management programmes for Black, White and Indian rhinoceros operating in various regions of the zoo world need to intensify and coordinate their efforts more.

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REFERENCES

Atkinson, M. W., Hull B., Gandolf, A. R. & Blumer, E. S. (2002): Long term medical and surgical management of chronic pododermatitis in greater one-horned rhinoceros *(Rhinoceros unicornis):* a progress report. In *A research update on elephants and rhinos. Proceedings of the international elephant and rhino research symposium, Vienna, June 7–11, 2001:* 159–163. Schwammer, H. M., Foose, T. J., Fouraker, M. & Olson, D. (Eds). Münster: Schuling Verlag.

Atkinson, S. J. (1997): *Possible determinants of skewed natal sex ratios in captive black and Indian rhinoceros in North America.* Cumberland, OH: International Rhino Foundation.

AZA (2005): *North American standardized guidelines for animal care: rhinoceros.* Silver Spring, MD: American Zoo and Aquarium Association.

AZA RAG (Rhinoceros Advisory Group) (2002): *Species survival plan for rhinoceros.* Cumberland, OH: American Zoo and Aquarium Association RAG.

AZA RAG (2004): *AZA Rhinoceros Advisory Group five-year research masterplan 2004.* Cumberland, OH: American Zoo and Aquarium Association RAG.

AZA RAG (2005): *Species survival plan for rhinoceros.* Cumberland, OH: American Zoo and Aquarium Association RAG.

AZA RAG (In press): *AZA regional collection plan for rhinoceros.* Cumberland, OH: American Zoo and Aquarium Association RAG.

Ballou, J. D. & Foose, T. J. (1996): Demographic and genetic management of captive populations. In *Wild mammals in captivity: principles and techniques* 263–283. Kleiman, D. G., Allen, M., Thompson, K.

& Lumpkin, S. (Eds). Chicago, IL: University of Chicago Press.

Ballou, J. D. & Lacy, R. C. (1995); Identifying genetically important individuals for management of genetic variation in pedigreed populations. In *Population management for survival and recovery:* 273–294. Ballou, J. D., Gilpin, M. & Foose, T. J. (Eds). New York, NY: Columbia University Press.

Dennis, P. M. (2005): *Executive summary: advanced veterinary epidemiology training program focusing on the health of captive black rhinoceros.* Yulee, FL: International Rhino Foundation.

Earnhardt, J. M., Lin, A., Faust, L. J. & Thompson, S. D. (2005): *ZooRisk: a risk assessment tool* version 2.53. Chicago, IL: Lincoln Park Zoo.

EEP Rhinoceros Advisory Group (EEP RAG) (2004): *Regional collection plan and EEP program reports.* Whipsnade: Zoological Society of London.

Emslie, R. H. & Brooks, P. M. (1999): *African rhinos: status survey and conservation action plan.* Gland & Cambridge: IUCN.

Faust, L. J. & Earnhardt, J. M. (2005): *ZooRisk: a assessment tool* version 2.53. *User's manual.* Chicago, IL: Lincoln Park Zoo.

Foose, T. J. (1983): The relevance of captive propagation to the conservation of biotic diversity. In *Genetics and conservation:* 374–401. Schonewald-Cox, C. M., Chambers, S. M., MacBryde, B. & Thomas, L. (Eds). Menlo Park, CA: Benjamin Cummings.

Foose, T. J. (1992): *Rhino global captive action plan.* Apple Valley, MN: IUCN/SSC CBSG.

Foose, T. J. (2000): Overview of global captive status for *Rhinoceros unicornis* and a proposal for a funding mechanism. In *Report of the regional meeting for Indian and Nepal of the IUCN/SSC Asian Rhino Specialist Group—Kaziranga 1999:* 172–174. van Strien, N. J. & Foose, T. J. (Eds). Yulee, FL: IUCN/SSC ASRSG & IRF.

Foose, T. J. (2005): *International studbook for Sumatran rhinoceros.* Waynesboro, PA: International Rhino Foundation.

Foose, T. J. & van Strien, N. J. (1997): *Asian rhinos: status survey and conservation action plan* (new edn). Gland & Cambridge: IUCN.

Foose, T. J., Lande, R., Flesness, N. R., Rabb, G. & Read, B. (1986): Propagation plans. *Zoo Biology* **5:** 139–146.

Foose, T. J., de Boer, L., Seal, U. S. & Lande, R. (1995): Conservation management strategies based on viable populations. In *Population management for survival and recovery:* 273–294. Ballou, J. D., Gilpin, M. & Foose, T. J. (Eds). New York, NY: Columbia University Press.

Fouraker, M. & Wagener, T. (1996): *AZA rhinoceros husbandry resource manual.* Fort Worth, TX: Forth Worth Zoological Park.

Guldenschuh, G. & von Houwald, F. (2002): *Husbandry manual for greater one-horned or Indian rhinoceros.* Basel: Basel Zoo.

Hermes, R., Schwarzenberger, F., Walzer, C., Göritz, F., Tomasova, K., Patton, L. & Hildebrandt, T. B. (2002): Fertility evaluation of the captive female white rhinoceros population. *Advances in Ethology* **37:** 138.

Hermes, R., Hildebrandt, T. B. & Göritz, F. (2004): Reproductive problems directly attributable to long-term captivity-asymmetric reproductive aging. *Animal Reproduction Science* **82–83:** 49–60.

Hermes, R., Hildebrandt, T., Blottner, S., Walzer, C., Silinski, S., Patton, M. L., Wibbelt, G., Schwarzenberger, F. & Göritz, F. (2005): Reproductive soundness of captive southern and northern white rhinoceroses *(Ceratotherium simum simum, C. s. cottoni):* evaluation of male genital tract morphology and semen quality before and after cryopreservation. *Theriogenology* **63:** 219–238.

Hermes, R., Hildebrandt, T. B., Walzer, C., Göritz, F., Patton, M. L., Silinski, S., Anderson, M. J., Reid, C. E., Wibbelt, G., Tomasova, K. & Schwarzenberger, F. (2006): The effect of long non-reproductive periods on the genital health in captive female white rhinoceroses *(Ceratotherium simum simum, C. s. cottoni). Theriogenology* **65:** 1492–1515.

Hlavacek, G. (2005): *International studbook for the greater one-horned or Indian rhinoceros* (13th edn). Basel: Basel Zoo.

von Houwald, F. (2001): *Foot problems in Indian rhinoceroses* ***Rhinoceros unicornis*** *in zoological gardens: macroscopic and microscopic anatomy, pathology and evaluation of the causes.* Doctoral dissertation, University of Zurich, Switzerland.

ISIS (2004): *SPARKS: single population animal record keeping system* version 1.54. Apple Valley/Eagan, MN: International Species Information System.

IUCN (2004): *2004 IUCN red list of threatened species.* Gland and Cambridge: IUCN. http://www.iucnredlist.org

Khan, M. M. K., Roth, T. L. & Foose, T. J. (1999): *In situ* and *ex situ* efforts to save the Sumatran rhinoceros *(Dicerorhinus sumatrensis).* In *Seventh world conference on breeding endangered species: linking zoo and field research to advance conservation:* 163–174. Roth, T. L., Swanson, W. F. & Blattman, L. K. (Eds). Cincinnati, OH: Zoological Society of Cincinnati.

Lacy, R. C. (1989): Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. *Zoo Biology* **8:** 111–123.

Lacy, R. C. & Ballou, J. D. (2002): *Population management 2000 user's manual.* Brookfield, IL: Chicago Zoological Society.

Lindsay, N. (2002): *EAZA rhinoceros regional collection plan.* Whipsnade: The Zoological Society of London.

Lindsay, N. (2004): *EAZA rhinoceros TAG annual meeting report.* Whipsnade: The Zoological Society of London.

MILLER, M. (2004): *SSP black rhinoceros veterinary update.* Lake Buena Vista, FL: Disney's Animal Kingdom.

MILLER, R. E. (2003): Rhinocerotidae. In *Zoo and wild animal medicine* (5th edn): 558–568. Fowler, M. E. & Miller, R. E. (Eds). Philadelphia, PA: W. B. Saunders Co.

OCHS, A. & MERCADO, H. (2005a): *International studbook for the African black rhinoceros* **10.** Berlin: Zoologischer Garten Berlin.

OCHS, A. & MERCADO, H. (2005b): *International studbook for the African white rhinoceros* **10.** Berlin: Zoologischer Garten Berlin.

OSOFSKY, S. A., PAGLIA, D. E., RADCLIFFE, R. W., MILLER, R. E., EMSLIE, R. H., FOOSE, T. J., DU TOIT, R. & ATKINSON, M. W. (2001): First do no harm: a precautionary recommendation regarding the movement of black rhinos from overseas zoos back to Africa. *Pachyderm* **30:** 17–23.

PAGLIA, D. E. & DENNIS, P. (1999): Role of chronic iron overload in multiple disorders of captive black rhinoceroses *(Diceros bicornis). Proceedings of the American Association of Zoo Veterinarians* **1999:** 163–171.

PAGLIA, D. E., DIERENFELD, E. S. & TSU, I-HSIEN (2002): Pathological iron overloads acquired in captivity by browsing (but not by naturally grazing) rhinoceroses. In *A research update on elephants and rhinos. Proceedings of the international elephant and rhino research symposium, Vienna, June 7–11, 2001:* 217. Schwammer, H. M., Foose, T. J., Fouraker, M. & Olson, D. (Eds). Münster: Schuling Verlag.

PATTON, M. L., SWAISGOOD, R. R., CZEKALA, N. M., WHITE, A. M., FETTER, G. A., MONTAGNE, J. P., RIECHES, R. G. & LANCE, V. A. (1999): Reproductive cycle length and pregnancy in the southern white rhinoceros *(Ceratotherium simum simum)* as determined by fecal pregnane analysis and observations of mating behavior. *Zoo Biology* **18:** 111–127.

POLLAK, J. P., LACY, R. C. & BALLOU, J. D. (2002): *Population management 2000* version 1.205. Brookfield, IL: Chicago Zoological Society.

RADCLIFFE, R. W., CITINO, S. B., DIERENFELD, E. S., FOOSE, T. J., PAGLIA, D. E. & ROMO, J. S. (2002): *Intensive management and preventative medicine for the Sumatran rhinoceros.* Glen Rose, TX: Fossil Rim Wildlife Center.

ROOKMAAKER, R. C. (1998): *The rhinoceros in captivity.* The Hague: SPB Academic Publishing.

ROTH, T. L. (2002a): The role of reproductive science and technology in achieving the birth of the first Sumatran rhino calf produced in captivity in 112 years. *Proceedings of the American Association of Zoo Veterinarians* **2002:** 210–212.

ROTH, T. L. (2002b): Integrating science, technology and animal management to produce the first Sumatran rhino calf in captivity in 112 years. *Proceedings of the AZA Annual Conference* **2002:** 63–65.

ROTH, T. L., O'BRIEN, J. K., MCRAE, M. A., BELLEM, A. C., ROMO, S. J., KROLL, J. L. & BROWN, J. L. (2001): Ultrasound and endocrine evaluation of ovarian cyclicity and early pregnancy in the Sumatran rhinoceros *(Dicerorhinus sumatrensis). Reproduction* **121:** 139–149.

ROTH, T. L., BATEMAN, H. L., KROLL, J. L., STEINETZ, B. G., PARLOW, A. F. & REINHART, P. R. (2004): Endocrine and ultrasonographic characterization of a successful pregnancy in a Sumatran rhinoceros *(Dicerorhinus sumatrensis)* supplemented with progesterone. *Zoo Biology* **23:** 219–238.

SMITH, R. L. & READ, B. (1992): Management parameters affecting the reproductive potential of captive, female black rhinoceros. *Zoo Biology* **11:** 375–383.

SWAISGOOD, R. R. (2003): Behavioral research for captive breeding problem-solving in southern white rhinoceros: lessons from captivity and the field. *Abstracts, Animal Behavior Meeting: Annual Meeting* **2003:** 33.

SWAISGOOD, R. R., DICKMAN, D. M. & WHITE, A. M. (2006): A captive population in crisis: testing hypotheses for reproductive failure in captive-born southern white rhinoceros females. *Biological Conservation* **129:** 468–476.

TOMASOVA, K. (2005): *Husbandry guidelines for white rhinoceros in captivity.* Dvur Kralove: Dvur Kralove Zoo.

TRIVERS, R. I. & WILLARD, D. E. (1973): Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179:** 90–91.

WAZA (2005): *Building a future for wildlife: the world zoo and aquarium conservation strategy.* Bern, Switzerland: World Association of Zoos and Aquariums.

WEBER, B., PAGLIA, D. & HARLEY, E. H. (2002): Red cell metabolism in the black rhinoceros: relevance to haemolytic disease. In *A research update on elephants and rhinos. Proceedings of the international elephant and rhino research symposium, Vienna, June 7–11, 2001:* 181. Schwammer, H. M., Foose, T. J., Fouraker, M. & Olson, D. (Eds). Münster: Schuling Verlag.

WIESE, R. J. & HUTCHINS, M. (1994): *Species Survival Plans: strategies for wildlife conservation.* Bethesda, MD: American Zoo and Aquarium Association.

WIESE, R. J. & WILLIS, K. (2005): *AZA studbook analysis and population management handbook.* Chevy Chase, MD: American Zoo and Aquarium Association.

ZSCHOKKE, S & BAUR, B. (2002): Inbreeding, outbreeding, infant growth, and size dimorphism in captive Indian rhinoceros *(Rhinoceros unicornis). Canadian Journal of Zoology* **80:** 2014–2023.

ZSCHOKKE, S., STUDER, P. & BAUR, B. (1998): Past and future breeding of the Indian rhinoceros in captivity. *International Zoo News* **45:** 261–276.

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APPENDIX
USEFUL ACRONYMS FOR POPULATION MANAGEMENT PLANNING

EEP	European Endangered Species Programme
FGE	Founder Genome Equivalent
GCAP	Global Captive Action Plan
GD	Gene Diversity
GU	Genome Uniqueness
MK	Mean Kinships
PM2000	Population Management 2000
RCP	Regional Collection Plan
REGASP	Regional Animal Species Collection Plan
SPARKS	Single Population Animal Record Keeping System
SSP	Species Survival Plan
TAG	Taxon Advisory Group
TP	Target Population
ZIMS	Zoological Information Management System