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An assessment of demographic parameters of African rhinoceros species (*Diceros bicornis* and *Ceratotherium simum*) and their significance to management in captivity.

by

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GENERAL ABSTRACT

Captive-breeding has been identified as an integral part of the conservation of threatened species. The black rhinoceros (*Diceros bicornis*) as a species is currently listed by the IUCN as critically endangered (CR), while the white rhinoceros's (*Ceratotherium simum*) current status is near-threatened (NT). Three African rhinoceros subspecies currently occur in captive populations in regional population management programmes, namely the South-central black rhinoceros (*Diceros bicornis minor*), the Eastern black rhinoceros (*Diceros bicornis michaeli*) and the Southern white rhinoceros (*Ceratotherium simum simum*). Concerns have been raised, however, that these populations are not self-sustainable. This study aims to analyze the demographic parameters that contribute to the growth rates of the global captive populations of African rhinoceros. The study sets out to determine if these global captive populations are currently self-sustaining, which demographic factors have the most influence on the population growth rates, and whether or not 50- and 100- year targets set for the captive African rhinoceros populations are attainable. Demographic data from 1 January 2010 until 31 December 2010 were analysed through population census, life table and age structure analyses. Two additional concerns, namely poor reproductive performance of the female F_1 generation and male-biased birth sex ratios, were also assessed. The results indicate that the captive populations of *D. b. minor* and *C. s. simum* are not self-sustainable, with population growth rates (λ) of 0.98 and 0.99, respectively. *Diceros bicornis michaeli* is the only subspecies with a growing population, with a population growth rate of 1.02. Sensitivity analyses conclude that fecundity rates, and not mortality rates, are the limiting factor to population growth in all three subspecies. While lifetime reproductive success values for *D. b. minor* and *C. s. simum* captive-born females are far lower than those of the founder generation, several factors need further investigation to determine the true cause of this. Birth sex ratio analysis shows no significant difference from parity for both black rhinoceros subspecies, however, quadratic logit regression conducted on the white rhinoceros data indicated a statistically significant male-bias. In all three subspecies, no significant link was found between maternal age and the sex of the offspring. Overall, the results of this study show that the 50 year and 100 year targets set at the GCAP workshop in 1992 are achievable. However, *D. b. minor* will only be able to achieve the target population sizes with an increase in fecundity rate of around 170% or alternatively, additional supplementation from the wild. Recommendations for the future include a global study of breeding husbandry at an institutional level, and the formalisation of a Global Species Management plan for *D. b. minor*.

KEY WORDS: *Diceros bicornis minor*, *Diceros bicornis michaeli*, *Ceratotherium simum simum*, global captive population sustainability, demographic analysis, target population size, F_1 female reproductive performance.

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DECLARATION

I, the undersigned hereby declare that the dissertation, which I hereby submit for the degree of Master of Science (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE:

DATE: 2014/07/18

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DISCLAIMER

This dissertation consists of a series of chapters that have been prepared as stand-alone manuscripts for subsequent submission for publication purposes. Consequently, unavoidable overlaps and/or repetitions may occur between chapters.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Background

Swaisgood (2006) stated that neither the European nor the North American captive populations of southern white rhinoceros (*Ceratotherium simum simum*) were self-sustainable. Foose & Wiese (2006) reported that the two subspecies of black rhinoceros (*Diceros bicornis minor* and *Diceros bicornis michaeli*) were only marginally self-sustaining in the North American captive populations with population growth rates of 0.996 and 1.017 for *D. b. minor* and *D. b. michaeli*, respectively. Foose & Wiese (2006) also indicated that the performance of the European population of *D. b. michaeli* was similar to the performance of the North American population. At the end of 2004, Europe and North America held 62% of the captive black and 78% of the captive white rhinoceros populations, respectively (Foose & Wiese 2006). This therefore raises concerns regarding the contribution of the captive population in the conservation of these subspecies. While captive populations can play many supportive roles that serve conservation purposes, ideally the populations should be self-sustaining without having to rely on the wild population for additional founders.

Currently, the greatest threat to both black and white *in situ* African rhinoceros populations is poaching, with figures released for the number of rhinoceros poached in South Africa alone increasing dramatically over the past few years. As indicated in Figure 1, in 2007, 13 rhinoceros were poached in South Africa; this number had risen to 448 by 2011 (Borchert 2012). 2012 figures released by the South African Department of Environmental Affairs (DEA) identified 668 poached rhinos for the year, and as of 22 November 2013, 860 rhinoceros had been poached in South Africa so far, already exceeding the poached figures of all previous years (DEA 2013). It is predicted that if the current growth rate of poaching continues, South Africa will experience a decline in South African rhinoceros populations from 2016 (Borchert 2012). Poaching incidents have also been recorded in the past six years in Botswana, the Democratic Republic of Congo (DRC), Kenya, Malawi, Mozambique, Namibia, Swaziland, Tanzania, Zambia and Zimbabwe, with Zimbabwe and Kenya recording the next highest poaching figures to South Africa between 2006 and 2012 (See Figure 2). In 2012, 745 rhinoceros were poached in Africa (Emslie *et al*. 2013).

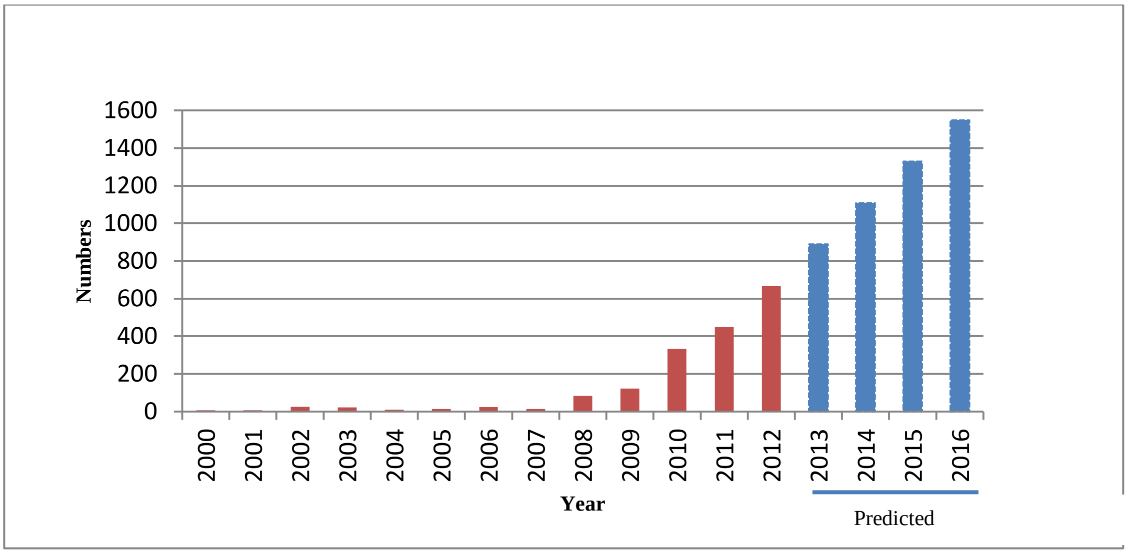

Figure 1: Rhino poaching figures for the Republic of South Africa: 2000-2012.

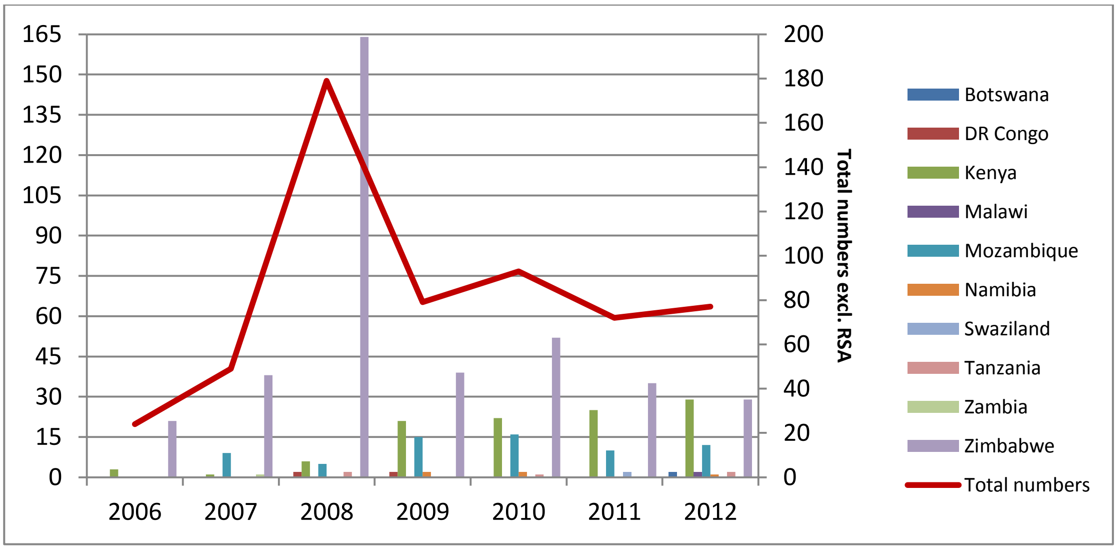

Figure 2: Minimum rhino poaching figures for Africa outside of the Republic of South Africa: 2006-2012.

Genuine concerns exist that world captive populations in general put a strain on wild populations if there is a continuous need to supplement numbers from the wild, adding pressure to already precarious populations. Although the removal of individuals of African rhinoceros populations to supplement captive numbers has not been identified as a significant factor in reducing wild rhinoceros numbers, if the current global captive population is not self-sustainable, the value of the *ex situ* population for the conservation of these species is diminished and it may have a negative impact on the wild population in future, either through the need to draw additional founders from the wild to sustain the captive population, or through the lack of surplus animals for re-introduction should the need arise.

1.1.1. The role of captive-breeding programmes in the conservation of species

Captive breeding is an integral part of the conservation of threatened species. It has been recognized by the International Union for Conservation of Nature and Natural Resources (IUCN) that with the increasing number of threatened taxa, it will not be possible to ensure the survival of most species without the utilization of complementary conservation approaches, including for some taxa, the practical use of *ex situ* techniques (IUCN 2002). This includes maintaining captive populations of threatened species as a form of insurance population. If the wild population is hit by a catastrophe (an epidemic, rampant poaching, habitat destruction, or a natural disaster) this will not lead to complete extinction of the species if there are still captive individuals (WAZA 2005; Hunter & Gibbs 2007). Provided that the species breeds and survives in captivity, there is still a possibility for it to be re-introduced into the wild when the cause of its extinction is no longer there. This has been successfully achieved for a number of species declared extinct in the wild, for example, the Yarqon Bleak (*Acanthobrama telavivensis*), European bison (*Bison bonasus*), Red wolf (*Canis rufus*), Przewalski horse (*Equus ferus przewalski*) and the Arabian oryx (*Oryx leucoryx*) (Maas 2012). Other re-introductions are in progress, but it still remains to be seen if these *in situ* populations will become self-sustaining (Maas 2012). All of these re-introductions, including the most recent, that of the Kihansi Spray Toad (*Nectophrynoides asperginus*) back into Tanzania in October 2012 (IUCN 2012), were only possible because the captive populations were both demographically and genetically self-sustaining.

The goals of *ex situ* populations are highlighted in the "*Draft IUCN guidelines on the use of ex situ management for species conservation*" (unpublished), that were developed to replace the "*IUCN Technical Guidelines on the Management of ex situ populations for Conservation*" (IUCN 2002). The goals have been identified as follows:

- Insurance population (maintaining a viable *ex situ* population of the species to prevent predicted local, regional or global species extinction and preserve options for future conservation strategies);
- Temporary rescue (temporarily remove from the wild to protect from catastrophes or predicted imminent threats, e.g., hurricanes, disease, oil spill). This could be appropriate at either local or global scales;
- Demographic manipulation (removal from the wild to reduce mortality during a specific life stage and then subsequently return to the wild, e.g., head-start programmes);
- Source for population restoration, either to re-establish the species into part of its former range from which it has disappeared, or to reinforce an existing population (e.g., for demographic, behavioural or genetic purposes);
- Source for ecological replacement to re-establish a lost ecological function and/or modify habitats. This may well involve species that are not themselves threatened but that contribute to the conservation of other taxa through their ecological role;
- Source for assisted colonisation to introduce the species outside of its indigenous range to avoid extinction;
- Research and/or training that will directly benefit conservation of the species, or a similar species, in the wild (e.g., monitoring methods, life history information, disease transmission/treatment); and
- Basis for an education and awareness programme that addresses specific threats or constraints to the conservation of the species or its habitat.

In order to develop viable populations in captivity, population management itself needs to achieve the following goals (Foose *et al*. 1995; Ballou & Foose 1996; WAZA 2005):

- Self-sustaining reproduction;
- Demographic security and stability:
    - A 95–99% probability that the population will demographically survive for a predetermined time period (e.g., 100 years) (Foose *et al*.1995);

- Genetic diversity adequate for:
    - Individual fitness, i.e. the ability to survive and reproduce well under current environmental conditions;
    - Population adaptability, i.e. the capacity to adapt to changing environments in the future (Foose & Wiese 2006);
- The goal accepted by the captive community is 90% retention of the wild genetic diversity over a pre-determined period of time (e.g. 100 years); and
- Target population sizes that are large enough to achieve these genetic and demographic goals.

The target size required for the genetic goals should also realise the demographic ones. Also of importance is for the population to attain the target population size as rapidly as possible (Foose *et al*. 1995).

1.1.2. Free-ranging black and white rhinoceros subspecies and their status

Of the five extant rhino species, i.e., the Indian rhinoceros (*Rhinoceros unicornis*; Linnaeus, 1758), Javan rhinoceros (*Rhinoceros sondaicus*; Desmarest, 1822), Sumatran rhinoceros (*Dicerorhinus sumatrensis*; Fischer, 1814), white rhinoceros (*Ceratotherium simum*; Lydekker, 1908) and the black rhinoceros (*Diceros bicornis*; Drummond, 1826), two species are found on the African continent, namely the black and the white rhinoceros (Skinner & Smithers 1990). The white rhinoceros is believed to have derived its name from the Dutch word *wijd*, or wide, allegedly referring to its wide lip (Emslie & Brooks 1999). It is uncertain how the black rhinoceros derived its common name as both species are grey in colour (Emslie & Brooks 1999).

The black rhinoceros on a species level, is currently listed by the IUCN as critically endangered (CR; Emslie 2012b). Between 1980 and 1995, black rhinoceros numbers in Africa decreased dramatically from an estimated 14,785 individuals to an extreme low of 2,410 individuals in 1995, but have since made a remarkable recovery and estimates at the end of 2007 were in the region of 4,200 individuals (Emslie & Brooks 1995; Emslie 2008). Numbers have continued to increase and at the end of 2010, 4,880 were recorded, with current figures reported to be around 5,055 (Emslie 2012b; IUCN 2013).

The white rhinoceros is faring much better and its current status is near-threatened (NT; Emslie 2012a). An estimate of the number in Africa at the end of 2007 was 17,500 individuals (Emslie 2008), with numbers increasing to 20,174 and 20,405 at the end of 2010 and 2012, respectively (Emslie 2012a; IUCN 2013). As outlined below, both species have recognized subspecies.

Black rhinoceros subspecies

Western black rhinoceros (*Diceros bicornis longipes*)

Eastern black rhinoceros (*Diceros bicornis michaeli*)

South-western black rhinoceros (*Diceros bicornis bicornis*)

South-central black rhinoceros (*Diceros bicornis minor*)

The four subspecies of black rhinoceros have historically occupied ranges that do not have clearly defined boundaries. Four subspecies have been classified however, as the core area for each group differs significantly in habitat and climate, and therefore the different populations in each area are likely to differ in behaviour and/or genetic adaptive traits (Emslie & Brooks 1999). Certain differences in morphology and temperament have been noted between the four subspecies (Emslie & Brooks 1999). For this reason, conservationists sometimes refer to the black rhinoceros subspecies as ecotypes, rather than subspecies (Emslie & Brooks 1999).

Western black rhinoceros (*Diceros bicornis longipes*)

Until recently, this was the most rare and endangered of the black rhinoceros subspecies, with 1999 estimates suggesting that a few scattered individuals remained in northern Cameroon and possibly in Chad (Emslie & Brooks 1999). These individuals lived in widely scattered groups that appeared to have limited breeding encounters with each other (Emslie & Brooks 1999). A re-assessment of the numbers of individuals in 2008 suggested that this subspecies is now extinct, as surveys through much of the range in northern Cameroon failed to record any individuals, but found widespread evidence of poaching (Emslie 2008; IUCN 2008e). A review of the IUCN Red list status in 2011 re-classified the subspecies as extinct (Emslie 2011b).

Eastern black rhinoceros (*Diceros bicornis michaeli*)

The current stronghold of this subspecies is Kenya, where numbers seem to be steadily increasing (Emslie 2008; IUCN 2008f). Rwanda and Tanzania still hold small numbers, but its presence in Ethiopia needs to be confirmed (Emslie & Brooks 1999; Emslie 2008). An important free-ranging population was established in 1961 outside of its natural geographic range at Addo Elephant National Park in South Africa. At a later stage, these animals were moved to a private reserve somewhere else in South Africa. Contractually, these animals may only be re-located back to their natural range, and not to any other reserve in South Africa, nor transferred into zoos (IUCN 2008f). The first five descendants of the original seven individuals were translocated to the Serengeti National Park in Tanzania on 21st May 2010, one of which was poached shortly thereafter in November 2010 (Anon 2010; 2011). One of the translocated females gave birth in February 2011, however, the mother and her calf were poached in May 2012, resulting in four senior wildlife officials and 28 game wardens being suspended as the deaths were not discovered until several days after the event (Anon 2011; Cota-Larson 2012). Initially, a further 27 individuals were expected to be translocated from South Africa to the Serengeti National Park between 2010 and 2012 (Anon 2010), but after the first poaching event United States Fish and Wildlife Services, which was planning the translocation, issued a statement that any further relocation plans were being “re-assessed” (Cota-Larson 2012). Numbers of *in situ* eastern black rhinoceros at the end of 2007 were estimated to be around 700 individuals, increasing to 740 by the end of 2010 (Emslie 2008; Emslie 2011c). This subspecies is listed as critically endangered by the IUCN (Emslie 2011c).

South-western black rhinoceros (*Diceros bicornis bicornis*)

This subspecies is adapted to more arid conditions than the other subspecies, and is the only black rhinoceros subspecies listed as vulnerable (VU) by the IUCN (Emslie 2011a). Currently, the stronghold for this subspecies is Namibia, where significant populations remain in the desert and arid savannah areas of the country (Emslie & Brooks 1999). In recent years, other small populations have been re-established elsewhere in Namibia and in the south-western part of South Africa (Emslie & Brooks 1999). A possibility also exists that a few animals may still occur in Angola (Emslie & Brooks 1999). In 2007, continental total estimates for this subspecies was 1,505 individuals, which by the end of 2010 had risen to 1,920 (Emslie 2008; IUCN 2008d; Emslie 2011a).

South-central black rhinoceros (*Diceros bicornis minor*)

This is the most common of the black rhinoceros subspecies, with South Africa holding the strongest population and to a lesser extent Zimbabwe, with smaller numbers remaining in southern Tanzania. The south-central black rhinoceros is now believed to be extinct in Angola and possibly also in Mozambique (IUCN 2008g). Re-introductions have been undertaken in Botswana, Malawi, Swaziland and Zambia (IUCN 2008g). This subspecies is listed as critically endangered as the population is estimated as having declined by an amount exceeding 80% over the past three generations (Emslie 2011d). This subspecies, however, is making a steady recovery in its current major range state of South Africa. Numbers increased from 110 individuals in 1930, to 1,094 individuals by 2001 and 1,684 individuals by the end of 2010 (Emslie 2008; Emslie 2011d). Numbers in the second largest range state, Zimbabwe, have unfortunately declined resulting in total current numbers still being lower than three generations ago. Therefore, its Red list status remains as critically endangered despite the positive growth seen in South Africa (Emslie 2011d).

White rhinoceros subspecies

Northern white rhinoceros (*Ceratotherium simum cottoni*)

Southern white rhinoceros (*Ceratotherium simum simum*)

The two white rhinoceros subspecies, the northern and the southern white rhinoceros, have a clear discontinuous distributional range (IUCN 2008a). With a call for taxonomic re-assessment by Groves *et al*. (2010), the remaining northern white rhinoceros have become a profoundly important group for conservation efforts. Groves *et al*. (2010) indicated that there is sufficient morphological and genetic evidence to warrant recognition of the two subspecies as two separate species, *C. simum* and *C. cottoni*. This has not been universally agreed on, however, as there are a number of ways to classify species (Emslie 2012a). For the purpose of this dissertation, I will continue to treat them as subspecies.

Northern white rhinoceros (*Ceratotherium simum cottoni*)

Historically, the northern white rhinoceros occurred over parts of north-western Uganda, southern Chad, south-western Sudan, the eastern part of the Central African Republic and north-eastern Democratic Republic of Congo (DRC) (IUCN 2008b). At the time of the 2008 IUCN assessment, Garamba National Park held the only confirmed extant population in the DRC. Between 1984 and 1995, numbers in Garamba National Park increased from 15 to 31, with 24 births recorded during that time period (Smith *et al*. 1995). Later surveys confirmed that the population in the DRC decreased to 25 individuals by June 1998 (Mackie 1998). A further survey brought the number down to only four individuals. Listed as critically endangered (CR), the most recent assessment failed to confirm the presence of this subspecies at all, raising concerns that this subspecies may now be extinct in the wild (IUCN 2008b). In an effort to try and save this subspecies from imminent extinction, four potentially breeding individuals were translocated from Dvur Kralove Zoo in the Czech Republic to Ol Pejeta Reserve in northern Kenya in late 2009. It was hoped that the change in environment might trigger breeding (Rookmaaker 2010), but although mating was witnessed, there has been no successful breeding (Ol Pejeta Conservancy 2013). The latest strategy, given the high mean kinship amongst the four surviving Northern white rhinoceros, is to cross-breed them with Southern white rhinoceros in the hope to retain some *C. s. cottoni* genes for later adaptation back to their natural wild habitat (Emslie 2012a).

Southern white rhinoceros (*Ceratotherium simum simum*)

Historically restricted to bushveld areas in southern Africa, south of the Zambezi, the southern white rhinoceros is currently the most numerous of the rhinoceros taxa; a remarkable feat as towards the end of the 19th century it numbered only in the region of 20 animals in a single population found in KwaZulu-Natal, South Africa (Emslie & Brooks 1999; IUCN 2008c). Its recovery has been globally acclaimed as one of the world’s greatest conservation successes and numbers in 1999 were estimated at around 8,440 individuals (Emslie & Brooks 1999). Currently, South Africa is the stronghold for this subspecies, with much smaller re-introduced populations occurring within its former range in Swaziland, Botswana, Namibia, Zimbabwe and Mozambique. Free-ranging populations of southern white rhinoceros have also been established in Ivory Coast, Kenya and Zambia, outside of their historical range (Emslie & Brooks 1999). By December 2007, there were an estimated 17,500 animals in 433 populations in Africa (Emslie 2008). Numbers published recently by the IUCN indicates an increase to 20,170 in 2010 and further up to 20,405 at the end of 2012 (Emslie 2012a; IUCN 2013).

1.1.3. The status and breeding performance of captive African rhinoceroses

At a 1992 Global Captive Action Plan (GCAP) workshop, target population sizes for the global *ex situ* populations of black and white rhinoceros were formulated with the primary target of preserving 90% genetic diversity for 100 years (Foose & Wiese 2006). The target captive population size is a compromise between the optimum population to ensure maximum genetic and demographic integrity, and the availability of captive capacity, taking enclosure space and resources into consideration (Foose & Wiese 2006). Ten-, 50- and 100-year target population sizes were set at 200, 240 and 240 for *D. b. michaeli*, 80, 160 and 400 for *D. b. minor* and 515, 525 and 500 for *C. s. simum*, respectively, with a total 10-, 50- and 100-year target of 795, 925 and 1,140 individuals, respectively (Foose & Wiese 2006). No targets were set for the Northern white rhinoceros (*C. s. cottoni*) and no captive programmes were recommended for either the South-western black rhinoceros (*D. b. bicornis*) or the Western black rhinoceros (*D. b. longipes*) (Foose & Wiese 2006). Commenting on these target populations sizes set in 1992, Emslie & Brooks (1999) stated that as a very high proportion of captive white rhinoceros were over 25 years old (approximately 42%), a reduction in the population was expected to happen automatically. At the end of 1998, 948 African rhinoceros were recorded in captivity world-wide; 60 *D. b. minor*, 175 *D. b. michaeli*, 9 *C. s. cottoni* and 704 *C. s. simum* (Emslie & Brooks 1999). By 2004, these figures had increased to 997; 69 *D. b. minor*, 171 *D. b. michaeli*, 10 *C. s. cottoni* and 757 *C. s. simum* (Foose & Wiese 2006). While the total number of African rhinoceroses in captivity at the end of 2004 met the 10 year target number set in 1992, it was identified that the proportion of black rhinoceros in relation to the number of white rhinoceros needs to be increased in order to meet the targets on the species level (Foose & Wiese 2006). The targets to be achieved in the next 30 years (in order to reach the 50 year target) are now 160 *D. b. minor*, 240 *D. b. michaeli* and 525 *C. s. simum* (Emslie & Brooks 1999; Foose & Wiese 2006).

Generally, both the black and white rhinoceroses in captivity have the potential for genetic viability with excellent founder stock at the species level (Foose & Wiese 2006). However, population growth rates for the eastern black rhinoceros and both subspecies of white rhinoceros in captivity have historically been inadequate (Leader-Williams 1993; Stanley-Price 1993). Future efforts should focus on a high growth rate for black rhinoceros, and a self-sustaining population of white rhinoceros. It is estimated that there are *ca*. 300 zoos worldwide that currently hold rhinoceros species in their collections (Foose & Wiese 2006).

Black rhinoceros in captivity

Currently, there are no captive populations of south-western black rhinoceros (*D. b. bicornis*) or the western black rhinoceros (*D. b. longipes*). Separate captive-breeding programmes do exist for the two other subspecies of black rhinoceros, namely the eastern black rhinoceros (*D. b. michaeli*) and south-central black rhinoceros (*D. b. minor*) (Foose & Wiese 2006).

With black rhinoceros, high mortality rates, sub-optimal reproductive performance as well as a number of health and husbandry problems have been identified as hampering successful captive breeding (Smith & Read 1992; Paglia & Dennis 1999; Paglia *et al*. 2002; Weber *et al*. 2002; Miller 2003; Dennis 2005; Dennis *et al*. 2007; Linklater 2007). Major causes of death have been identified as haemolytic anaemia, mucocutaneous ulcer disease, cholestatic hepatopathy, encephalomacia, fungal pneumonia, leptospirosis and tuberculosis (Miller 1994; Foose 1995). In a survey of captive black rhinoceros in North America, 40% of all adult deaths were caused by haemolytic anaemia (Miller 1994). Ill health from mucocutaneous ulcer syndrome has also been very high (Miller 1994). Research shows that the diseases may be related to unusual blood chemistry found in black rhinoceros, and in the 1990s concern was also raised that the diets of captive black rhinoceros had been deficient, possibly contributing to poor *ex situ* breeding rates recorded in some institutions (Emslie & Brooks 1999).

One further concern for the sustainability of the North American captive black rhinoceros population was identified by the American Association of Zoos and Aquariums (AZA) in their 2002 Rhinoceros Species Survival Plan (SSP) Masterplan (AZA 2002), which states that the skew toward males in the sex ratio of calves is an increasing concern for the captive population of black rhinoceroses in North America. A male bias creates difficulties in managing large animals such as these in a captive environment as excess males take up zoo space, which is limited as it is (Dennis *et al*. 2007).

Eastern black rhinoceros (*Diceros bicornis michaeli*)

The population growth rate of the eastern black rhinoceros in captivity has been disappointing, with the population at the end of 1998 standing at 175, having shown a net increase from births and deaths of only 2 (65 births and 63 deaths) between 1993 and 1998; and with a further decrease to 171 by 2004 (Emslie & Brooks 1999; Foose & Wiese 2006). The reason for this poor performance suggested by Emslie & Brooks (1999), is that the eastern black rhinoceros in captivity are generally older animals (17% over the age of 25 as opposed to 3% older than 25 for *D. b. minor*), that were born well before the advances in rhinoceros research and husbandry techniques that are currently available. The 171 living animals recorded as being in captivity at the end of 2004 were then housed in 51 separate captive institutions (Foose & Wiese 2006).

South-central black rhinoceros (*Diceros bicornis minor*)

Emslie & Brooks (1999) reported that a significant achievement has been made with the captive south-central black rhinoceros population slowly increasing, with a world-wide net increase of 13 animals to a population of 60 animals (a result of 29 births and 16 deaths) between 1993 and the end of 1998. World-wide figures given by Foose & Wiese (2006) seem to verify this trend, with numbers of the south-central subspecies increasing further by 9 to 69 between 1999 and 2004. An increase in numbers is encouraging (Emslie & Brooks 1999; Foose & Wiese 2006), with the relative success of the south-central black rhinoceros attributed to the population having been established more recently, was younger and had the full benefit of advanced scientific husbandry (Emslie & Brooks 1999). In 2004, 69 individuals of this subspecies were located in 16 institutions (Foose & Wiese 2006).

White rhinoceros in captivity

In the Status Survey and Conservation Action Plan for African Rhino compiled by Emslie & Brooks (1999), it was estimated that the North American captive population of white rhinoceros declined between 1996 and 1998 by 3.5% per year. Slightly more optimistic figures were reported by Foose & Wiese (2006), according to whom the North American population was marginally self-sustaining from 2001 until 2005, with a population growth rate (λ) of 1.001. At the time of drafting the Action Plan, analyses were not available for the European population, but crude assessments conducted by Foose & Wiese (2006) suggested a similar situation. In contrast, wild populations held in well protected areas below the ecological carrying capacity can achieve a growth rate of between 6.5% and 10% per year (Emslie & Brooks 1999). Emslie & Brooks (1999) stated that it remained to be seen whether a combination of improved diets and husbandry, the development of more extensive paddock systems, and the application of results from reproduction research, would result in captive rates of productivity that consistently approach levels seen in protected areas in the wild (Emslie & Brooks 1999). The comparatively low growth rate of white rhinoceros in captivity may be due to fertility issues (Patton *et al*. 1999; Hermes *et al.* 2002, 2004, 2005, 2006), in particular poor reproductive performance of the captive-born F_1 generation (Swaisgood *et al*. 2006). Swaisgood *et al*. (2006) expressed concern that the reproductive performance of the captive population would worsen as the breeding founders that previously drove the growth in the population began to die off, necessitating the capture of additional founders to support the captive population. Taking the GCAP targets into consideration, growth rates comparable to those of the wild population are clearly not the management goal for *C. s. simum*, which aims to have a sustainable population at a reduced number than is currently found in captivity. Any reduction in numbers, however, should be due to a controlled decline, and not because of either reproductive or mortality issues which would affect sustainability in the future.

Northern white rhinoceros (*Ceratotherium simum cottoni*)

Captive reproduction of Northern white rhinoceros has been slow with six births recorded since 1977. Efforts have been made to stimulate reproduction in the small and ailing captive population of this subspecies, considering the potentially extinct status of this subspecies in the wild (Hermes *et al*. 2005). The last birth in captivity was in 2000 (Christman 2008). At the end of 2008, only 9 individuals of this subspecies (1:1 at San Diego Wild Animal Park in the United States and 2:5 at Dvur Kralove Zoo in the Czech Republic) were present in captive facilities, these possibly being the world’s last individuals (Christman 2008). This included one hybrid *C.s. simum* x *C.s. cottoni* located at Dvur Kralove Zoo (Christman 2008). As noted before, four of these remaining captive animals were translocated to a reserve in northern Kenya in 2009 in the hope that the change in environment would trigger breeding (Rookmaaker 2010). In May 2011, one of the remaining captive animals died at Dvur Kralove Zoo, leaving only three pure bred *C. s. cottoni* in captivity, a 29 year old female at Dvur Kralove Zoo; and a 41 year old male and 38 year old female at San Diego Wild Animal Park (Johnston 2011).

Southern white rhinoceros (*Ceratotherium simum simum*)

Regional captive population programmes exist for the Southern white rhinoceros subspecies (Foose & Wiese 2006). Reproductive success of the southern white rhinoceros in captivity has been noted on several occasions, especially where a number of animals, including more than one male, have been held in large enclosures that more closely simulate wild conditions. One cow at the San Diego Wild Animal Park, U.S.A., for example, has produced 10 calves in captivity and since 1971, 14 cows there have given birth to 75 calves (Reiches 1993). Southern white rhinoceros are less prone to fatal diseases in captivity than black rhinoceros and, being grazers, are easier to feed than the browsing black rhinoceros. Despite these successes, the overall annual rates of increase obtained in captivity are still well below those of well-protected free-ranging populations. From 1993 to 1998, six more southern white rhinoceros died than were born in captivity world-wide (Emslie & Brooks 1999). The South African Natal Parks Board exported 658 southern white rhinoceros to destinations outside Africa between 1962 and 1994 (Emslie & Brooks 1999). As there were only an estimated 646 southern white rhinoceros in captivity in 1997, Emslie & Brooks (1999) reported that captive breeding programmes overall had failed to increase numbers. It is unclear however, whether all the animals exported went into the regional breeding programmes or to non-participating facilities, as international studbook data indicate that only 639 individuals entered the breeding programmes during that period, originating not only from KwaZulu-Natal, South Africa but also from the Kruger National Park, South Africa and other *in situ* locations (Frese 2008). Updated 2004 figures compiled by Foose & Wiese (2006) showed an increase by 101 to 747 individuals in seven years (including 27 captures), which corresponds to an increase of 1.93% per annum. By comparison, the white rhinoceros re-introduced into the Kruger National Park, South Africa achieved an average growth rate of 8.4% per year, potentially causing a doubling of numbers every nine years (Emslie & Brooks 1999). Similarly, 20 animals taken to Kenya in the 1970s had increased at a rate of 11% per annum causing the population to increase three and a half times up until 1992 (Brett 1993). On the downside, in a number of African range states where law enforcement efforts were not sufficient to prevent poaching, some re-established wild populations of southern white rhinoceros have performed worse than out-of-range zoos and safari parks (Emslie & Brooks 1999).

The latest analysis of the North American captive population demonstrates that the population has shown a marginal increase with a λ of 1.001 (Foose & Wiese 2006). This is considerably better than the -3.5% growth rate reported in Emslie & Brooks (1999) for the same population, but is still a major contrast to net population growth rates of 6.5% to 11% per year achieved by well-protected wild populations held below ecological carrying capacity (Brett 1993; Emslie & Brooks 1999). Studies of zoo populations of white rhinoceros by Lindemann (1982) showed that the breeding success of groups of white rhinoceros females with only one male was significantly lower than in groups with more than one male. It has also been suggested that pairs of rhinoceros that mature together from a young age in captivity usually do not breed, but a change to a new facility may trigger breeding (Emslie & Brooks 1999). It also appears that larger groups have higher reproductive success (Reece 1993). In 1999, it was felt that the problem of poor population growth rates was largely due to most zoos having display animals only, with many white rhinoceros in North America found in non-breeding pairs in small enclosures (Emslie & Brooks 1999). Concerns have also recently been raised regarding the reproductive failure of the F_1 generation of southern white rhino, further contributing to the lowering of the captive population growth rate (Swaisgood *et al*. 2006). Whether the 2006 growth rate has been achieved as a result of changes to captive management is uncertain. What is important now is that the population will stabilise at the target population numbers that have been set, and does not decline further due to the concerns mentioned above.

1.2 Problem statement

Based on studies of captive populations of black and white rhinoceros subspecies in North America and Europe, it has been claimed that the captive populations of these animals are not self-sustaining, or if they are, only marginally so (Foose & Wiese 2006, Swaisgood 2006). If global captive populations prove to be unsustainable without the assistance of additional founders, the conservation value of the captive population is diminished. In addition, global target population sizes will not be achievable. While many reasons for this have been proposed and analyzed, age-specific demographic dynamics have not been truly assessed, and previous studies are based on regional populations rather than the global captive population.

1.3 Aims of the study

Given the above background, the aims of the present study are to analyze the demographic parameters that contribute to the growth rates of the global captive populations of African rhinoceros, and to make management recommendations to maximize growth potential within the target population goals set out at the GCAP workshop (Foose 1995).

1.4 Study objectives

Given the aims above, the objectives of the present study are:

- To determine if the current captive populations of *D. b. minor*, *D. b. michaeli* and *C. s. simum* currently rely on supplementation of wild-caught animals for their sustainability;
- To ascertain if the captive population can be sustainable into the future without the need for additional founders and reliance on their breeding;
- To determine if the current age structures of the captive rhinoceros populations differ significantly from stable age structures thereby affecting population growth rates;
- To examine if there are significant differences in age-specific fecundity and mortality rates of the captive populations compared to *in situ* populations;
- To investigate which changes to fecundity or mortality rates in specific age classes would have the most significant effect on future population growth rates;
- To determine if the fecundity and mortality rates of the F_1 generation differs significantly from the F_0 generation and if these differences occur in specific age classes;
- To examine if the birth sex ratios differ significantly from the expected 1:1 norm; and
- To examine if the birth sex ratio is male biased and if the bias is dependent on the age of the dam.

1.5 Scope of study

The present study focuses on three of the six African rhino subspecies as they are currently found globally in zoological gardens in sufficient numbers for data collection and analysis. Private game reserves or game farms, which may be considered captive or *ex situ*, generally do not participate in regional zoological population management programmes and therefore do not form part of this study. The three subspecies are the south-central black rhinoceros, *Diceros bicornis minor*, the eastern black rhinoceros, *Diceros bicornis michaeli*, and the southern white rhino, *Ceratotherium simum simum.* In Chapter 2, data collated from the captive population between 1 January 2001 and 31 December 2010 were assessed. For Chapters 3 and 4, all data from the first available captive records were analyzed.

1.6 Research Questions

For all three subspecies, the present study will attempt to address the following specific research questions:

- Based on 2010 figures, are the global captive populations of *D. b. minor*, *D. b. michaeli* and *C. s. simum* currently self-sustaining?
- Which demographic factors have the most influence on the population growth rate of the three sub-species? and
- Are the 50- and 100- year targets set for the captive African rhinoceros populations attainable?

1.7 Research hypotheses

Given the above specific research questions, the present study will test the following specific research hypotheses relating to *D. b. minor*, *D. b. michaeli* and *C. s. simum*:

- *Null* (H_0) *hypothesis*: The global captive rhinoceros populations have age structures that are stable;
- *Alternative* (H_A) *hypothesis*: The global captive rhinoceros populations have age structures that are not stable;
- *Null* (H_0) *hypothesis*: There are no significant differences in age-specific mortality and fecundity rates in global captive rhinoceros populations in comparison to *in situ* populations;
- *Alternative* (H_A) *hypothesis*: There are significant differences in age-specific mortality and fecundity rates in global captive rhinoceros populations in comparison to *in situ* populations;

- *Null (H_0) hypothesis*: Lifetime reproductive success of F_1 generation females is not significantly different to that of the founder population;
- *Alternative (H_A) hypothesis*: Lifetime reproductive success of F_1 generation females is significantly different to that of the founder population;
- *Null (H_0) hypothesis*: Aging of the F_0 generation will not significantly affect future growth rates of the global captive population;
- *Alternative (H_A) hypothesis*: Aging of the F_0 generation will significantly affect future growth rates of the global captive population;
- *Null (H_0) hypothesis*: Birth sex ratios do not differ from the theoretical 1:1 sex ratio;
- *Alternative (H_A) hypothesis*: Birth sex ratios differ from the theoretical 1:1 sex ratio;
- *Null (H_0) hypothesis*: Females of prime breeding age produce equal numbers of male and female offspring;
- *Alternative (H_{A1}) hypothesis*: Females of prime breeding age produce more male than female offspring; and
- *Alternative (H_{A2}) hypothesis*: Females of prime breeding age give birth to more female than male offspring.

1.8 Relevance of the study

Captive-breeding is an integral part of the conservation of threatened species. It has been recognized by the IUCN that with the increasing number of threatened taxa, it will not be possible to ensure the survival of most species without the utilization of complementary conservation approaches, including for some taxa, the practical use of *ex situ* techniques (IUCN 2002). This includes maintaining captive populations of threatened species as a form of insurance. This will only be possible if the captive population is both demographically and genetically self-sustaining. Black rhinoceros and white rhinoceros are listed by the IUCN as being critically endangered (CR) and near threatened (NT), respectively (Emslie 2012a; 2012b).

In the 1999 Status Survey and Conservation Action Plan for African Rhino, captive populations were identified as potential safety nets should field conservation efforts fail (Emslie & Brooks 1999).

Concerns however, have been raised that neither the European nor the North American captive populations of the southern white rhinoceros (*C. s. simum*) and the black rhinoceros subspecies (*D. b. minor* and *D. b. michaeli*) are self-sustaining (Foose & Wiese 2006; Swaisgood 2006). At the end of 2004 these two continents held 78% of the captive white and 62% of the captive black rhinoceros populations, respectively (Foose & Wiese 2006).

1.9 Thesis outline

The present thesis is structured as follows. Chapter 2 aims to determine if the captive populations of *D. b. minor*, *D. b. michaeli* and *C. s. simum* are self-sustainable, and to identify factors that are impacting population growth rates. Population census and life history data of the three subspecies under review are investigated, and bench-marked to the data reported for the *in situ* population. Sensitivity analysis is conducted to determine whether fecundity or mortality factors affect population growth rates and how various changes in these might influence the population growth rates. Furthermore, age structure analyses are conducted to determine if the current populations have stable age distributions, thereby making it possible to predict future growth accurately. Chapter 3 aims to determine whether female captive-born rhinoceros have lower fecundity rates to founder females in the population, as claimed by Swaisgood *et al*. (2006) for *C. s. simum*. This chapter assesses founder *versus* captive-born female life tables in order to compare fecundity and mortality rates; and ultimately overall lifetime reproductive rates for all three subspecies. Chapter 4 evaluates birth sex ratios to determine if a male biased birth sex ratio exists in any of the three populations under analysis. Also investigated is whether any change in birth sex ratio bias occurs as dams age, linking this to maternal condition. Chapter 5 provides a general discussion of the major findings of the study and discusses future research directions. Finally, Chapter 6 provides general conclusions and recommendations.

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CHAPTER 2

POPULATION CENSUS AND LIFE TABLE ANALYSIS OF THREE AFRICAN RHINOCEROS SUBSPECIES (*DICEROS BICORNIS MINOR, DICEROS BICORNIS MICHAELI* AND *CERATOTHERIUM SIMUM SIMUM*) IN CAPTIVITY

2.1 Abstract

Population census and life table analyses are essential tools in the field of population ecology and when assessing the status of a population. The current global captive populations of three subspecies of African rhinoceros (*Diceros bicornis minor, Diceros bicornis michaeli* and *Ceratotherium simum simum*) were analysed through population census, life table and age structure analyses to determine whether their respective captive populations are self-sustaining, therefore not having to rely on the addition of founders from the wild population. The results indicate that the captive populations of *D. b. minor* and *C. s. simum* are not self-sustainable, with a λ below 1.0 (0.98 and 0.99 respectively). However, *D. b. michaeli* shows a positive population growth rate of 1.02. Sensitivity analysis conducted on a number of fecundity and mortality factors, including bench-marking to *in situ* populations, indicates that fecundity rates, and not mortality rates, are the limiting factor to population growth in all three subspecies. Age structure analysis indicates that the female population of *D. b. minor* has a stable age structure whereas the male population does not. In the case of *C s. simum*, both males and females have age distributions that are significantly different to a stable age distribution. Finally, both male and female *D. b. michaeli* show stable age distributions adding weight to future predictions of a positive population growth rate for this subspecies.

Key words: Stable age structure, population growth rate, self-sustainable global captive population.

2.2 Introduction

Captive-breeding is an integral part of the conservation of threatened species. It has been recognized by the IUCN that with the increasing number of threatened taxa, it will not be possible to ensure the survival of most species without the utilization of complementary conservation approaches, including for some taxa, the practical use of *ex situ* techniques (IUCN 2002). This includes maintaining captive populations of threatened species as a form of insurance. This will only be possible if the captive population is both demographically and genetically self-sustaining.

Black rhinoceros (*Diceros bicornis*; Drummond, 1826) and white rhinoceros (*Ceratotherium simum*; Lydekker, 1908) are listed by the IUCN as being critically endangered (CR) and near threatened (NT), respectively (Emslie 2012a; 2012b). In the 1999 Status Survey and Conservation Action Plan for African Rhino, captive populations were identified as potential safety nets should field conservation efforts fail (Emslie & Brooks 1999). Concerns however, have been raised that neither the European nor North American captive populations of the southern white rhinoceros (*Ceratotherium simum simum*) are self-sustaining, while black rhinoceros subspecies (*Diceros bicornis minor* and *Diceros bicornis michaeli*) are marginally self-sustaining (Foose & Wiese 2006; Swaisgood 2006). At the end of 2004, these two continents held 78% of the captive white and 62% of the captive black rhinoceros populations, respectively (Foose & Wiese 2006).

At a 1992 Global Captive Action Plan (GCAP) workshop, target population sizes for the global *ex situ* populations of black and white rhinoceros were formulated using the preservation of 90% genetic diversity for 100 years as the primary target (Foose & Wiese 2006). The target captive population size is a compromise between the optimum population to ensure maximum genetic and demographic integrity, and the availability of captive capacity, taking enclosure space and resources into consideration (Foose & Wiese 2006). Ten, 50 and 100 year target population sizes were set at 200, 240 and 240 for *D. b. michaeli*, 80, 160 and 400 for *D. b. minor* and 515, 525 and 500 for *C. s. simum*, respectively, with a total 10, 50 and 100 year target of 795, 925 and 1,140 individuals, respectively (Foose & Wiese 2006).

Population growth rate is the key unifying variable of population ecology and plays a central role in forecasting future population trends (Sibly & Hone 2002). Population growth rate is typically estimated using census data over time; or from demographic life history data (Sibly & Hone 2002). The most basic calculation of population growth rate can be derived from population census data and is described as the factor by which population size increases per year, conventionally given the symbol λ (lambda) (Sibly & Hone 2002). Although this gives a good indication in the population trend over time, the drawback of this approach is that it does not specify the individual effects that births, deaths, immigration and emigration have on the population, or how birth (fecundity) and death (mortality) rates vary throughout an animals' lifespan and therefore the effect a populations age structure will have on population growth rate into the future. The analysis of life history traits ignores the effect of immigration and emigration, focusing on the effect that age structured fecundity and mortality rates have on population growth.

The analysis of life history traits has been used as an important tool for conservation managers across a variety of animal taxa, such as birds (Dennis *et al*. 1991; Heppel *et al*. 2000; Low & Pärt 2009; Mitchell *et al*. 2009; Ortega *et al*. 2009; Schaub *et al*. 2009; Sim *et al*. 2011), eutherian mammals (Dennis *et al*. 1991; Coulson 2005), marsupials (Lachish *et al*. 2009) and reptiles (Heppel 1998; Enneson & Litzgus 2008). Once the life history data have been collated and the life tables and survival curves constructed, several analyses are possible. The data can be used to construct Leslie matrices, the first Eigen value of which equals λ assuming a stable age distribution, and the corresponding right Eigen vector represents the stable age distribution. If the life table λ differs significantly from the actual population growth rate (λ derived from population census data), it is an indication that either the current age distribution is far removed from the stable distribution or that immigration and emigration play a significant role on population growth rate. A simulation run starting with the current age distribution will show how the population will develop towards the stable age distribution, provided that the life table does not change. The entries in the Leslie matrix can be manipulated to separately evaluate the effects of the captive environment on population growth through reproduction and mortality, respectively. Furthermore, a sensitivity analysis can be carried out to evaluate changes at different ages, and the data can be used to calculate and subsequently analyze the resulting growth rates (Stearns 1992; Roff 1992).

Both survivorship and fertility differ greatly across species and there is a need to understand the effects that age-specific survivorship and fertility have on the dynamics of a population before implementing a management plan that would actually be effective in promoting its long-term survival (Rockwood 2006). Understanding how these rates drive the variation in population growth rate (λ) is the key to predicting population dynamics, and is therefore, central to both fundamental and applied population ecology (Sim *et al*. 2011).

Life history traits are directly linked to fitness and are continuously exposed to strong selection pressures (Roff 1992; Stearns 1992). It is therefore assumed that a species life-history in its natural environment is closest possible to the optimal for that environment (Roff 1992; Mayr 1983). The captive environment is in most cases vastly different from the wild, and reproduction in this environment is to a large extent controlled by humans. Captive populations are managed to be self-sustaining, so that no capture of wild animals is necessary. In some cases, however, captive populations may decline despite all attempts to manage them for growth. To understand the cause of such a decline, examination of the life table and the age structure of the population are necessary. The life table for growing wild populations, if available, can serve as a benchmark for comparison. These tools can be used to establish whether low performance of a population is due to high mortality, low reproductive rates, late onset of reproduction or a combination of these. The important variables which describe a life history and determine the population growth rate (λ) are age at first and last reproduction, age-specific mortality and age-specific fecundity (Roff 1992; Stearns 1992). Depending on how the life history is configured, the population growth rate can be more or less sensitive to changes in any of these variables (Rockwood 2006).

The present study uses the life tables of wild rhinoceros as the benchmark because wild populations of both black and white rhinoceros have achieved population growth rates of up to 11% which gives a good indication of the growth potential of the species (Brett 1993). The bench-marking exercise will in all likelihood reveal differences in a number of variables. However, not all variables are of equal importance. From a management point of view, it would be sensible to prioritize those variables with the largest impact on population growth. The use of sensitivity analysis on the life tables will assist in identifying the variables that have the largest effect on the population growth rate, and thereby guide management recommendations (Sim *et al.* 2011). Life table analysis will also provide an expected stable age structure, which can be compared with the current age structure. If the current age structure is similar to the predicted stable age distribution it can be predicted, through simulation runs, how the population will develop into the future, starting from the current situation.

Given the above background, the aims of the present chapter are to analyse the demographic parameters that contribute to the growth rates of the global captive populations of African rhinoceros, and to make management recommendations to maximize growth potential within the target population goals set out at the GCAP workshop (Foose 1995).

For all three subspecies, the present study will attempt to address the following specific research questions:

- Based on 2010 figures, are the global captive populations of *D. b. minor*, *D. b. michaeli* and *C. s. simum* currently self-sustaining?
- Which demographic factors have the most influence on the population growth rate of the three sub-species? and
- Are the 50- and 100-year targets set for the captive African rhinoceros populations attainable?

Given the questions above, the objectives of the present study are therefore:

- To determine if the current captive populations of rhinoceros currently rely on supplementation of wild-caught animals for their sustainability;
- To ascertain if the captive population can be sustainable into the future without the need for additional founders and reliance on their breeding;
- To determine if the current age structure of the captive rhinoceros populations differ significantly from a stable age structure and, if so, how this affects population growth rates;
- To examine if there are significant differences in age-specific fecundity and mortality rates of the captive populations compared to *in situ* populations; and
- To investigate which changes to fecundity or mortality rates in specific age classes would have the most significant effect on future population growth rates.

The present study focuses on three of the six African rhino subspecies, the south-central black rhinoceros, *D. b. minor*, the eastern black rhinoceros, *D. b. michaeli*, and the southern white rhino, *C. s. simum* and uses demographic data for a ten-year period between 2001 and 2010.

The present study will test the following specific research hypotheses:

- *Null (H_0) hypothesis*: The global captive rhinoceros populations have age structures that are stable;
- *Alternative (H_A) hypothesis*: The global captive rhinoceros populations have age structures that are not stable;
- *Null (H_0) hypothesis*: There are no significant differences in age-specific mortality and fecundity rates in global captive rhinoceros populations in comparison to *in situ* populations;
- *Alternative (H_A) hypothesis*: There are significant differences in age-specific mortality and fecundity rates in global captive rhinoceros populations in comparison to *in situ* populations;
- *Null (H_0) hypothesis*: Aging of the F_0 generation will not significantly affect future growth rates of the global captive population;
- *Alternative (H_A) hypothesis*: Aging of the F_0 generation will significantly affect future growth rates of the global captive population.

2.3 Materials and Methods

2.3.1 Annual census analysis

Ex situ population data were collected from the International Studbook for Rhinoceros (Ochs 2001; 2005) and the Zoological Information Management System database (ZIMS) developed and administrated by International Species Information System (ISIS). ISIS is a worldwide organization that provides a world standard in zoological data collection and sharing software and contains information on 2.3 million animals (almost 15,000 taxa/10,000 species) and is constantly growing (ISIS 2011). The data were entered into the Single Population Animal Record Keeping System version 1.66 (SPARKS) database programme, a studbook programme also developed and distributed by ISIS (ISIS 2004; 2011). With SPARKS, it is possible to record data on a single species or population, and life history parameters such as birth dates, death dates and causes; and pedigree history are logged. These data were then exported to Population Management X version 1.2 (PMx) data analysis programme (Ballou *et al.* 2011). Annual census figures for each subspecies were assessed from the date each was first recorded in the studbook *viz.* 1914 for *D. b. minor*, 1906 for *D. b. michaeli* and 1946 for *C. s. simum*. Wild-born, captive-born and unknown birth type animals were assessed separately. Sexes were also assessed separately to determine if one sex is more reliant on wild-born individuals for their sustainability than the other. As only one individual of both *D. b. minor* and *C. s. simum* and zero individuals of *D. b. michaeli* were recorded as their sex not having been determined, the unknown sex category was omitted from the analysis. Census population growth rates per annum (λ) were calculated for each subspecies using the formula: $\lambda = N_{x+1}/N_x$, where N_x is population size at time x, and N_{x+1} is population size one year later (Rockwood 2006). For the census analysis, a total sample size of 159, 845 and 1650 specimens were analysed through the studbook for *D. b. minor*, *D. b. michaeli* and *C. s. simum* respectively.

2.3.2 Life table analysis

Life tables were constructed for both the *in situ* and ex *situ* populations of the three subspecies of rhinoceros (*D. b. minor, D. b. michaeli* and *C. s. simum*) under analysis. *In situ* life tables were compiled from range and out of range states where the subspecies occur in free-ranging populations, using population data published by Owen-Smith (1988). Only female life tables were constructed for comparison to *ex situ* data. Life tables were constructed using Microsoft Excel 2010 (www.microsoft.com). Age classes of one year were assigned starting from age class 0 to maximum age of longevity reported. As *in situ* data was reported using life stages rather than age classes, age classes were assigned to the different life stages based on the following rationale:

- Neonate: From date of birth to one year of age;
- Juvenile: Age where offspring is still reliant on the mother for sustenance until weaning at approximately three years of age;
- Sub-adult: Age between weaning and first reported breeding event; and
- Adult: Animals of breeding age.. As minimal *in situ* life history data were found for *D. b. michaeli*, the life table of *D. b. minor* was used for both *Diceros bicornis* subspecies.

Table **1** specifies which age classes correspond to the life stages described above. As minimal *in situ* life history data were found for *D. b. michaeli*, the life table of *D. b. minor* was used for both *Diceros bicornis* subspecies.

Table 1: Age classes assigned to life stages for *Diceros bicornis minor*, *Diceros bicornis michaeli* and *Ceratotherium simum simum in situ* data.

	D. b. minor	*D. b. michaeli*	*C s. simum*
Neonate	0	0	0
Juvenile	1 to 2	1 to 2	1 to 2
Sub-adult	3 to 5	3 to 5	3 to 6
Adult	6 to 40	6 to 40	6 to 45

Values for mortality rates (q_x), survival rates (p_x), age-specific survivorship (l_x), age-specific fertility (m_x), realised fecundity (F_x) and net lifetime reproduction (R_o) were calculated as follows:

- q_x – the proportion of individuals that die within an age class. Percentage mortality rates reported were converted into proportions and assigned to the relevant age classes (Rockwood 2006). For example, 8.3% neonate mortality equates to a q_x of 0.083 for age class 0; 3.5% juvenile mortality is equal to q_x of 0.035 (Owen-Smith 1988); and so forth;

- p_x – the probability of an individual alive at the beginning of age class x surviving to the beginning of age class x+1. $p_x = 1 - q_x$ (Rockwood 2006);
- l_x – the proportion of individuals that survive from birth to the beginning of age class x. $l_{x+1} = l_x * p_x$ (Rockwood 2006);
- m_x – the average number of same-sexed young born to animals in age class x. Inter-birth intervals were obtained and converted into m_x values for males and females using the formula:

  $$m_x = 0.5 * (1/\text{inter-birth interval})$$

  It was reported that younger cows gave birth more frequently than older cows (Owen-Smith 1988), therefore the minimum inter-birth interval reported was assigned to the age class where the first breeding event was reported, and the maximum inter-birth interval reported was assumed to be at the last breeding age reported. Inter-birth intervals for the ages in between were derived from interpolation from minimum to maximum across the breeding age classes from youngest to oldest;
- F_x – the number of female offspring produced in the next age class weighted by the probability of the dam reaching that age class after surviving to age x. $F_x = p_x m_{x+1}$ (Rockwood 2006); and
- R_o – the average number of same sex offspring produced by an individual per lifetime. $R_o = \sum l_x m_x$ (Begon *et al.* 2006; Rockwood 2006).

As with the census analysis data, in order to create the *ex situ* population life table, data were collected from the International Studbook for Rhinoceros (Ochs 2001) and the ZIMS database and entered into SPARKS 1.66 database programme. These data were then exported to PMx 1.2 data analysis programme (Ballou *et al.* 2011), where life tables for males and females of the three subspecies were constructed. The PMx programme calculates Kaplan-Meier estimates of survivorship (l_x), annual age-specific survival (p_x) and mortality rates (q_x), age-specific fertility (m_x), and the sample sizes used to calculate these estimates, as described by Kaplan & Meier (1958) and Lacy *et al.* (2012). F_x and R_o were calculated as described above for the *in situ* population life tables (Rockwood 2006).

In order to reflect the current captive population dynamics as closely as possible, demographic data in all three subspecies were limited to between 1st January 2001 and 31st December 2010, representing a ten-year period. It needs to be noted however, that this limits the sample size, with the numbers of south-central black rhinoceros in each age class being especially low. More details on the sample sizes used in the life table analyses can be viewed in Appendixes 1 to 3, where sample sizes are reflected under the Risk columns for both q_x and m_x. Age classes with sample sizes below 30 are recommended to be viewed with caution, as small sample size may produce misleading information (Traylor-Holzer 2011). Sample sizes are summarised in Table 2, showing that the sample size available for the analysis of the life table for *D. b. minor* is indeed small and should therefore be viewed with caution. Sample size available for *D. b. michaeli* is greater than 30 animals for age classes 0 to around age 15, but later years yielded a small sample size. Most age classes for *C. s. simum* can be viewed as reliable, as the majority are based on sample sizes larger than 30 individuals.

Table 2: Age class sample size used to determine life tables for male and female *Diceros bicornis minor*, *Diceros bicornis michaeli* and *Ceratotherium simum simum*.

Subspecies		Age class with sample size > 30	Age class with sample size < 30
D. b. minor	Males	None	0 to 33
	Females	None	0 to 34
D. b. michaeli	Males	0 to 15	16 to 48
	Females	0 to 17	18 to 48
C. s. simum	Males	0 to 40	41 to 45
	Females	0 to 40	41 to 46

The statistical package, Statistica™ (www.statsoft.com) was used to compare Kaplan-Meier survival curves of founder and captive-born females (Kaplan & Meier 1958). Five different (mostly nonparametric) tests for censored data are available for this comparison: Gehan's generalized Wilcoxon test, the Cox-Mantel test, the Cox's *F* test , the log-rank test, and Peto and Peto's generalized Wilcoxon test (Statsoft Inc 2013). Cox's *F* test tends to be more powerful than Gehan's generalized Wilcoxon test when:

- Sample sizes are small (i.e., *n* per group less than 50);
- Samples are from an exponential or Weibull curve; and
- There are no censored observations (Statsoft Inc 2013).

As the data currently under analyses contains censored data points, Cox's *F* test was therefore omitted. Little difference has previously been found between the Cox-Mantel test and the log-rank test when the samples are drawn from a population that follows an exponential or Weibull distribution, therefore the log-rank test was also omitted (Statsoft Inc 2013). The three statistical tests performed were therefore:

1. Gehan's Wilcoxon Test (Gehan 1965)
2. Cox-Mantel Test (Cox 1959; Mantel 1966; Mantel & Haenszel 1959)
3. Peto & Peto Wilcoxon Test (Peto & Peto 1972)

All tests were deemed to be significantly different when $P < 0.05$.

The data calculated for the life table analysis were transferred into Mathematica 8 in the form of a Leslie matrix, with the realized fecundity (F_x) forming the first row of the Leslie matrix, and the p_x values entered in the sub-diagonal (Rockwood 2006). The Eigen value of the Leslie matrix was calculated to determine λ, the finite population growth rate parameter and the right Eigen vector, the stable age distribution (Rockwood 2006). To assist with the bench-marking comparisons between *in situ* and *ex situ* rhinoceros populations, fecundity (m_x), mortality (q_x) and age-specific survivorship curves were created from the life tables (Rockwood 2006).

2.3.3 Sensitivity analysis

Sensitivity analysis was conducted on the Leslie matrix for the female population to analyse the effect on the population growth rate. The following fecundity and mortality related variables were assessed and included variables to allow bench-marking comparisons between the *in situ* and *ex situ* populations:

Fecundity variables:

a) Increase of fecundity (m_x) across all breeding ages by 5%;
b) Lowering age of first reproduction by 1 age class;
c) Extending age of reproduction past current senescence by one age class;
d) Alter fecundity (m_x) across all breeding ages to match those reported in *in situ* populations; and
e) Increase fecundity (m_x) to the median captive breeding rate for females of all breeding age classes.

Mortality variables:

f) Increase age specific survivorship (p_x) rate by 5% over the age classes which constitute the different life stages:

    1. Neonate (p_0);
    2. Juvenile (p_1 and p_2);
    3. Sub-adult (p_3 to one age class before first recorded breeding event); and
    4. Adult (from age class at first breeding event).

g) Change neonatal survivorship (p_0) rate to match that of *in situ* populations;

h) Alter p_x across all ages to match that of the *in situ* population;

i) Increase survivorship (p_x) by 5% across all age classes;

j) Increase survivorship (p_x) rate by 5% over the top 5 age classes with the highest mortality; and

k) Increase survivorship (p_x) rate to 100% over all age classes until maximum life span.

Percentage change in λ was calculated to determine which factor had the most effect on the observed population growth rate obtained from the life tables in PMx.

Further sensitivity analysis was conducted in Mathematica 8 on current female fecundity rates, in order to calculate the change in fecundity needed to achieve the required λ to meet the 50 and 100 year population goals set in 1992. Required intrinsic rate of growth (r) was calculated using the formulae:

$$r_{50} = \frac{\ln(\mathrm{N2042}/\mathrm{N2010})}{2042-2010} \quad \text{and} \quad r_{100} = \frac{\ln(\mathrm{N2092}/\mathrm{N2010})}{2092-2010}$$

In this equation, N2042 and N2092 equals the 50- and 100-year population targets set in the 1992 GCAP meeting (Foose and Wiese 2006), and N2010 equals the number of individuals in the population as of 31 December 2010. Corresponding $\lambda = e^r$ (Rockwood 2006).

With current female λ assigned a value of 1, population growth rate was extrapolated to determine λ at 0.5, 1.5, 2 and 2.5 times the current fecundity rate. The change in m_x was then determined for the required λ needed to achieve the population targets.

2.3.4 Age structure analysis

Age pyramid graphs were constructed to assess the current age distribution of *D. b. minor*, *D. b. michaeli* and *C. s. simum* from census data as of 31 December 2010, with males indicated on the left of the graph, and females on the right. As with the life table analysis, age classes of one year were assigned, starting from age class 0 until maximum longevity recorded. The shapes of the age pyramid graphs were assessed visually to determine if the population was declining, stationary or growing.

The stable age distribution was determined for each of the three subspecies by calculating the Eigen vector of the ten-year Leslie matrix using Mathematica 8. Where age classes showed a sample size of zero, these age classes were grouped with adjacent age classes to achieve a large enough sample size for statistical purposes in both the observed and the stable age structure frequency tables (Sokal & Rohlf 1995). Number of age classes grouped in this manner varied between the subspecies, depending on the sample size available. The stable age distribution was then compared statistically with the current age distribution using a *G*-test for goodness of fit where the expected frequencies are intrinsic to the sampled data, therefore using the number of age classes minus 2 degrees of freedom,

$$\mathrm{G} = 2\sum^{a} \mathrm{O} \ln\left(\frac{\mathrm{O}}{\mathrm{E}}\right)$$

where:

a = Number of age classes;

O = Observed frequency; and

E = Expected frequency.

William's correction (q) was applied to the result of the *G*-test analysis as suggested by Sokal & Rohlf (1995) through the following formula:

$$q = 1 + (a^2 - 1)/6nv$$

where:

a = number of age classes;

n = number of individuals in the population; and

$v = a - 1$.

Therefore: $$G_{\mathrm{adj}} = \frac{G}{q}$$

All tests were deemed to be significantly different when $P < 0.05$.

2.4 Results

2.4.1 Annual census analysis

Diceros bicornis minor

Captive records for *D. b. minor* date back to 1912, with numbers recorded being consistently below ten individuals until the late 1970s. A sharp increase in total numbers occurred in the early 1980s, with the number reaching a climax in 2001 with 69 individuals (Figure 3). Since 2001, there has been a steady decrease in total numbers with the final figure standing at 61 animals at the end of 2010, consisting of 32 males and 29 females.

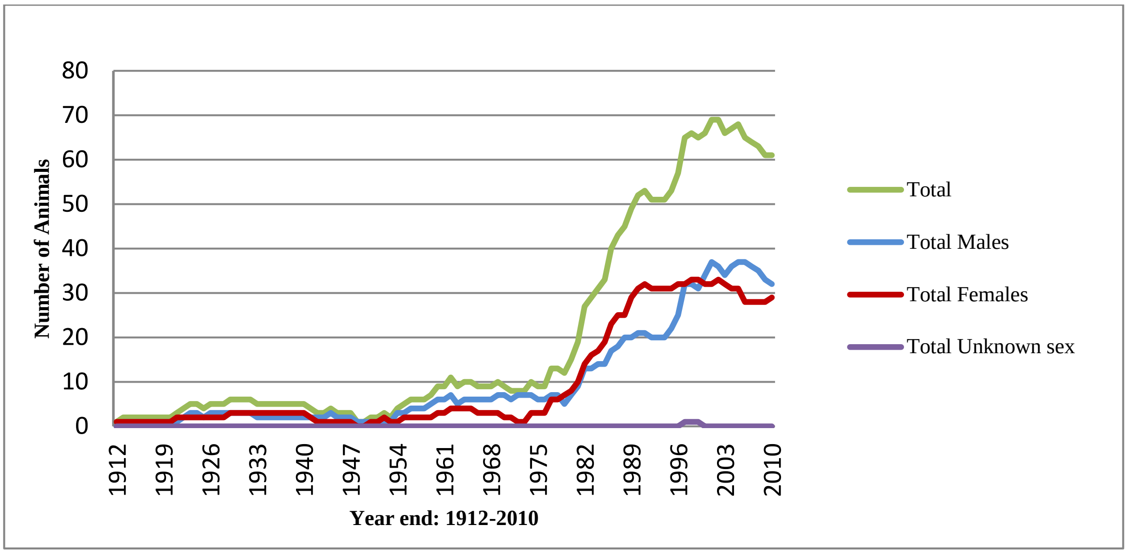

Figure 3: Annual census – *Diceros bicornis minor*. Total numbers by sex.

The first captive birth was recorded in 1965 at Lisbon Zoo, but captive-born animal numbers remained very low until the influx of new founders into the population in the 1980s, which seems to have boosted the captive breeding rate. From 1990, captive births increased until a high of 11 captive births recorded in 1997 and numbers of captive-born individuals peaked in 2005 at 43 individuals. The decrease in total population numbers over the past decade is reflected in both the wild-caught individuals and captive-born individuals, which showed decreases in numbers since 1991 and 2005, respectively (Figure 4). The ratio of captive-born individuals *versus* wild-caught individuals has steadily increased over the past 20 years, with captive-born figures rising from 16% of the population to 63% between 1990 and 2010. There have been 21 captive-births reported in the last 10 years, but only one occurring in the past 5 years.

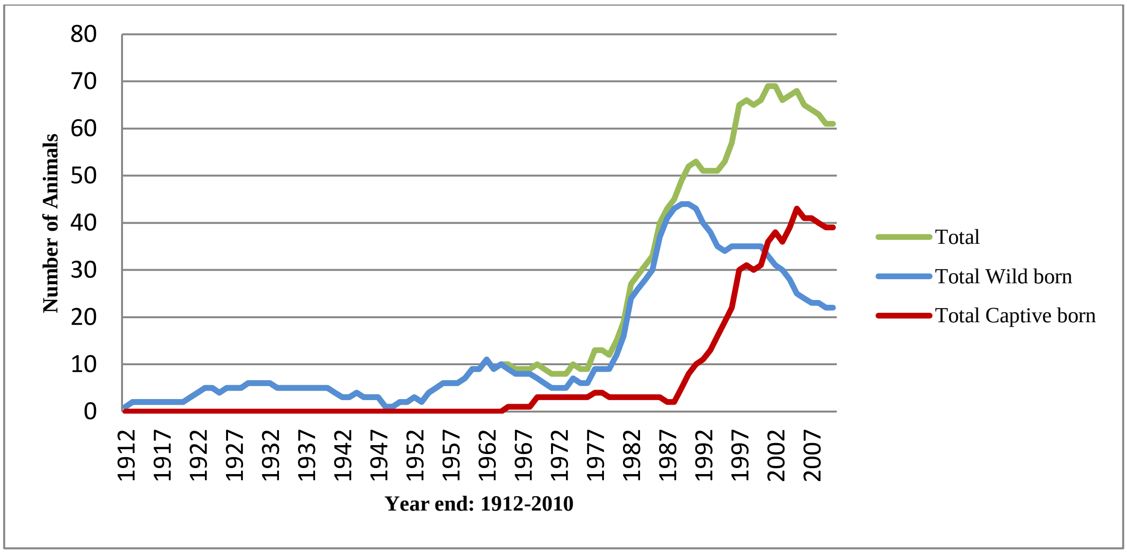

Figure 4: Annual census - *Diceros bicornis minor*. Total wild-born *versus* captive-born individuals in the population**.**

During the 1980s, a total of 43 animals were imported from the wild, increasing the founder population to a total of 44 animals by 1989 (Figure 4 and Figure 5). After 1990, no new founders were imported into the captive population, so a steady decrease in founder numbers due to natural attrition is to be expected. At the end of 2010, 22 founders remained in the population (Figure 5).

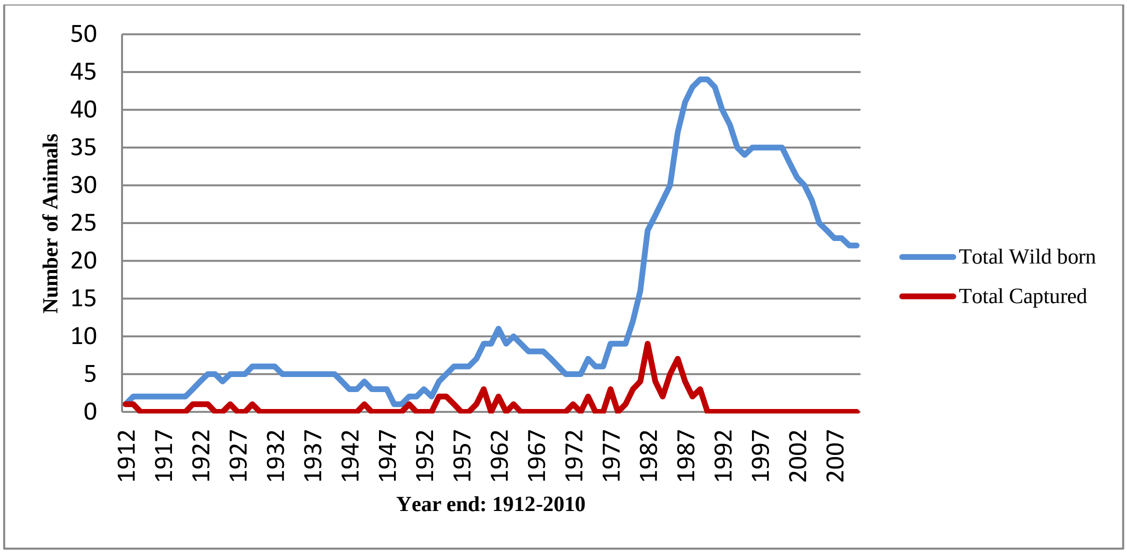

Figure 5: Annual census – *Diceros bicornis minor*. Total wild-born individuals *versus* total captured per annum.

As males and females in a population often react differently to similar situations, a comparison between wild-born and captive-born numbers was conducted separately for each sex, as can be seen for males in Figure 6 and for females in Figure 7. Initially, more females than males were imported into captive institutions, with numbers of founders standing at 26 and 19 for females and males, respectively at the end of the 1980s. Both founder populations then started to decline and at the end of 2010, the female population showed a drop of 42.5% down to a total of 15 individuals, while the male decline was higher, with a drop of 63% down to a total of 7 animals. Conversely, captive-born males increased from one individual to 28 individuals from 1988 to 2008 before numbers started declining, while females increased from one to 15 individuals over the same time period. Both sexes have shown a slight decline in the past decade.

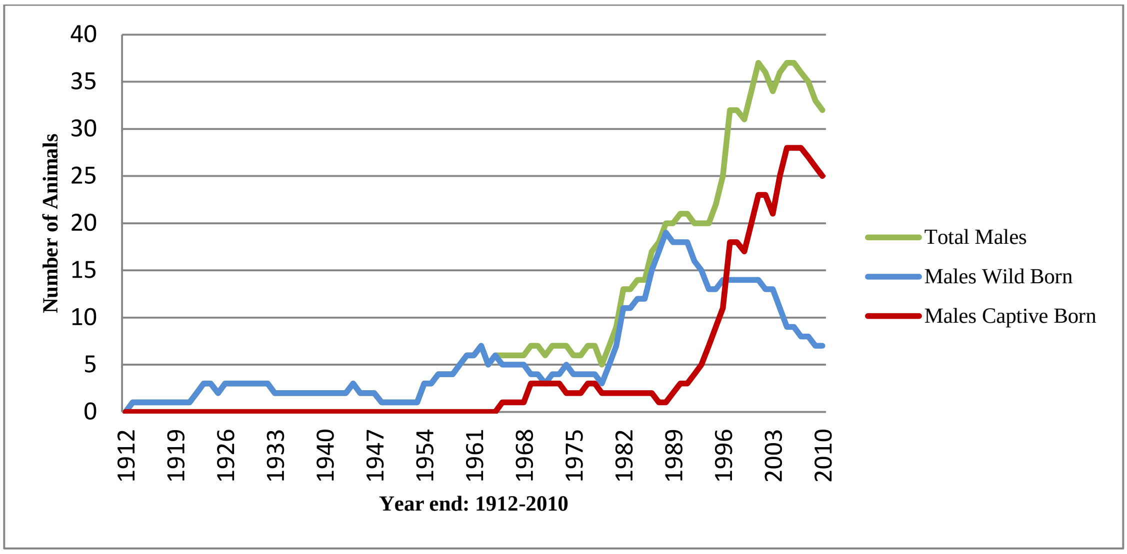

Figure 6: Annual census - *Diceros bicornis minor*. Males - Wild-born *versus* captive-born population totals.

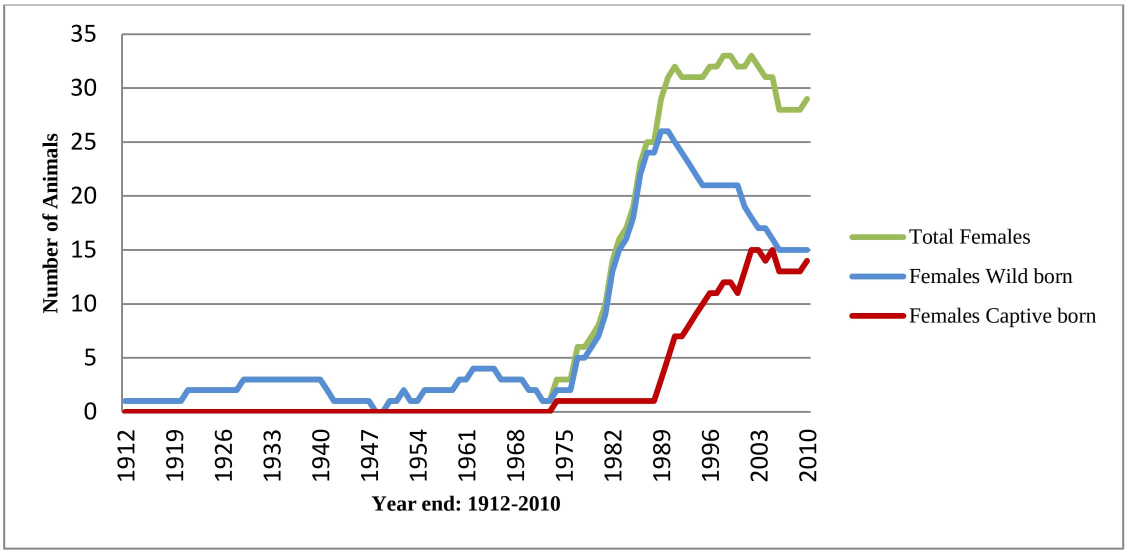

Figure 7: Annual census - *Diceros bicornis minor*. Females - Wild-born *versus* captive-born population totals.

Diceros bicornis michaeli

Records of *D. b. michaeli* in captivity date back to 1905. Population numbers steadily increased from this time up until 1973 when a total population size of 193 was recorded. After a period of decline for just over a decade after that, the population recovered and has shown an overall increase in numbers since 1986 (Figure 8). The total population size at the end of the study period stood at 249 individuals, consisting of 95 males, 132 females and 22 individuals that had not as yet been sexed.

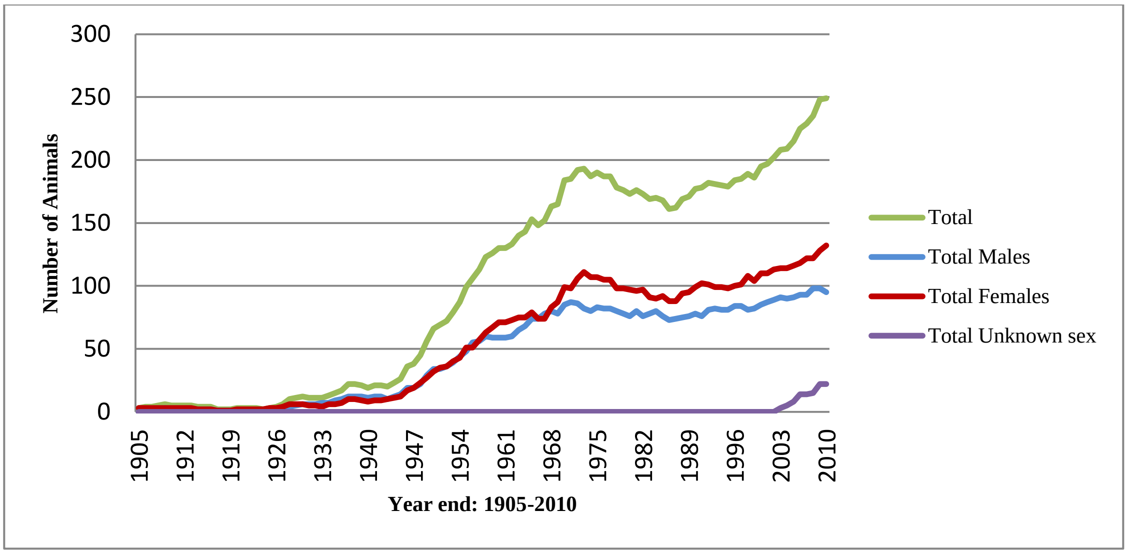

Figure 8: Annual census – *Diceros bicornis michaeli*. Total numbers by sex.

The first captive birth for *D. b. michaeli* was reported in 1941 by the Chicago Zoological Society. After a slow start, captive breeding took off in the late 1950s, and numbers of captive bred individuals stood at 233 at the end of 2010. As with *D. b. minor*, the founder population of *D. b. michaeli* has decreased significantly since its peak of 149 individuals in 1972 (Figure 9).

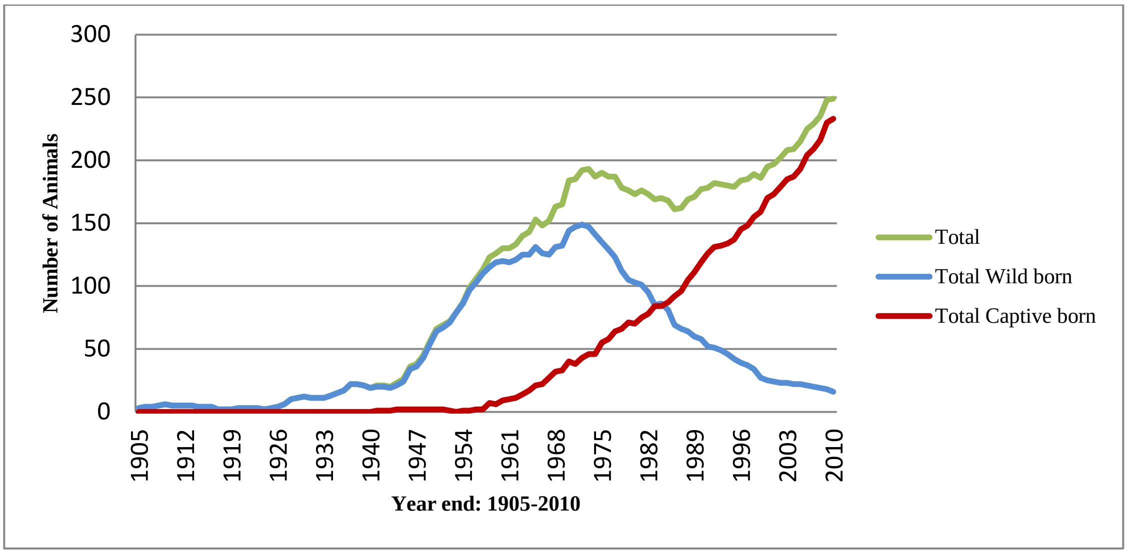

Figure 9: Annual census - *Diceros bicornis michaeli*. Total wild-born *versus* captive-born individuals in the population.

While the addition of new founders was reportedly very low and inconsistent up until 1945, the next three decades shows a consistent influx of wild-born individuals, boosting numbers up to a total of 147 individuals in 1971. However, since 1975, few new founders have been recruited with no new founders entering the captive population since 1994. Currently, there are only 16 founders remaining in the population (Figure 10).

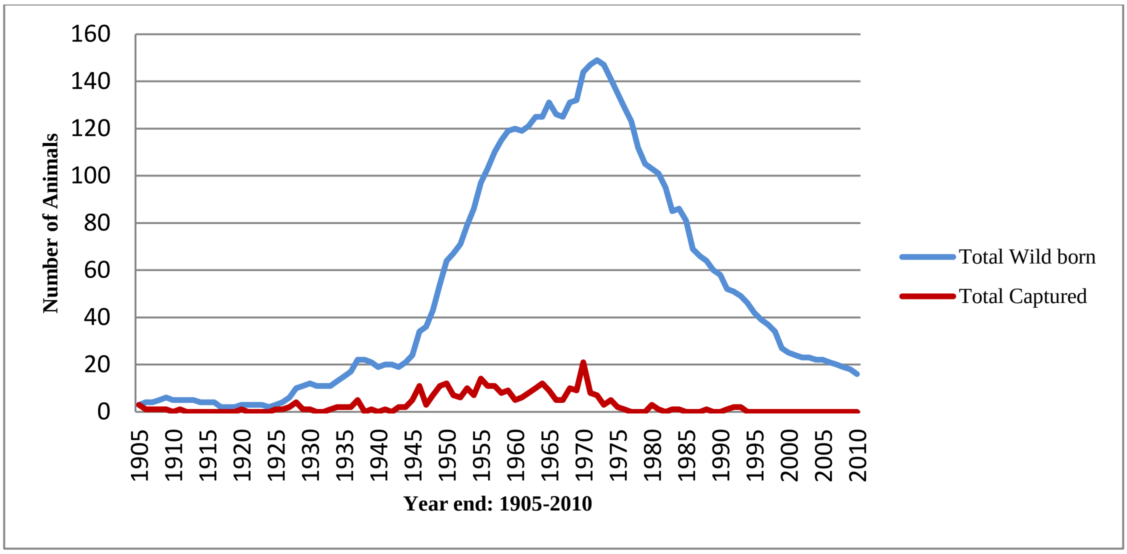

Figure 10: Annual census - *Diceros bicornis michaeli*. Total wild-born *versus* total captured per annum.

On comparing male and female founder *versus* captive-born populations, both sexes of *D. b. michaeli* show similar census patterns. After peaking around 1970, the founder population numbers then went into a steady decline, with male numbers decreasing by 96% between 1970 and 2010 to a total of three individuals, and the female founder population decreasing by 84% to a total of 13 individuals. The success of the captive-breeding programme seems to have counteracted this decline however, with captive-born individuals numbering 92 males and 119 females at the end of 2010 (Figure 11; Figure 12).

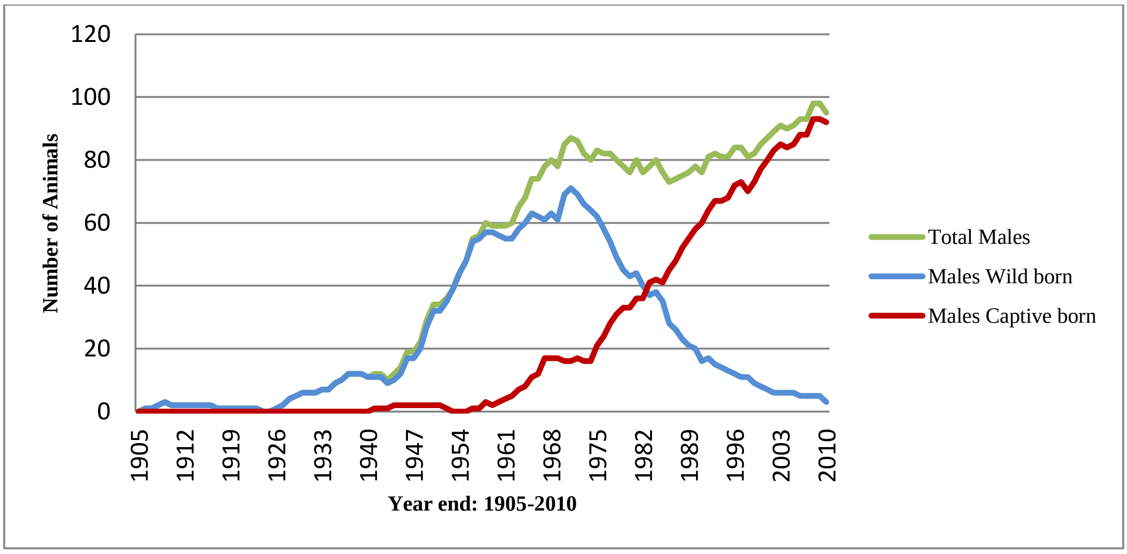

Figure 11: Annual census - *Diceros bicornis michaeli*. Males - Wild-born *versus* captive-born population totals.

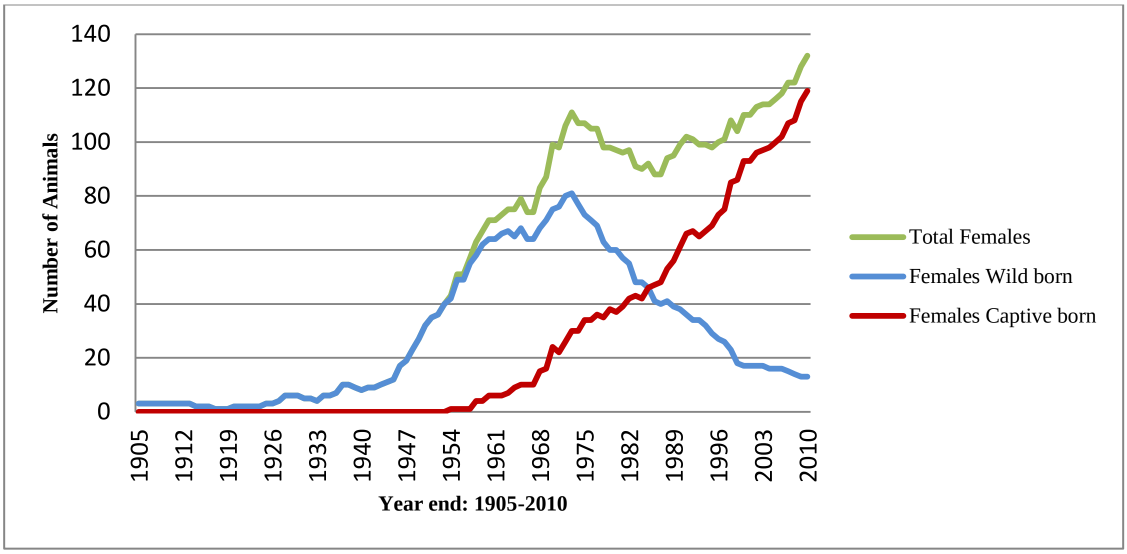

Figure 12: Annual census - *Diceros bicornis michaeli*. Females - Wild-born *versus* captive-born population totals.

Ceratotherium simum simum

The captive population of *C. s. simum* is relatively young in comparison to *D. b. minor* and *D. b. michaeli*, with captive records only dating back to 1946. Numbers stayed below ten until 1958, where an influx of new founders as well as a successful captive-breeding programme over the next couple of years boosted the population quickly to over 500 individuals by 1972 and a decade later to over 600 animals. Numbers at the end of 2010 indicate their highest ever, with 673 individuals in the population comprising 290 males and 383 females (Figure 13).

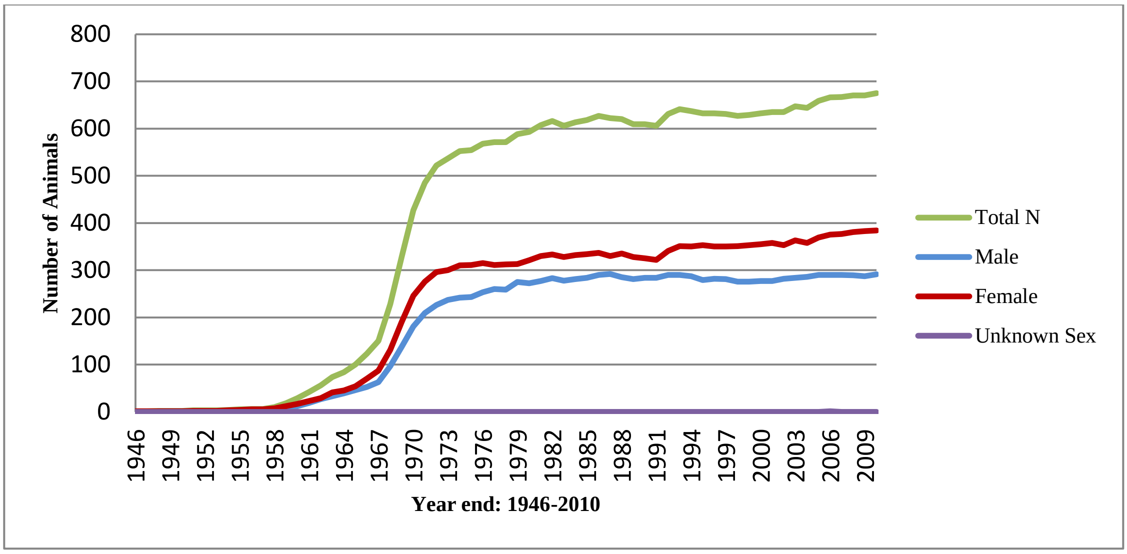

Figure 13: Annual census – *Ceratotherium simum simum*. Total numbers by sex.

The first captive birth was recorded in 1967 and took place at the National Zoological Gardens of South Africa in Pretoria, a result of a female founder that had conceived in the wild. The first captive birth that was conceived in captivity was also recorded at this zoo in 1969. The number of captive-born individuals has steadily increased over the past 40 years, with captive-born animals numbering 402 at the end of 2010 (Figure 14).

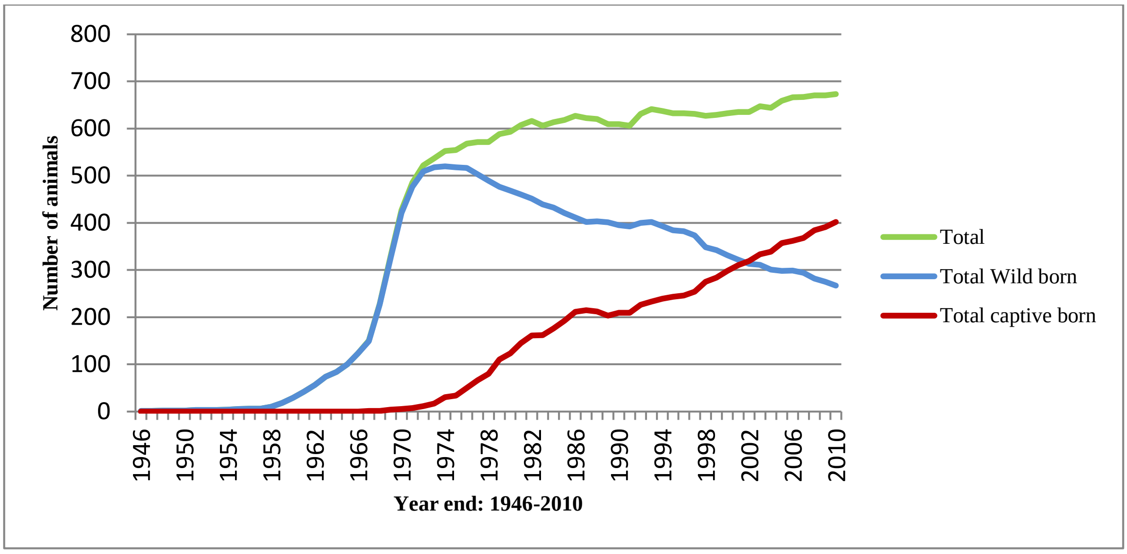

Figure 14: Annual census - *Ceratotherium simum simum*. Total wild-born *versus* captive-born individuals in the population.

In 1969, the largest number of founders entered the captive population in a single year when 83 animals were added. A staggering 399 new founders were recorded in the studbook in a ten-year period from 1966 to 1975. Since 1976 however, although there has still been a regular influx, the number of founders entering the population has decreased significantly, with a total of 134 captured between 1976 and 2010, generally at a rate of below ten per annum and with no captures taking place at all during several years. Total numbers recorded as founders for the entire history of the captive population is 607 individuals. The current number of founders in the population is 267, with the last new founders entering the population in 2008, when two new animals were added (Figure 15).

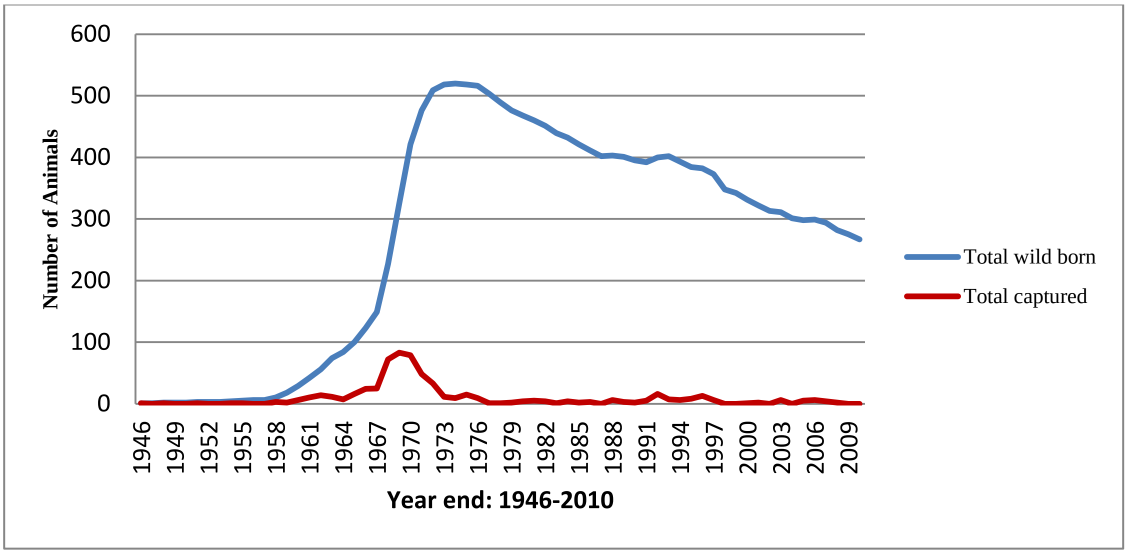

Figure 15: Annual census - *Ceratotherium simum simum*. Total wild-born in population *versus* total captured per annum.

Census data on male wild-born *versus* captive-born animals; and female wild-born *versus* captive-born animals show a similar pattern. Both sexes indicate a peak in founders in the late 1970s, with a steady decline thereafter, and at the end of 2010 there were 88 and 179 founder males and females, respectively. The first captive-birth reported in 1967 was that of a male offspring, while the first female to be born in captivity arrived a few years later, in 1971. Both male and female captive-born generations have since shown a relatively steady increase, and captive-born individuals are currently at their highest ever, with equal numbers of 201 for both males and females in the population at the end of the study period (Figure 16 and Figure 17).

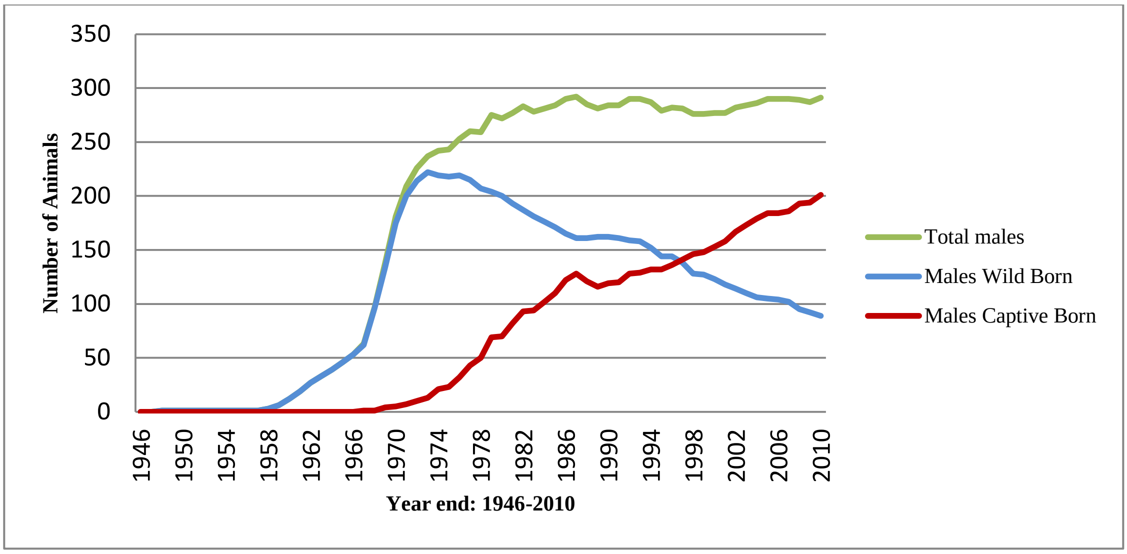

Figure 16: Annual census - *Ceratotherium simum simum*. Males - Wild-born *versus* captive-born in population.

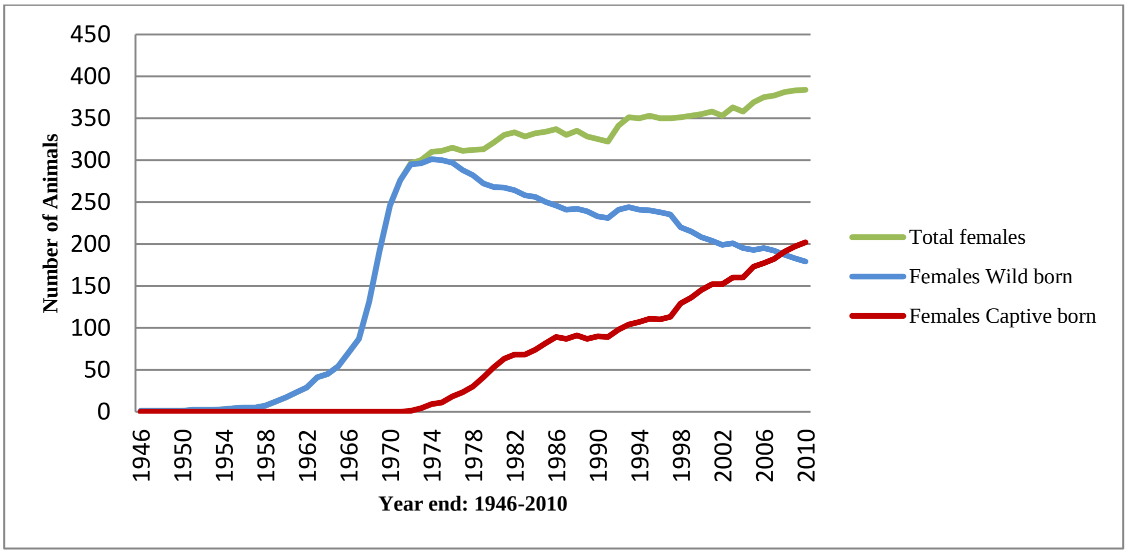

Figure 17: Annual census - *Ceratotherium simum simum*. Females - Wild-born *versus* captive-born in population.

Population growth rates from census analysis

Census population growth rate over the final year of the study was zero for *D. b. minor*, and 0.4% for *D. b. michaeli* and *C. s. simum*. However, in order to eliminate the effect of random fluctuations, a ten-year average was calculated. The finite population growth rates indicate a mean 2.5% growth per annum over the past ten years for *D. b. michaeli*, an almost stationary population (0.6% per annum) in the case of *C. s. simum*, and a declining population of just less than 1% per annum for *D. b. minor*.

Population growth rates calculated from annual census figures for the three subspecies are presented in Table 3.

.

Table 3: λ derived from census data for *Diceros bicornis minor*, *Diceros bicornis michaeli* and *Ceratotherium simum simum*: 2001 – 2010.

Year	*D. b. minor*	*D. b michaeli*	*C. s. simum*
2001	1.045	1.010	1.005
2002	1.000	1.025	1.000
2003	0.957	1.030	1.019
2004	1.015	1.005	0.995
2005	1.015	1.029	1.023
2006	0.956	1.047	1.011
2007	0.985	1.018	1.002
2008	0.984	1.026	1.004
2009	0.968	1.055	1.000
2010	1.000	1.004	1.004
Mean	0.993	1.025	1.006

2.4.2 Life table analysis

Complete life tables for *D. b. minor*, *D. b. michaeli* and *C. s. simum* are presented in Appendices 1, 2 and 3.

Diceros bicornis minor

Sample sizes for *D. b. minor* were very small and therefore should be viewed with caution. No smoothing exercise has been done on the data, so spikes and anomalies may exist because of the small sample size. Fecundity rates begin at age 5 for both male and female *D. b. minor* with last recorded m_x values occurring at age 27 for females and age 32 for males. This upper age limit for males however, has to be viewed with caution, as it is based on the reproduction of a single individual, which also created an anomaly of an m_x rate of 0.5 at age class 29 and 32. Excluding the two unusual peaks in male fecundity at age classes 29 and 32, fecundity appears to peak at age 14 for both sexes, where a female fecundity of 0.17 and a male fecundity of 0.13 are recorded (Figure 18).

Figure 18: Fecundity rates (m_x) of *ex situ* male and female *Diceros bicornis minor*.

Initial mortality in the first year of life is relatively high for females compared to that of males, the result of two females dying out of a sample size of 6.4 giving a neonate mortality of 33%. In contrast, only one male offspring died out of a sample size of 13.2. Males show a spike in mortality at age 18 and 27 but this cannot be linked to any other life stage event and are more likely the result of small sample size. The oldest recorded male was 32.1 years old, while the oldest recorded female was 35 years (Figure 19). Currently, the ages of the oldest animals alive are 29 and 34 years for males and females, respectively.

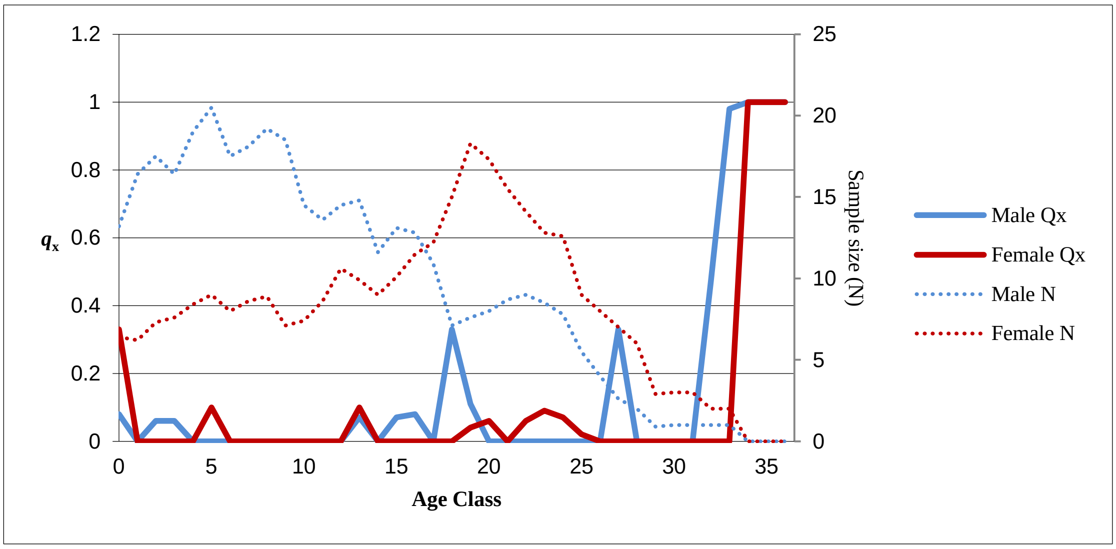

Figure 19: Mortality rates (q_x) of *ex situ* male and female *Diceros bicornis minor*.

After initial high mortality in the first age class, female survivorship is high throughout the lifespan, with a 38% survivorship up until age 34, one year before the oldest recorded female. Median survival time is recorded at age 20.6 for females and 18.7 for males. 81% of males are recorded as surviving until breeding age, whereas of females, only 67% survive until breeding; a direct result of the neonate mortality as no further mortalities were recorded up until breeding age (Figure 20).

Figure 20: Kaplan-Meier survivorship (l_x) of *ex situ* male and female *Diceros bicornis minor*.

Statistical analysis shows no significant difference between male and female survivorship as $P > 0.05$ for all three statistical tests conducted, the results of which are presented in Table 4. The survivorship graphs however, show that the male and female curves appear very different. Two factors that may be affecting the outcome of the statistical analyses: 1) small sample size (*n* = 47♂;41♀) and 2) large amount of censored data (*n* = 32♂; 29♀) compared to uncensored data (*n* = 15♂; 12♀). This equates to 68% censored data for the male population and 71% censored data in the female population.

Table 4: Survivorship curve statistical analyses: Male *versus* female *Diceros bicornis minor*.

	Test statistic	Probability (*P*)
Gehan's Wilcoxon	0.51	0.61
Peto & Peto Wilcoxon	-1.20	0.23
Cox-Mantel	1.45	0.15

A period of reproductive senescence seems to occur in the captive female population, with last reproduction occurring at age 27, while longevity of 35 years is obtained. Males do not seem to exhibit this, as age at last reproduction of 32 is close to the longevity of 34 observed. Overall R_o for males is

0.79 and for females is 0.56, indicating that with current fecundity and mortality rates, neither sex are able to sustain their numbers.

Diceros bicornis michaeli

Earliest age of reproduction for females is 5 years while the highest age at last reproduction recorded is 36 years. This indicates earliest conception age of females at around 3.5 years of age given a gestation period of approximately 15 months. Youngest males inseminated at 6 years of age and the oldest at 33 years of age. Male fecundity peaked at 25 years with a value of 0.26. Peak female fecundity is much lower than that of males, only reaching 0.12, but this rate is seen across several age classes up until age 32 (Figure 21).

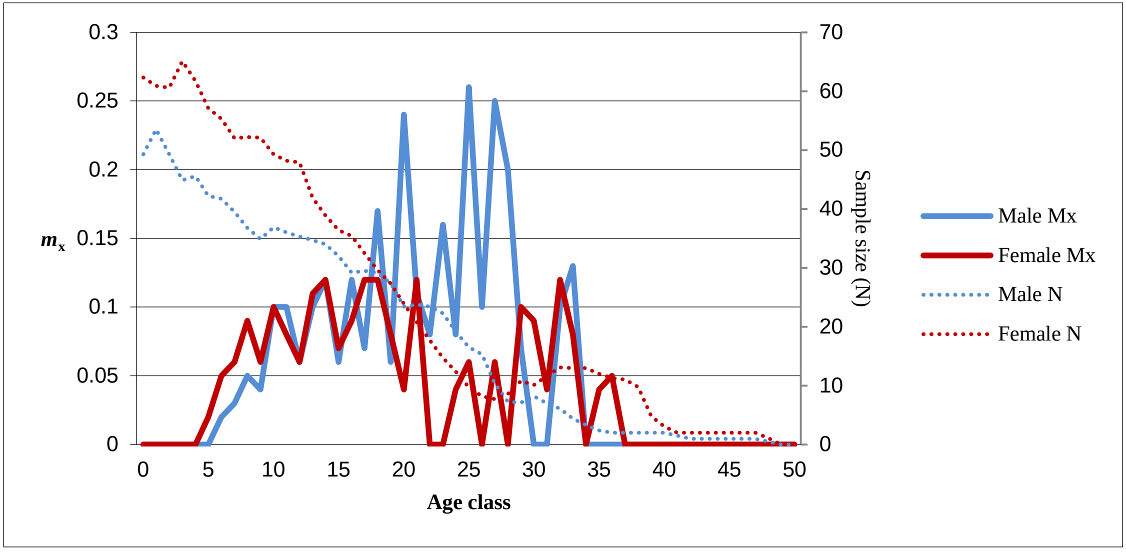

Figure 21: Fecundity rates (m_x) of *ex situ* male and female *Diceros bicornis michaeli*.

Neonate mortality rate for males and females is almost identical with a rate of 0.13 and 0.12, respectively. Mortality rates for both sexes remain relatively low until approximately the age of 30, where mortality rates become less constant with males showing spikes in the later years at ages 32, 35 and 41. Female mortality spiked at age 39 with a value of 0.28. The oldest recorded female was 46 years of age, and oldest living female on 31 December 2010 was 41 years. The oldest recorded male was 49.5 years of age. At the end of the study period, the oldest living male was also 41 years of age.

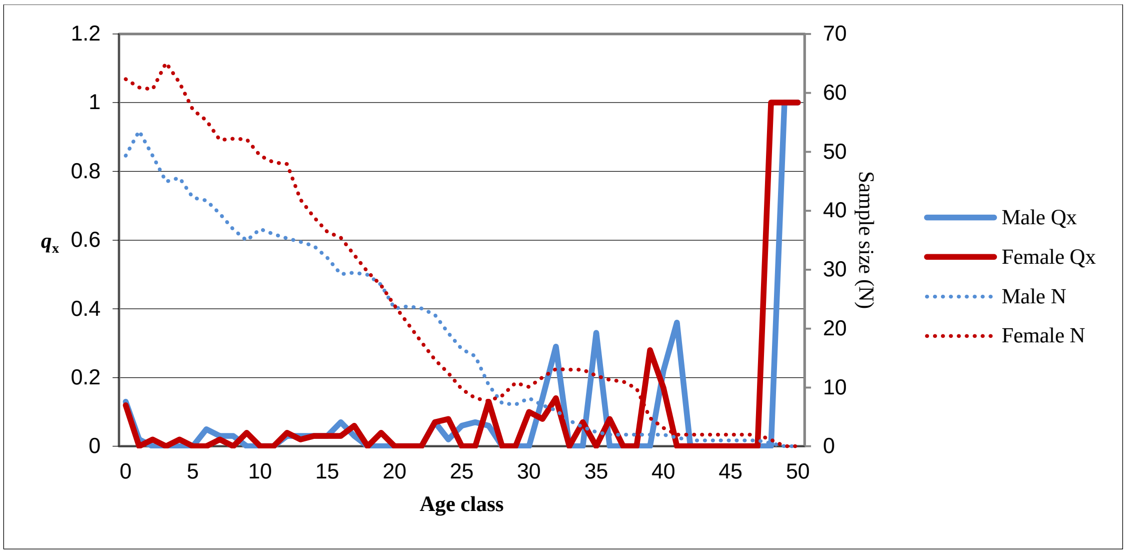

Figure 22: Mortality rates (q_x) of *ex situ* male and female *Diceros bicornis michaeli*.

After an initial small drop during age class 0, age-specific survivorship shows a steady rate of decline until around the age of 30 for both sexes. After the age of 30, some dips in the survivorship can be noted, which may be a reflection of the smaller sample sizes available for the older age classes. Median survival time is reached at the age of 26.8 and 27.6 for males and females, respectively. 85% of both male and female populations survive until the age of first reproduction.

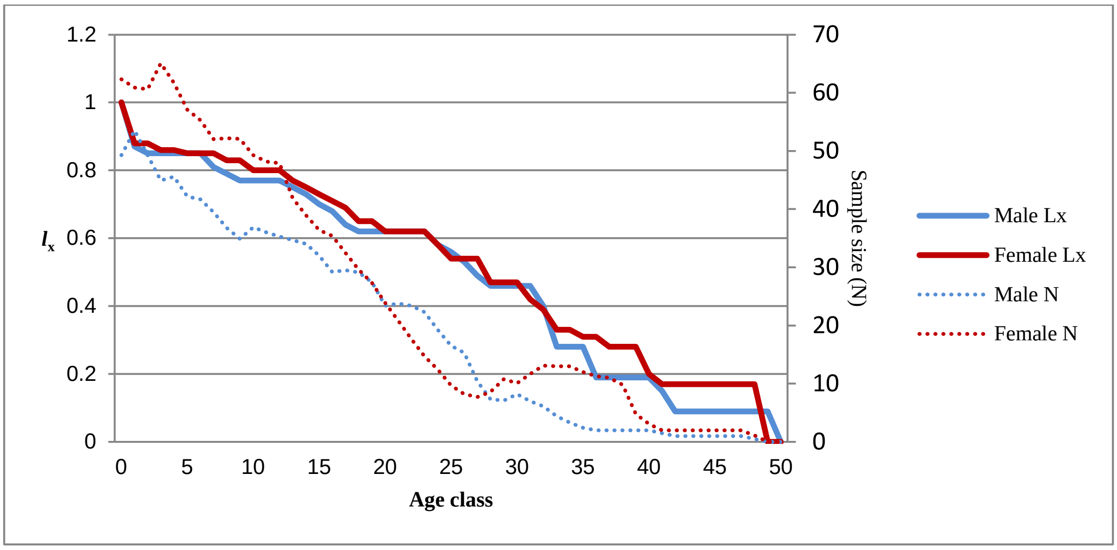

Figure 23: Kaplan-Meier survivorship (l_x) of *ex situ* male and female *Diceros bicornis michaeli*.

Statistical analyses of the survivorship curves of male *versus* female *D. b. michaeli* shows no statistically significant difference with all three test indicating a $P > 0.05$; $n = 129$♂; 167♀ (Table 5).

As with *D. b. minor* 74% of the male data and 79% of the female data was censored data points (censored data *n* = 95♂; 132♀; uncensored data *n* = 34♂; 35♀).

Table 5: Survivorship curve statistical analysis: Male *versus* female *Diceros bicornis michaeli.*

	Test statistic	Probability (*P*)
Gehan's Wilcoxon	0.72	0.47
Peto & Peto Wilcoxon	-0.93	0.35
Cox-Mantel	-0.96	0.33

Reproductive senescence seems to occur in both male and female captive *D. b. michaeli*, with age of last reproduction recorded at 33 and 36 years, respectively. R_o is 1.7 for the male population, and 1.3 for the females, indicating that both sexes are currently able to reproduce in sufficient numbers to replace themselves during a generation time.

Ceratotherium simum simum

In the case of *C. s. simum*, first reproduction occurs at the age of 4 for females and 7 for males, indicating that females start reproductive cycling at approximately 3 years of age. Female reproduction seems to peak between the ages of 9 and 11 where peaks in fecundity of 0.08 are observed, gradually decreasing thereafter until last reproduction at age 36. A dip seen at age 12 is unusual given the sample size of over 100. Male data indicate a peak between ages 15 and 20 years, and follow a similar pattern of decline to the females, with a last reproductive event being recorded at the age of 40. Males of *C. s. simum*, as with *D. b. michaeli*, show a higher reproductive output over many of the age classes, almost double that of the females (Figure 24).

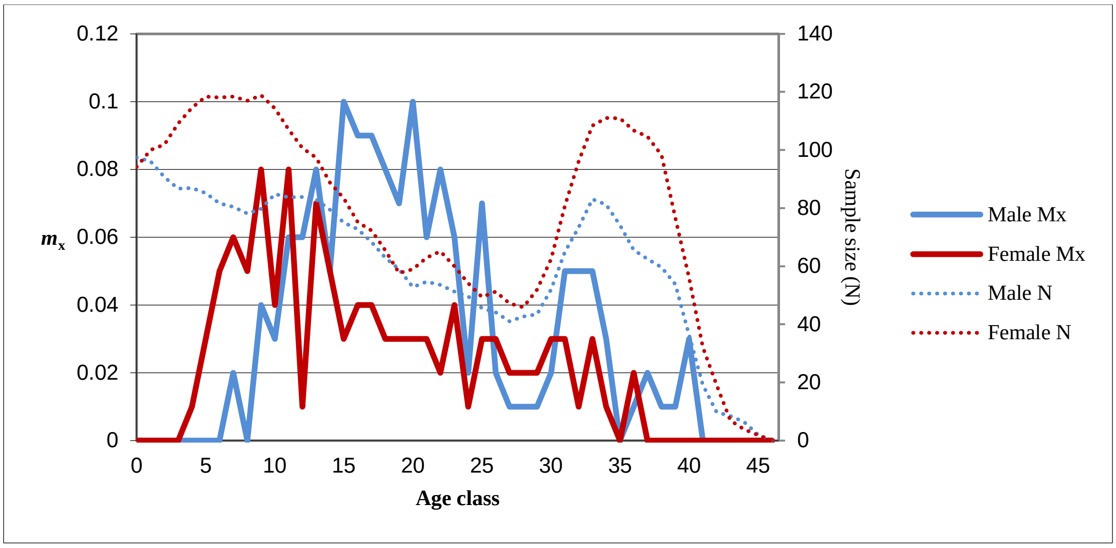

Figure 24: Fecundity rates (m_x) of *ex situ* male and female *Ceratotherium simum simum*.

Males and females show very similar patterns of mortality, with neonate mortality at 15% for females and 17% for males. Males also show a slight spike at age 3 compared to the females, but rates then remaining under 5% per annum throughout most of their adult lives. From the age of around 37, the rates then start to rise until maximum longevity is reached at age 46 for males and 45.4 for females (Figure 25). On 31 December 2010, the oldest living animals were 45 years for both sexes.

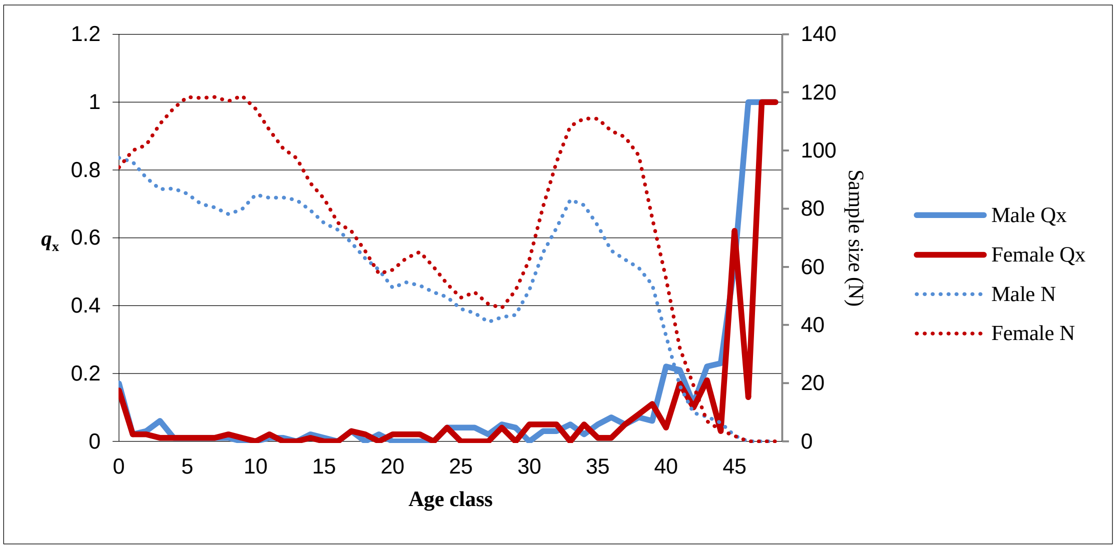

Figure 25: Mortality rates (q_x) of *ex situ* male and female *Ceratotherium simum simum.*

The survival rate of males is consistently lower than that of females, as a result of the slightly higher initial mortality rates at age class 0 and 3. Both sexes show an initial drop in the first age class. Male survival rate until first breeding age is 72%, whereas the female rate is much higher at 81%. Median survival time is 29.5 for males and 37 for females (Figure 26).

Figure 26: Kaplan-Meier survivorship (l_x) of *ex situ* male and female *Ceratotherium simum simum*.

Survivorship curve analyses indicate statistically significant difference between the male and female curves for all three tests as $P < 0.05$; male $n = 408$, female $n = 489$ (Table 6). This can be clearly observed on the survivorship graph, where male survivorship is consistently below that of female survivorship due to the higher mortality rates between age classes 0 to 3 mentioned before. The large proportion of censored data points may also influence these analyses as censored data n = 290♂:383♀, while uncensored n = 118♂:106♀ (71% and 78% censored data for males and females, respectively).

Table 6: Survivorship curve statistical analyses: Male *versus* female *Ceratotherium simum simum.*

	Test statistic	Probability (*P*)
Gehan’s Wilcoxon	-2.88	0.00
Peto & Peto Wilcoxon	2.79	0.01
Cox-Mantel	2.69	0.01

As with the black rhinoceros subspecies, a period of reproductive senescence is evident in female *C. s. simum*, with an age of last reproduction at 36 years, and longevity of 47 years. For the male population this is less evident, with age of last reproduction seen at 40 years, compared to a longevity of 46 years. PMx calculation of R_o for males is 0.91 and for females is 0.788 indicating that both the males and females in the population are in decline.

Population growth rates from life table analysis

Population growth rates (λ) derived from Leslie matrices based on data between 1 January 2001 and 31 December 2010 are presented in Table 7. *Diceros bicornis minor* shows a slight decline of close to 2% using life table analysis *versus* the census analysis which indicates a stationary population. *Diceros bicornis michaeli* in contrast shows a positive growth for both sets of analyses, with a growth rate of 2.4% per annum at stable age distribution calculated from the life table analysis, but less positive with a stationary population indicated using the census data. *Ceratotherium simum simum* has a life table λ of 0.99 *versus* census λ of 1.00, life table analysis therefore indicating a 1% decline per annum. Data from all three subspecies indicate the possibility that the age distribution of the populations are not stable, as λ calculated from the two different methods are not equivalent. Stochasticity may also play a role in the results seen from the census data, as the λ calculated from the life tables is deterministic, and some stochastic variation due to small sample size is likely to have occurred.

Table 7: Finite population growth rates (λ) from Leslie matrix first Eigen value calculations (Using Mathematica 8) and PMx census data

	Leslie matrix Eigen value			Census analysis λ (2009-2010)		
Subspecies	Population Total	Males	Females	Population Total	Males	Females
D. b. minor	0.98	0.99	0.96	1.00	0.97	1.03
D. b. michaeli	1.02	1.03	1.02	1.00	0.97	1.03
C. s. simum	0.99	1.00	0.98	1.00	1.01	1.00

Wild *versus* captive populations

For the benchmarking exercise between wild populations *versus ex situ* populations, only female data have been assessed. Additionally, due to limited information, the same life table for wild populations was used for both Black rhinoceros subspecies. Full *in situ* population life tables used for these analyses are indicated in Appendices 4 and 5.

Diceros bicornis minor

Wild females reportedly first give birth at age 6 compared to age 5 observed in the captive populations. No reported age of last reproduction could be found for wild females, so m_x for *in situ* females was calculated up until maximum longevity reported at age 40. The m_x calculated for *in situ* females was consistently higher than that reported for *ex situ* females, giving an indication that fecundity is a factor in low growth rates reported in the *ex situ* population compared to that of the wild population. In *in situ* populations, inter-birth intervals ranged between 2.1 years for young animals and 3.9 years for older animals, with a mean of approximately 2.7 years (Owen-Smith 1988). This translates to a maximum m_x value of 0.24 and minimum of 0.13 with a mean of 0.15. Mean inter-birth interval for the *ex situ* population was 3.2 years, with a minimum of 1.3 years and a maximum of 7.3 years (possibly as a result of a skipped birthing season). Maximum m_x value observed for *ex situ* females was 0.17 at the age of 14 years (Figure 27).

Figure 27: Fecundity rates (m_x) of *ex situ versus in situ* female *Diceros bicornis minor*.

In situ females have longevity of up to 40 years (Owen-Smith 1988) which exceeds the maximum reported longevity of *ex situ* females of 35 years. *Ex situ* mortality rates for neonate animals is high compared to that of the *in situ* population (33% compared to 9%), but the opposite can be said for juvenile mortalities, where mortality in wild populations was reported at around 16% per annum compared to zero in the *ex situ* population. In the captive population, no mortalities have been reported during sub-adulthood and a mean q_x value of 0.02 (2%) is calculated for adult age classes. This is compared to 5.7% sub-adult and 3.5% annual adult mortality recorded for wild population (Owen-

Smith 1988), indicating that average mortality is higher in wild populations compared to their *ex situ* counterparts (Figure 28).

Figure 28: Mortality rates (q_x) of *ex situ* vs *in situ* female *Diceros bicornis minor*.

Except for the first year of life, survival rates appear higher in the *ex situ* population than the *in situ* population, until longevity records are reached. This may be due to no mortalities having been recorded for a number of age classes in the *ex situ* population, possibly again a factor of low sample size (Figure 29).

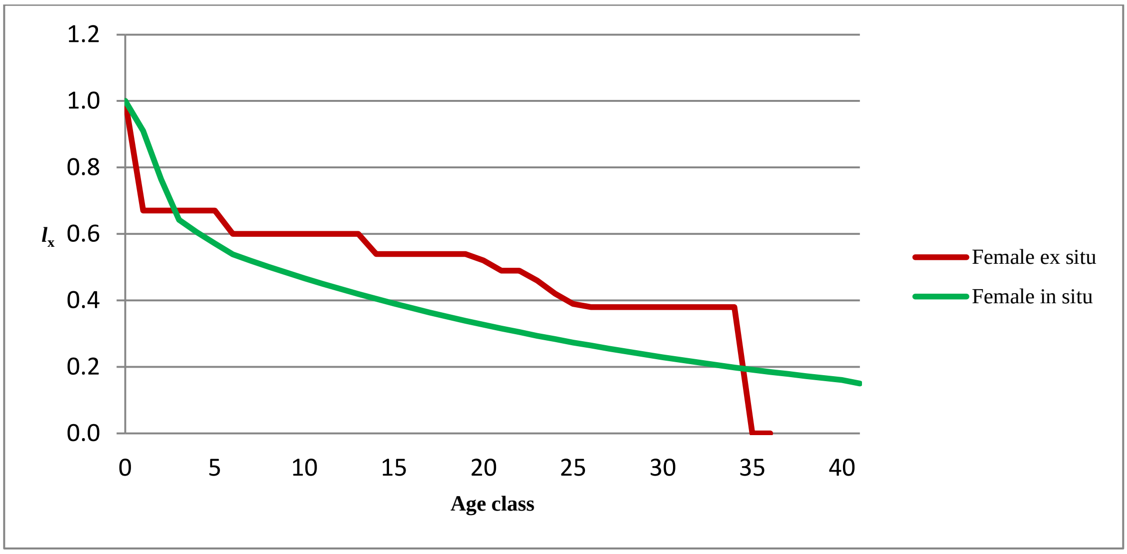

Figure 29: Survivorship (l_x) of *ex situ versus in situ* female *Diceros bicornis minor*.

R_o calculated from life table fecundity and mortality figures is 0.534 for *ex situ* females compared to 2.01 for *in situ* females.

Diceros bicornis michaeli

As with *D. b. minor*, *ex situ* reproduction is reported to start a year earlier at age 5 compared to age 6 noted for *in situ* females. Age of last reproduction between the two populations is much closer together than that of *D. b. minor*, as *D. b. michaeli ex situ* females are reported to breed until at least 36 years of age compared to females in the wild which reportedly breed until the age of 40. Once again, m_x rates appear vastly higher in the *in situ* environment (Figure 30).

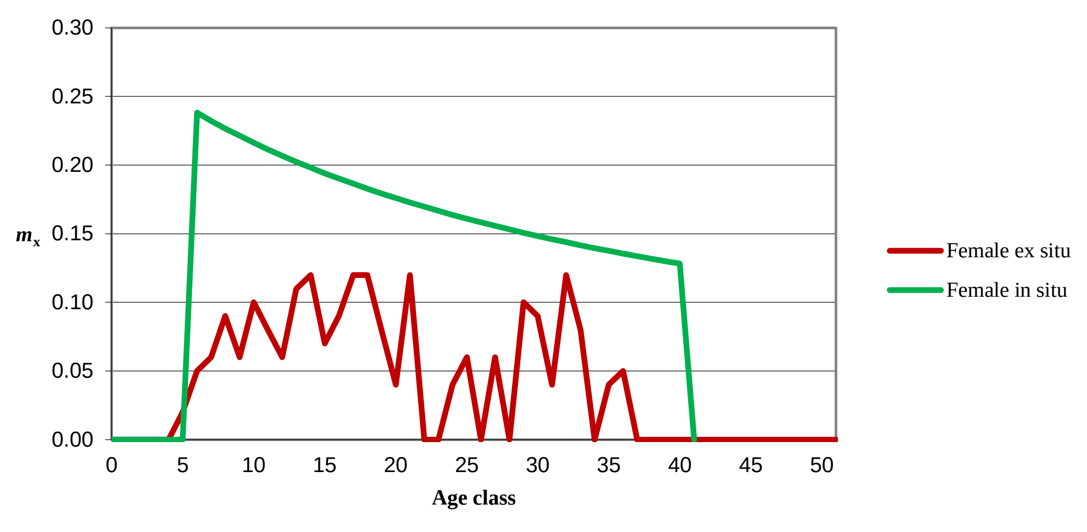

Figure 30: Fecundity rates (m_x) of *ex situ versus in situ* female *Diceros bicornis michaeli*.

Neonate mortality is similar for both *ex situ* and *in situ* females, with figures of 0.12 and 0.9, respectively. Juvenile mortality, however, is higher for the *in situ* population, an average of 16% juvenile mortality per annum reported compared to 1% in the *ex situ* population. Average adult mortality rates are identical with a mean q_x of 0.035 calculated for both the *in situ* and *ex situ* population. Longevity appears to be higher in the captive populations (48 years *versus* 40 years) (Figure 31).

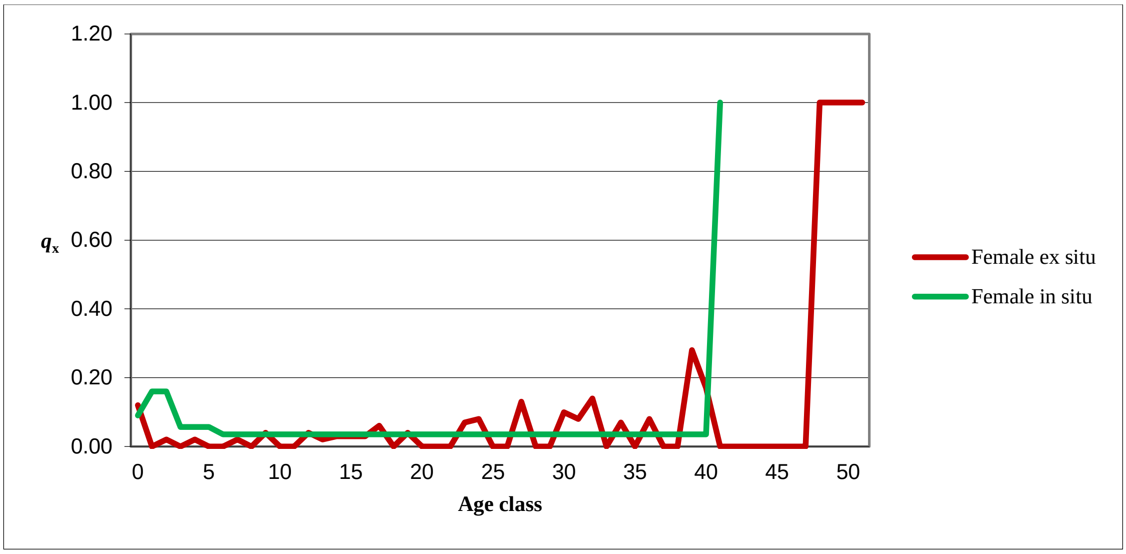

Figure 31: Mortality rates (q_x) of *ex situ versus in situ* female *Diceros bicornis michaeli*.

The survivorship curve shows a much higher survival rate in the captive population than that of the wild population. The median survival time is 27.6 years for the captive females, but much earlier at 8 years of age for the wild population. This is mostly due to the higher juvenile mortality *in situ* (Figure 32).

Figure 32: Survivorship (l_x) of *ex situ versus in situ* female *Diceros bicornis michaeli*.

R_o for *in situ* females is 2.01 compared to the 1.3 for *ex situ* females, indicating a much higher possible reproductive rate than is currently observed in the *ex situ* population.

Ceratotherium simum simum

Fecundity rates for captive *C. s. simum* are very low in comparison to the average reported for the *in situ* population. Captive female however, have been reported breeding from age 4, whereas first reproductive event for the *in situ* population only occurred at age 7. As with *D. b. minor* and *D. b. michaeli*, no senescence was reported for free ranging female rhinoceros, so m_x values are continuous until longevity is reached at age 46. For *ex situ* females, age of last reproduction is recorded at 36 years (Figure 33).

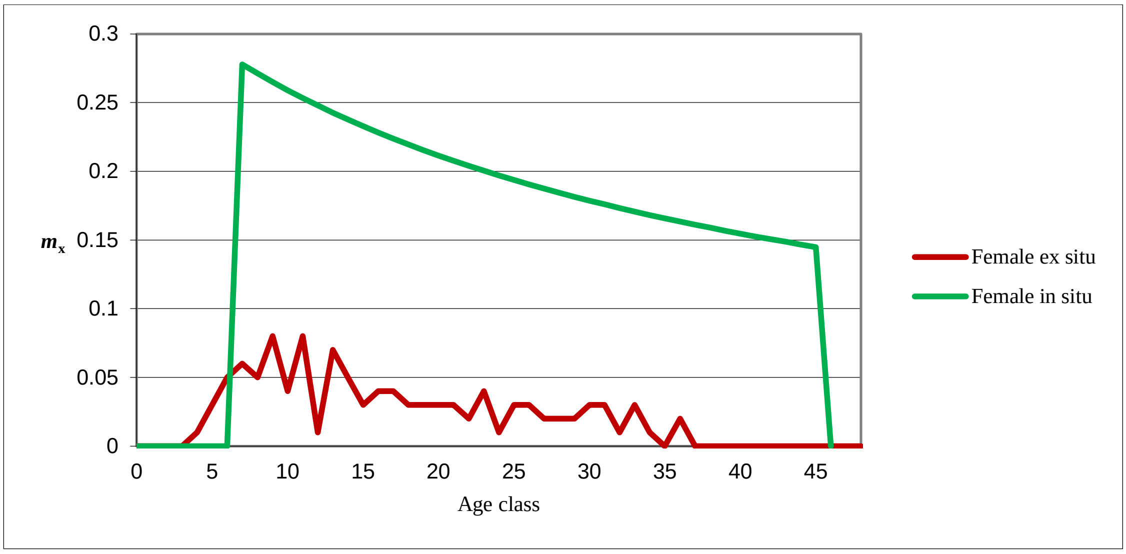

Figure 33: Fecundity rates (m_x) of *ex situ versus in situ* female *Ceratotherium simum simum*.

Mortality rates are comparable for the *ex situ* and *in situ* populations, but with higher mortality occurring after the age of 30 in the *ex situ* population. The oldest female reported in captivity reached an age of 45.4 years, compared to the longevity of 45 years reported for wild females (Figure 34). Mean adult q_x is 0.01 for *in situ* population *versus* 0.03 in the *ex situ* population.

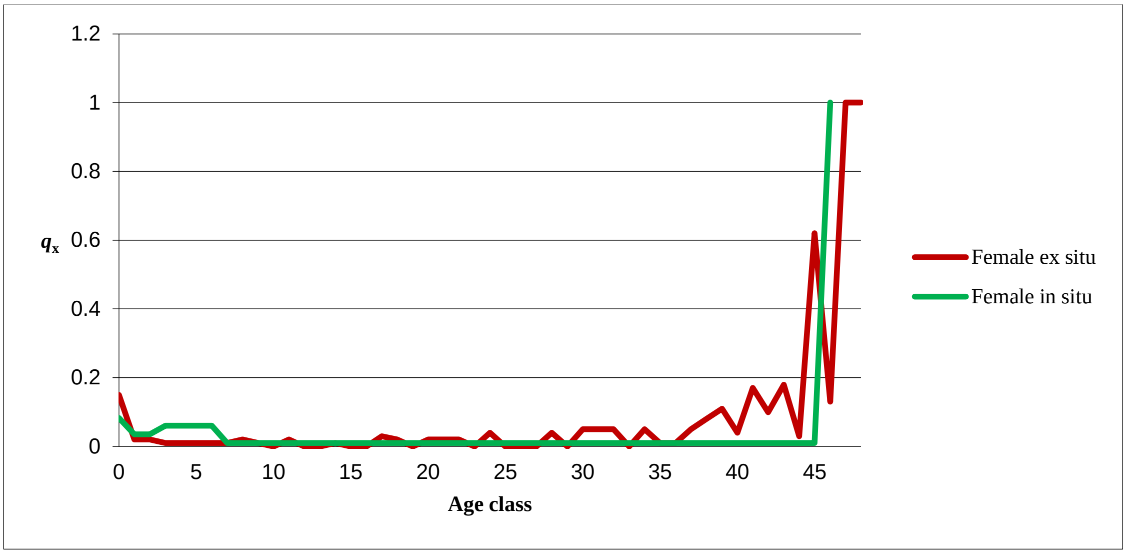

Figure 34: Mortality rates (q_x) of *ex situ versus in situ* female *Ceratotherium simum simum.*

Neonate survival is reported to be lower in captive populations compared to wild populations. After this, however, survival in captivity is noticeably higher than what is reported for the *in situ* population, until the age of 37, where *ex situ* survival after senescence seen in the captive population, seems to decline faster than that of the *in situ* population (Figure 35). Median survival time is around the age of 37 for the captive population and 35 for the wild population.

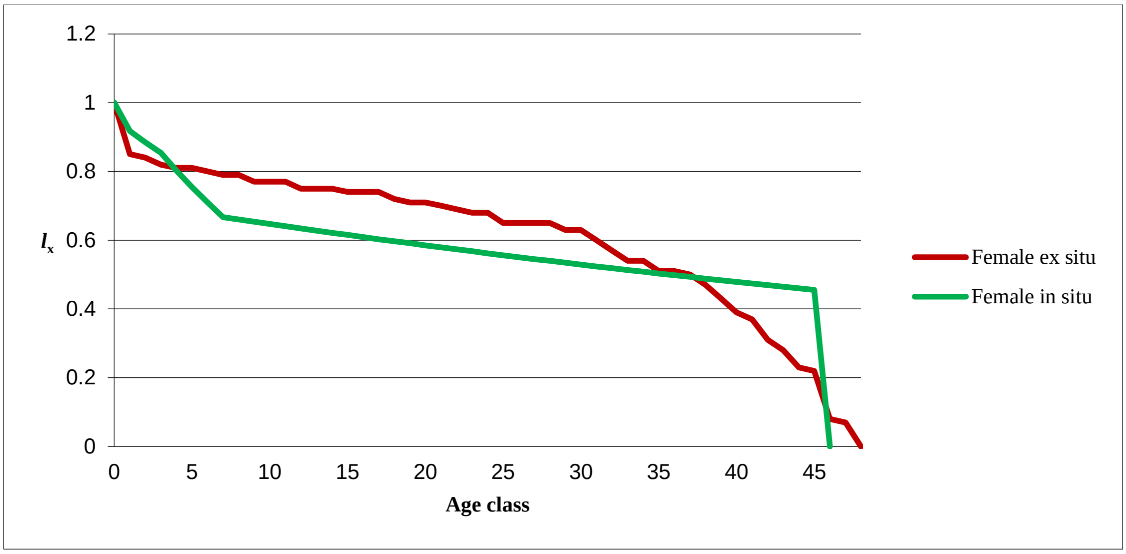

Figure 35: Survivorship (l_x) of *ex situ versus in situ* female *Ceratotherium simum simum*.

R_o figures are 4.4 for the *in situ* population *versus* that of 0.79 for *ex situ* females. This indicates a huge potential for replacement currently not seen in the captive population.

Summary of key demographic factors from the life table analysis

Table 8 compares some of the key life table factors observed in *D. b. minor, D. b. michaeli and C. s. simum,* both those reported in the *in situ* population and those calculated from *ex situ* population data. Age of first reproduction appears to be similar for all three sub-species, as reports are that females give birth to their first offspring between the age of four and seven. A captive female *C. s. simum* was the youngest female to give birth at the age of four years. While no reproductive senescence is reported in the wild population, captive animals seem to indicate some level of reproductive senescence, where a gap of approximately eight to ten years is observed between the age of last reproduction and maximum life span. This is particularly pronounced in male *D. b. michaeli*, where the oldest recorded male was 49.5 years of age, but last reported age of reproduction is 32. However, this should be viewed with caution as it may be a case of error in reporting as the longevity record is based on a single animal. Captive *D. b. minor* displays the lowest longevity of all three subspecies, with the oldest recorded male at 32.1 years and oldest female at 35 years of age.

Neonate mortality in the captive population is higher than the *in situ* populations for both sexes of *D. b. michaeli* and *C. s. simum***,** as well as for female *D. b. minor*. However, male *D. b. minor* data indicate the lowest neonate mortality of 0.8. The highest neonate mortality is seen in female *D. b. minor*, where a rate of 0.33 is recorded.

The data indicates that median survival times are much higher in captive *D. b. minor* and *D. b. michaeli* than their *in situ* counterparts. The difference is quite dramatic, as a median survival time of 18.7 and 26 years for male and female captive *D. b. minor*, and 26.8 and 27.6 years for male and female *D. b. michaeli* captive populations is recorded, while for the *in situ* population the median survival time is only eight years. This is due to high juvenile mortality reported in the *in situ* population compared to the *ex situ* population. This discrepancy is not seen in *C. s. simum***,** where median survival time for both the *in situ* and *ex situ* populations is around the age of 35 years.

Overall lifetime reproductive rate (R_o) is much lower in the captive populations than their wild counterparts in all three sub-species. Indications are that *D. b. michaeli* is the only sub-species currently able to sustain itself as R_o figures are greater than one for both male and female sub-populations.

Generation lengths (T) are similar for both *in situ* and *ex situ* populations of *D. b. minor* and *D. b. michaeli*, while *ex situ C. s. simum* has a slightly lower generation length than their wild counterparts.

Table 8: Summary of demographic parameters from life table analysis

	D. b. minor			*D. b. michaeli*			*C. s. simum*		
Parameter	*Ex situ*		*In situ*	*Ex situ*		*In situ*	*Ex situ*		*In situ*
	♂	♀	♀	♂	♀	♀	♂	♀	♀
Age at 1st reproduction	5	5	6	6	5	6	7	4	7
Highest age of reproduction	30	27	40	32	36	40	39	37	45
Oldest recorded animal	32.1	35	40	49.5	46	40	46	45.4	45
Oldest living animal	29	34	N/A	41	41	N/A	45	45	N/A
Neonate mortality	0.08	0.33	0.09	0.13	0.12	0.09	0.17	0.15	0.083
Median survival time	18.7	26	8	26.8	27.6	8	29.6	37.1	35.5
Age at which $l_x = 0.25$	32.1	34.3	27	35.4	39.4	27	41	43.5	45
Age at which $l_x = 0.1$	33.3	34.7	40	41.9	41.5	40	45.1	45.9	45
R_o	0.729	0.534	2.01	1.649	1.282	2.01	0.911	0.788	4.3
Generation time (T)	20.6	15.6	17.8	18.3	16	17.8	19.7	17.2	22.6

2.4.3 Sensitivity analysis

Sensitivity analysis was conducted on the female data for all three populations with the resultant change in λ recorded in Table 9. Out of all three subspecies in this study, only *D. b. michaeli* had a positive growth before sensitivity analysis was conducted. The scenario that had the most impact on *D. b. minor* was to increase the m_x value across all age classes to those matching fecundity rates of *in situ* populations. This was followed by increasing the m_x values to a value calculated using the median inter-birth interval reported in captivity. Increasing survival rate to 100% across all age classes had a nominal impact, with only a 4.16% increase in population growth rate. In the case of *D. b. michaeli* and *C. s. simum*, maximum impact was gained by matching fecundity rates across all age classes to those calculated from the median inter-birth interval from captive animals, thereafter, increasing the m_x values to match *in situ* values achieved the second highest impact. Third highest for these two sub-species was achieved by increasing p_x to 1 across all age classes, but as with *D. b. minor*, this did not have as profound an impact as was expected, with an increase of only 2.15% seen in the case of *C. s. simum* and 2.47% for *D. b. michaeli*. As was expected, given that survival was lower in the *in situ* populations of all three subspecies (Figure 29, Figure 32 and Figure 35), changing p_x rates to match those reported for *in situ* populations produced negative results.

Table 9: Sensitivity analysis

		D. b. minor	%	*D. b. michaeli*	%	*C. s. simum*	%
	Original λ	0.963		1.017		0.983	
a)	Increase of m_x across all breeding ages by 5%.	0.966	0.32	1.020	0.31	0.986	0.29
b)	Lowering age of first reproduction by 1 age class.	0.966	0.42	1.020	0.34	0.998	1.49
c)	Extending age of reproduction past current senescence by one age class.	0.967	0.46	1.017	0.05	0.984	0.05
d)	Alter m_x across all breeding ages to match those reported in *in situ* populations.	1.065	14.52	1.089	7.14	1.094	11.23
e)	Increase m_x to the median captive breeding rate for females of breeding age	1.052	9.31	1.092	7.39	1.120	13.86
f1)	Increase age specific survivorship (p_x) rate by 5% over the neonate (p_0) life stages.	0.966	0.32	1.020	0.31	0.986	0.29
f2)	Increase p_x by 5% over the juvenile (p_1 and p_2) life stages.	0.963	0.00	1.018	0.13	0.986	0.24
f3)	Increase p_x by 5% over the sub adult (p_3 to one age class before first recorded breeding event) life stages.	0.963	0.00	1.018	0.13	0.984	0.06
f4)	Increase p_x by 5% over the adult (from age class at first breeding event) life stages.	0.970	0.82	1.029	1.19	0.992	0.87
g)	Change neonatal survivorship (p_0) rate to match that of *in situ* populations.	0.982	2.03	1.019	0.21	0.988	0.45
h)	Alter p_x across all ages to match that of the *in situ* population.	0.943	-2.07	0.982	-3.42	0.976	-0.79
i)	Increase survivorship (p_x) by 5% across all age classes.	0.973	1.13	1.034	1.74	0.998	1.45
j)	Increase p_x rate by 5% over the top 5 age classes with the highest mortality.	0.971	0.90	1.020	0.35	0.986	0.29
k)	Increase p_x to 100% over all age classes until maximum life span.	1.003	4.16	1.042	2.47	1.005	2.15

At the current population growth rates calculated from the life table analysis, predicted numbers for the 50 year (2042) target set at the GCAP workshop are 35 for *D. b. minor*, 532 for *D. b. michaeli* and 503 for *C. s. simum*, with only *D. b. michaeli* achieving its target number. Theoretical population growth rates required to achieve population targets are presented in Table 10 below. Only *D. b. minor* requires a substantial increase in population growth rate in order to achieve the target population size set in 1992, with current life table λ calculated as 0.98 and the required λ to reach the 2042 target as 1.03.

Table 10: Growth rates for *Diceros bicornis minor*, *Diceros bicornis michaeli* and *Ceratotherium simum simum* required to reach GCAP target population size.

	Target N			Actual N		Current growth rates		Required growth rates	
Subspecies	2002	2042	2092	2004	2010	λ Census	λ Life table	λ 2042	λ 2092
D. b. minor	80	160	400	69	61	1.00	0.98	1.03	1.02
D. b. michaeli	200	240	240	171	249	1.00	1.02	1.00	1.00
C. s. simum	515	525	500	747	673	1.00	0.99	0.99	1.00

As fecundity has been identified as the main factor limiting population growth rate, further analyses were conducted to calculate the fecundity rates needed in order to produce the population growth rate required to achieve the population targets. The proportional changes required for the three subspecies are presented in Figure 36. In order to achieve the 50- and 100-year population targets, *D. b. minor* female fecundity would have to increase by 170% and 150%, respectively. In contrast, *C. s. simum* female fecundity would only have to increase by 30% to achieve the 100-year target. *Diceros bicornis michaeli* is the only subspecies where current female fecundity rates are above what is necessary to achieve the target population goals set, with the required λ corresponding to approximately minus 25% of the current fecundity rates.

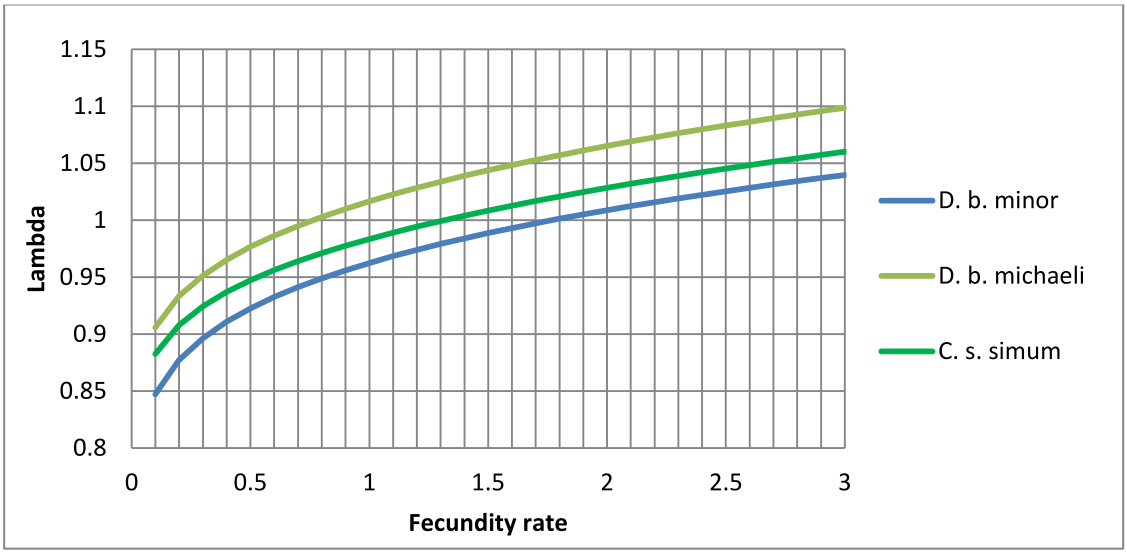

Figure 36: Proportional change in female fecundity rates (m_x) to achieve target GCAP population growth rates - *Diceros bicornis minor*, *Diceros bicornis michaeli* and *Ceratotherium simum simum.*

2.4.4 Age structure analysis

Diceros bicornis minor

Due to the small number of individuals in the *D. b. minor* population, it is fairly difficult to assess the state of the population from a visual assessment of the current populations age pyramid. However, the absence of any animals in age classes 1 to 4 is indicative of a very low rate of recruitment and a population in decline. *G*-test analysis on observed male and female age distribution of *D. b. minor* indicates a significant difference from the stable age distribution for males where $G_{adj} = 10.34 > X^2_{0.05\ [4]} = 9.49$; $n = 6$; $P < 0.05$, but no significant difference from a stable age distribution in females, where $G_{adj} = 6.50 > X^2_{0.5\ [4]} = 3.36$; $n = 6$; $P > 0.1$.

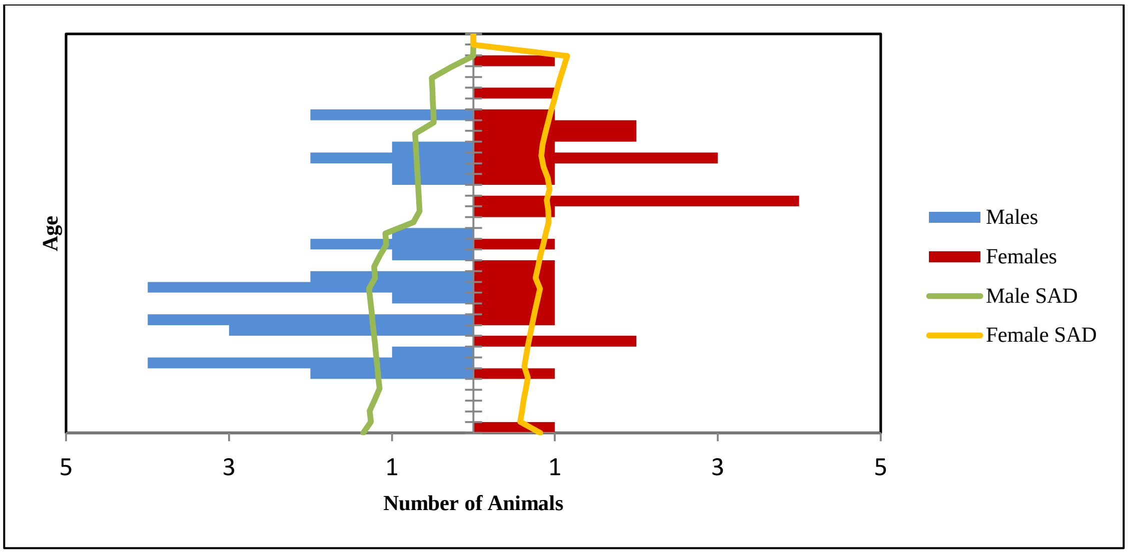

Figure 37: Age pyramid - *Diceros bicornis minor*.

On assessment of the census data and the age pyramid, 36% of the current population of *D. b. minor* are founders, all of which, except for one male, are over the age of 20. As last age of reproduction is 27 years for this subspecies, 33% of the female founders may already be past breeding age (Figure 38).

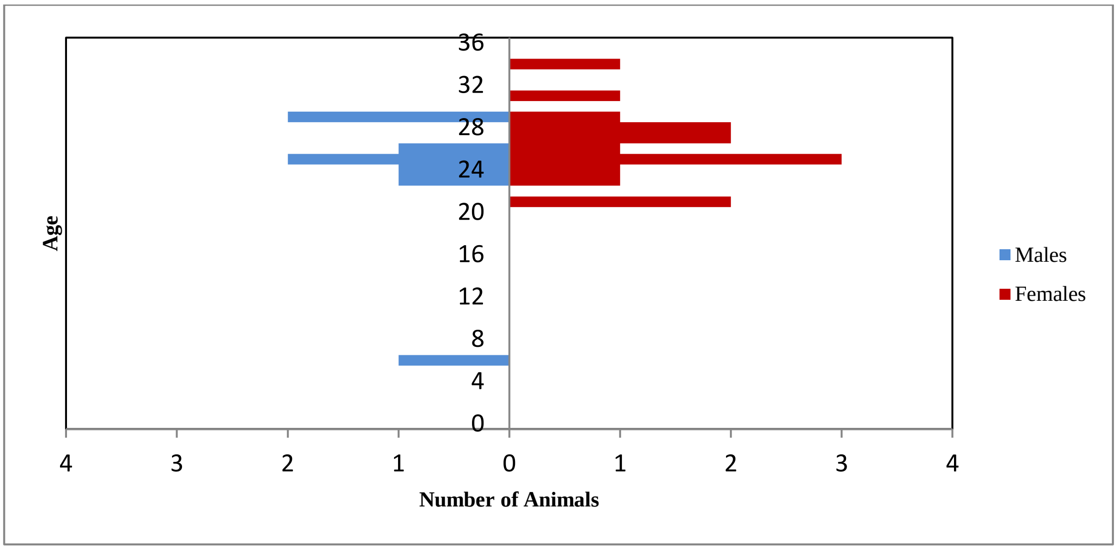

Figure 38: Founder age pyramid - *Diceros bicornis minor*.

The captive-born population on the other hand is all under the age of 22. The captive-born population shows a male bias, with 25 males and only 14 captive-born females (Figure 39). The oldest captive-born female is currently 21 years of age, while the oldest captive-born male is 18 years old.

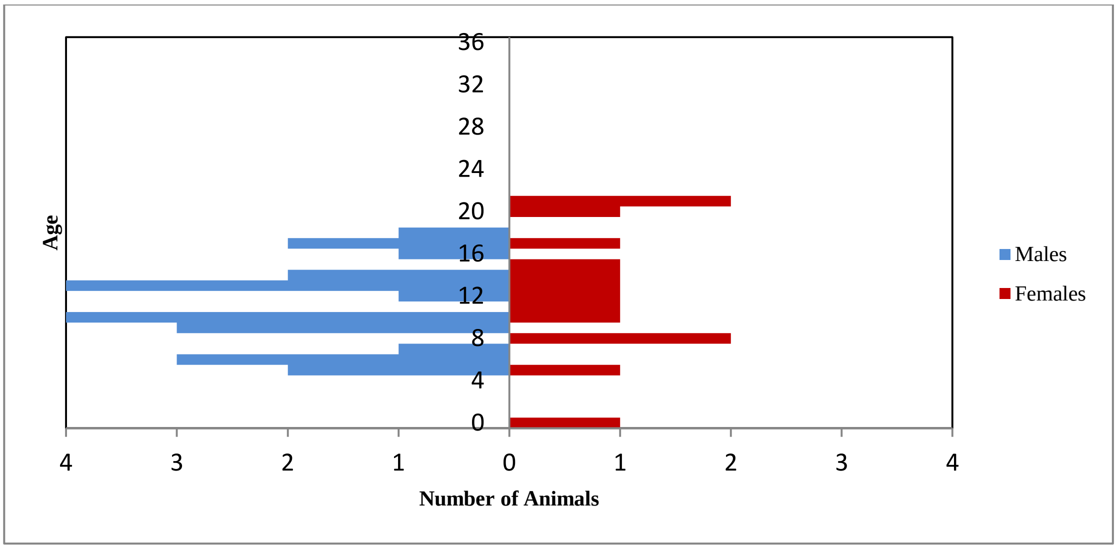

Figure 39: Captive-born age pyramid - *Diceros bicornis minor*.

Diceros bicornis michaeli

The shape of the age pyramid for *D. b. michaeli* is indicative of a growing population with constant recruitment into the lower age classes (Figure 40). Analysis of the stable age structure compared to the observed age structure for *D. b. michaeli* indicated that neither male nor female observed age distributions are significantly different to that of the stable age distribution with male $G_{adj} = 23.23 > X^2_{0.1\,[15]} = 22.31$; $n = 17$; $P > 0.05$, and female $G_{adj} = 12.48 > X^2_{0.9\,[15]} = 8.55$; $n = 17$; $P > 0.5$.

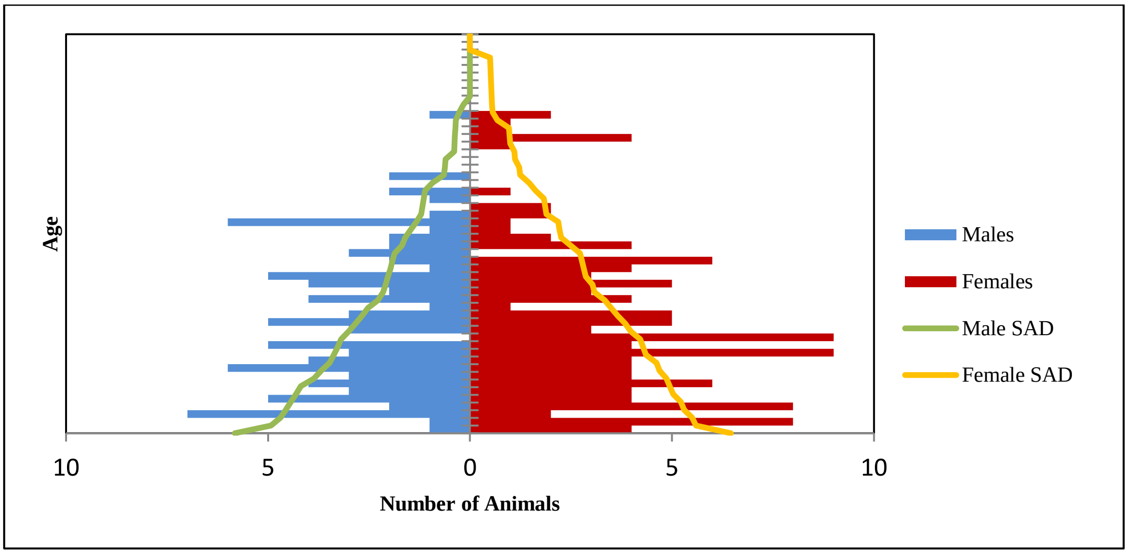

Figure 40: Age pyramid - *Diceros bicornis michaeli*.

As discussed earlier in the section on annual census analysis, founders make up only 6.4 % of the current population of *D. b. michaeli*. All the founders are over the age of 17 and 57% of female founders may already be past the maximum reproductive age of 37 years recorded in captivity (Figure 41).

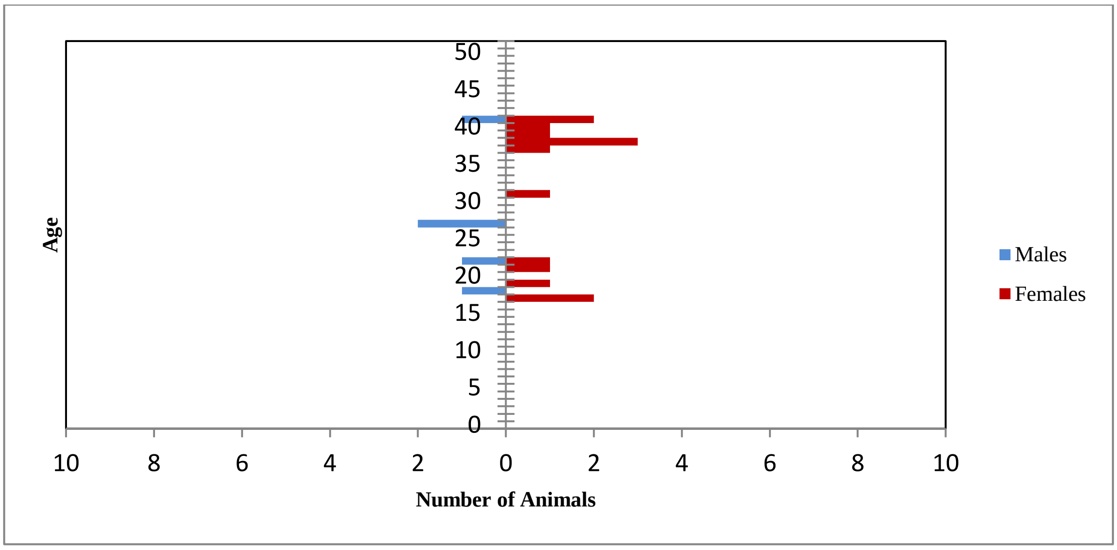

Figure 41: Founder age pyramid - *Diceros bicornis michaeli*.

Captive-born *D. b. michaeli* on the other hand are fairly well distributed throughout the age structure. (Figure 42). The oldest captive-born female is 38 years old and the oldest captive-born male is 33 years old.

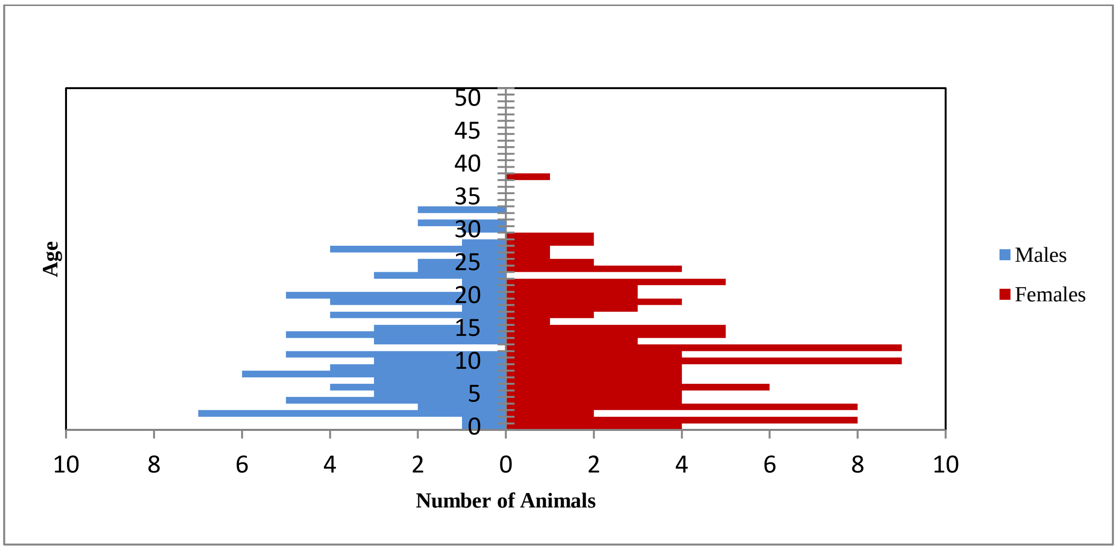

Figure 42: Captive-born age pyramid - *Diceros bicornis michaeli*.

Ceratotherium simum simum

The *C. s. simum* age pyramid structure resembles that of a population in decline, as numbers in the lower age classes are contracted compared to those of the breeding age classes. *Ceratotherium simum simum,* in comparison to *D. b. minor* and *D. b. michaeli*, shows significant difference for both males and females when comparing the stable age distribution to the current age distribution of the population. Male data showed a $G_{adj} = 53.35 > X^2_{0.005\ [21]} = 41.40$; $n = 23$; $P < 0.005$ and females gave a value of $G_{adj} = 124.33 > X^2_{0.005\ [21]} = 41.40$; $n = 23$; $P < 0.005$. This difference can mostly be attributed to the age classes 39 to 42 for males and 39 to 43 for females, where a large aging population exists (Figure 43).

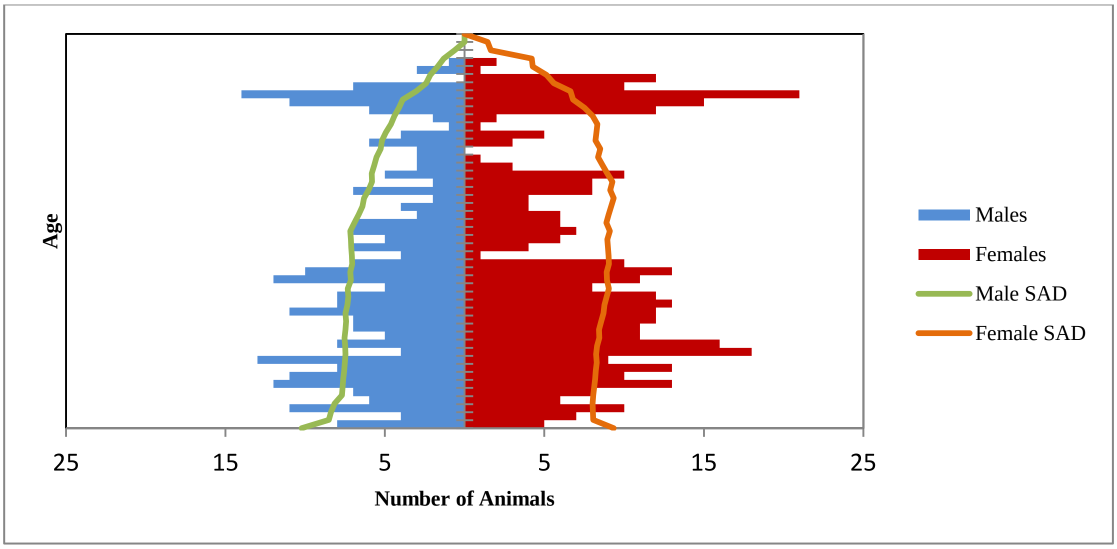

Figure 43: Age pyramid - *Ceratotherium simum simum*.

On assessment of the founder *versus* captive-born age pyramid structures, it can be seen that founders make up the majority of the large group of rhinoceros above the age of 40. However, there are still a number of founders throughout the population structure, starting at 2 years of age. The founder age structure has a female bias, with 200 females in the population compared to 97 males (Figure 44).

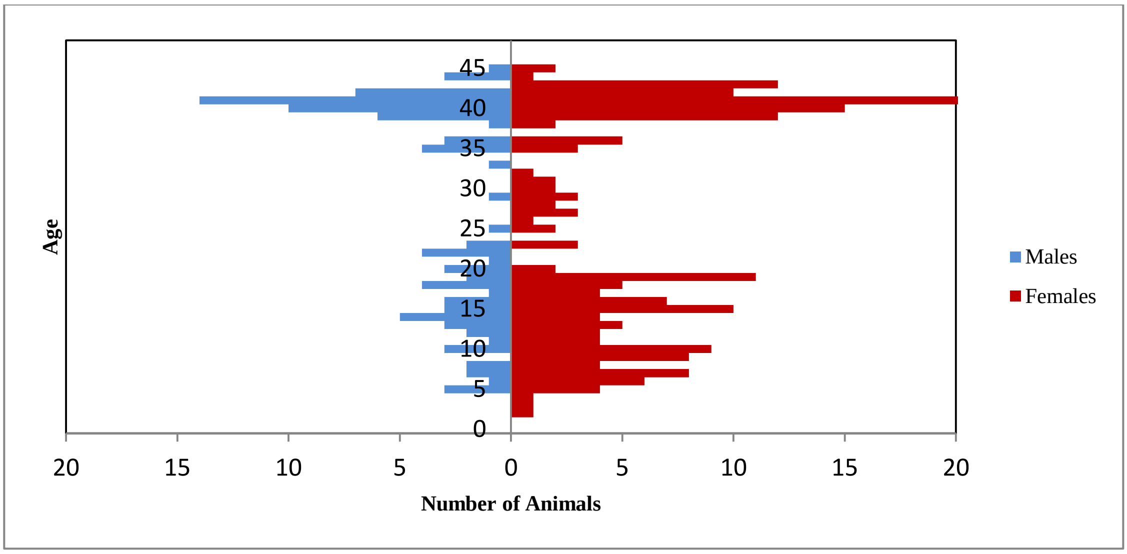

Figure 44: Founder age pyramid - *Ceratotherium simum simum*

Captive-born *C. s. simum* show a population structure that appears to be growing, with the base of the age pyramid appearing wider than the other age classes. Sex ratio is slightly male biased, with 192 males and 180 females in the population (Figure 45).

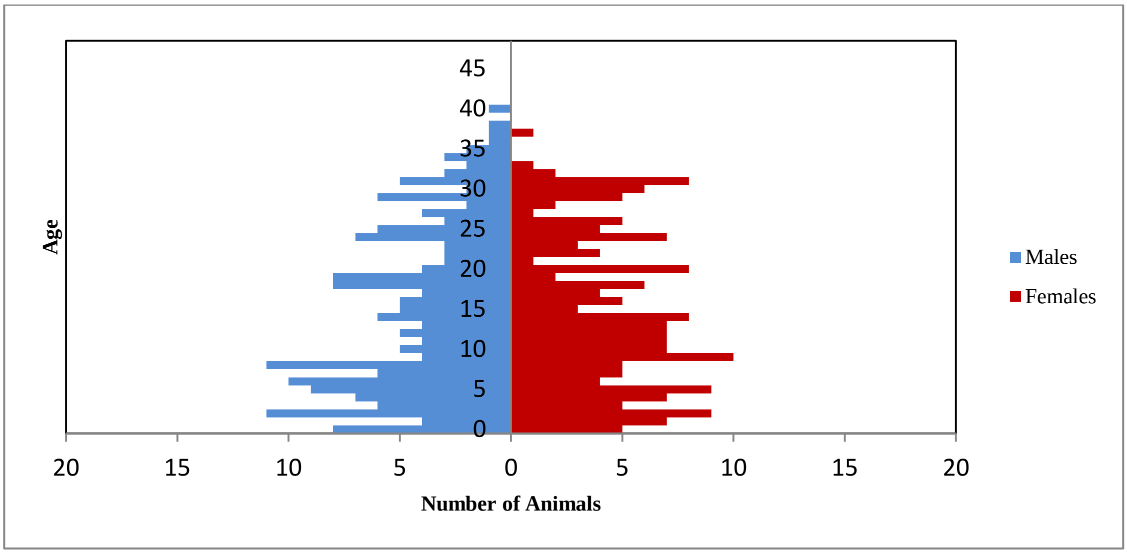

Figure 45: Captive-born age pyramid - *Ceratotherium simum simum*.

2.5 Discussion

Diceros bicornis minor

This study confirms that the captive population *Diceros bicornis minor* is currently in decline. Since no new founders have been imported into the population since 1990, the population has been reliant on captive breeding for the past 20 years for its growth and sustainability. While the population showed an average positive growth rate up until 2001, the overall growth rate for the past ten years is recorded as minus 1% (-0.01 per annum), corresponding to the λ of 0.996 reported by Foose & Wiese in 2006 for the North American population. The null (H_0) hypothesis proposed that aging of the F_0 population will not have a significant effect on the population growth rate may in fact be rejected based on what has been observed happening in the last ten years. Currently the founders make up 36% of the population, with 33% of the female founders over breeding age. Twenty-one births were offset by 23 deaths in the population over the study period, with 65% of these deaths consisting of founders. Further loss of founders will in all likelihood exacerbate the situation, unless the captive-born population is made to be self-sustainable.

Male growth rate during the ten year time period under investigation was stationary, with a λ of 1 recorded; the negative growth seen as the result of a 1% drop in the female population. However, there was no statistically significant difference between male and female age specific survivorship at P = 0.05. With a current overall R_o of 0.79 and 0.56 for males and females, respectively, neither sex will be able to sustain their numbers for much longer without additional founders being imported into the population.

Benchmarking to *in situ* populations, it is clear that fecundity, rather than mortality, is the negative factor affecting population growth rate. Altering mortality rate of the *ex situ* population to match that of the *in situ* population through sensitivity analysis resulted in a negative change in population growth rate, indicating that the captive population has a better survival rate than their wild counterparts. The opposite was however true when the fecundity rates were analysed. The null (H_0) hypothesis that there are no significant differences in age-specific mortality and fecundity rates in global *D. b. minor* population in comparison to *in situ* populations is rejected, as differences between the two populations are reported for both these demographic factors, albeit one resulting in a negative effect and the other a positive effect in comparison. Further sensitivity analysis supports the theory that fecundity has the larger bearing, as positive changes to fecundity rates have a much larger impact than changes to mortality rates. However, analysis conducted on this subspecies indicated that an 80% increase in current fecundity rate is needed before a positive growth rate is observed; and in order to reach the 50 year target population size set out in the 1992 GCAP meeting, the fecundity rate needs to increase by 170%. This is theoretically possible, as changing m_x rates to rates calculated by the median figure of inter-birth intervals currently seen in the captive population resulted in a 276% increase in fecundity.

Age structure analysis indicates that males of the population currently do not have a stable age distribution, whereas females do. Comparison of census data λ to life table λ does not seem to support this however, as the difference between the two λs for females is almost 7% while for the males it is only 1.8%. It has been stated before that data for the subspecies must be viewed with caution due to low sample size, and this discrepancy in λs may be a consequence of this. The null (H_0) hypothesis that the global captive *D. b. minor* population has an age structure that is stable is therefore rejected.

Diceros bicornis michaeli

The *D. b. michaeli* population is currently performing well, having reached its 50 years target population size set at the 1992 GCAP workshop by the end of 2009 (Foose & Wiese 2006). As no new founders have been introduced into the population since 1994, the positive growth has purely been due to captive births, with a mean growth of 2.5% per annum calculated from the annual census figures for the last ten years, although the last year indicated a growth of only 0.4%. The λ from the life table analysis shows a growth of 2.4%, very close to that of the figure achieved through the annual census reports. As founders only make up 6.4% of the current population, aging of the founder population is unlikely to have any significant effect on future population growth rates, therefore the null (H_0) that aging of the F_0 generation will not significantly affect future growth rates of the global captive population is accepted. The growth rates calculated suggest a stable age structure, which is confirmed by the age structure analysis where neither the current male nor female populations showed a significant difference to the stable age structure obtained from the eigen vector of the Leslie matrix.

This result supports the null hypothesis (H_0) that the global captive *D. b. michaeli* population has an age structure that is stable.

As with *D. b. minor*, sensitivity analysis indicates that fecundity rather than mortality is the critical factor preventing population growth rates that are equivalent to those witnessed in the wild. Although no statistical analysis was performed, the null (H_0) hypothesis that there are no significant differences in age-specific mortality and fecundity rates in the global *D. b. michaeli* captive rhinoceros populations in comparison to *in situ* populations is partly rejected based on the comparative graphs for age-specific fecundity and mortality rates between the *in situ* and *ex situ* population. Mortality rates are almost identical, with mean *qx* values of 0.035 calculated for both populations. However, fecundity rates are vastly different, with higher *in situ* fecundity recorded throughout the age classes. These rates are not impossible to achieve for the captive population, as sensitivity analysis using m_x values observed in the wild compared to the m_x values calculated from the median of the current inter-birth interval observed in captivity produced similar result in the growth rate of 8.9% and 9.2% respectively. However, if the 1992 GCAP targets are the end goal, population growth rate should at this stage actually be curtailed, rather than increased. A decrease in fecundity (-25%) would yield the required population growth rate to reach the target. Alternatively, it may be possible to supply extra individuals out of the studbook for release back into the wild if the opportunity exists, without compromising the captive population.

Ceratotherium simum simum

The *C. s. simum* population is the largest of the three rhinoceros subspecies under discussion, with a total of 673 held in captivity at the end of 2010. Although a reduction in numbers was suggested at the GCAP meeting in order to make captive space available for black rhinoceros, this has not happened and the population grew by 6.65% between 1992 and 2010. This is likely to change over the next five years, as 14.4% of the population is currently over the age of 40, and just the reduction of these population numbers alone will reduce the total number by 97. All except one of these individuals are founders. This natural attrition should not have any effect on current birth recruitment rate as minimal births have been recorded in this subspecies over the age of 40. The null (H_0) hypothesis that the aging of the F_0 population will not significantly affect the global population growth rate is therefore accepted for this subspecies.

Currently, population growth rate from annual census figures is recorded as 1.004 with an average of 1.006 over the past ten years. After the drop predicted in the next five years, the population should stabilize once again, as the current λ obtained from the life table is 0.99, indicating an almost stationary population. At the moment, the population shows an age distribution that is far from stable, showing significant difference for both the male and female populations. This, however, is an artefact of the aged founder population which is no longer contributing to recruitment, and is likely to improve as the aged population dies off, eliminating the main source of discrepancy in the current age distribution. The current data refutes the null hypothesis (H_0) that the global captive population has an age structure that is stable in the case of *C. s. simum*, but the population age structure is expected to stabilize within the next five years.

As with the black rhinoceros subspecies, the bench-marking exercise and sensitivity analysis indicates that fecundity rather than mortality is the significant factor currently restricting population growth rates. In the bench-marking exercise, average adult mortality in the *ex situ* population is identical to that reported in the wild, therefore by deduction, only fecundity can be different. Sensitivity analysis once again confirms this, as increasing the m_x rates to match those seen in the *in situ* population produces a population growth rate of 9.4%. In order to reach the 100-year target, a controlled decrease in *C. s. simum* numbers is needed. While female λ is currently 0.983, the required λ is in fact 0.9964. With a male λ of 1, a 30% increase in female fecundity will achieve this rate. The null (H_0) hypothesis that there are no significant differences in age-specific mortality and fecundity rates in global captive rhinoceros populations in comparison to *in situ* populations is therefore rejected, but only in part. No significant difference was found for age-specific mortality, but a difference is observed in the age-specific fecundity rates.

In conclusion, the global captive population growth rates calculated in this study for all three populations of African rhinoceros are consistent with those reported by Foose & Wiese (2006) for the North American captive populations. For all three subspecies, fecundity appears to be the limiting factor in the population growth rates observed, while no evidence could be found to suggest that mortality limits the global captive population’s growth rates reaching those observed in certain populations in the wild. While both *D. b. michaeli* and *C. s. simum* have already attained their global targets and are demographically stable, *D. b. minor* is unlikely to achieve its targets without the introduction of additional founders. Small population size and an age structure that is not stable are compounding factors that increase the risk of extinction for this subspecies.

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Appendix 1: Life table – *Diceros bicornis minor* (*ex situ*)

Males

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	l_xm_x	$x(l_xm_x)$
0	0.92	0.08	13.2	1	0	13.2	0.00	0.00	0.00
1	1	0	16.4	0.92	0	16.4	0.00	0.00	0.00
2	0.94	0.06	17.5	0.92	0	17.5	0.00	0.00	0.00
3	0.94	0.06	16.4	0.86	0	16.4	0.00	0.00	0.00
4	1	0	19	0.81	0	19	0.03	0.00	0.00
5	1	0	20.5	0.81	0.03	20.5	0.00	0.02	0.12
6	1	0	17.5	0.81	0	17.5	0.00	0.00	0.00
7	1	0	18.1	0.81	0	18.1	0.00	0.00	0.00
8	1	0	19.2	0.81	0	19.2	0.06	0.00	0.00
9	1	0	18.5	0.81	0.06	18.5	0.00	0.05	0.44
10	1	0	14.5	0.81	0	14.5	0.03	0.00	0.00
11	1	0	13.6	0.81	0.03	13.6	0.03	0.02	0.27
12	1	0	14.5	0.81	0.03	14.5	0.00	0.02	0.29
13	0.93	0.07	14.8	0.81	0	14.8	0.12	0.00	0.00
14	1	0	11.6	0.76	0.13	11.6	0.12	0.10	1.38
15	0.93	0.07	13.1	0.76	0.12	13.1	0.07	0.09	1.37
16	0.92	0.08	12.8	0.71	0.08	12.8	0.09	0.06	0.91
17	1	0	10.9	0.65	0.1	10.9	0.07	0.07	1.11
18	0.67	0.33	7.1	0.65	0.07	7.1	0.00	0.05	0.82
19	0.89	0.11	7.6	0.43	0	7.6	0.00	0.00	0.00
20	1	0	8	0.39	0	8	0.00	0.00	0.00
21	1	0	8.7	0.39	0	8.7	0.06	0.00	0.00
22	1	0	9	0.39	0.06	9	0.00	0.02	0.51
23	1	0	8.5	0.39	0	8.5	0.07	0.00	0.00
24	1	0	7.8	0.39	0.07	7.8	0.00	0.03	0.66
25	1	0	5.5	0.39	0	5.5	0.00	0.00	0.00
26	1	0	4	0.39	0	4	0.00	0.00	0.00
27	0.67	0.33	2.6	0.39	0	2.6	0.00	0.00	0.00
28	1	0	2	0.26	0	2	0.50	0.00	0.00
29	1	0	0.9	0.26	0.5	0.9	0.00	0.13	3.77
30	1	0	1	0.26	0	1	0.00	0.00	0.00
31	1	0	1	0.26	0	1	0.50	0.00	0.00
32	0.53	0.47	1	0.26	0.5	1	0.00	0.13	4.16
33	0.02	0.98	1	0.14	0	1	0.00	0.00	0.00
34	0	1	0	0	0	0	0.00	0.00	0.00
35	0	1	0	0	0	0	0.00	0.00	0.00
36	0	1	0	0	0	0	0.00	0.00	0.00

Females

Age	p_x	q_x	*Risk qx*	l_x	m_x	*Risk mx*	F_x	l_xm_x	$x(l_xm_x)$
0	0.67	0.33	6.40	1.00	0.00	6.40	0.00	0.00	0.00
1	1.00	0.00	6.20	0.67	0.00	6.20	0.00	0.00	0.00
2	1.00	0.00	7.30	0.67	0.00	7.30	0.00	0.00	0.00
3	1.00	0.00	7.60	0.67	0.00	7.60	0.00	0.00	0.00
4	1.00	0.00	8.40	0.67	0.00	8.40	0.06	0.00	0.00
5	0.90	0.10	9.00	0.67	0.06	9.00	0.00	0.04	0.20
6	1.00	0.00	8.00	0.60	0.00	8.00	0.06	0.00	0.00
7	1.00	0.00	8.60	0.60	0.06	8.60	0.00	0.04	0.25
8	1.00	0.00	8.90	0.60	0.00	8.90	0.07	0.00	0.00
9	1.00	0.00	7.10	0.60	0.07	7.10	0.07	0.04	0.38
10	1.00	0.00	7.40	0.60	0.07	7.40	0.00	0.04	0.42
11	1.00	0.00	8.60	0.60	0.00	8.60	0.05	0.00	0.00
12	1.00	0.00	10.60	0.60	0.05	10.60	0.15	0.03	0.36
13	0.90	0.10	9.90	0.60	0.15	9.90	0.15	0.09	1.17
14	1.00	0.00	9.00	0.54	0.17	9.00	0.05	0.09	1.29
15	1.00	0.00	10.10	0.54	0.05	10.10	0.05	0.03	0.41
16	1.00	0.00	11.50	0.54	0.05	11.50	0.04	0.03	0.43
17	1.00	0.00	12.20	0.54	0.04	12.20	0.00	0.02	0.37
18	1.00	0.00	15.00	0.54	0.00	15.00	0.00	0.00	0.00
19	0.96	0.04	18.30	0.54	0.00	18.30	0.03	0.00	0.00
20	0.94	0.06	17.30	0.52	0.03	17.30	0.03	0.02	0.31
21	1.00	0.00	15.50	0.49	0.03	15.50	0.04	0.01	0.31
22	0.94	0.06	14.10	0.49	0.04	14.10	0.00	0.02	0.43
23	0.91	0.09	12.80	0.46	0.00	12.80	0.04	0.00	0.00
24	0.93	0.07	12.60	0.42	0.04	12.60	0.06	0.02	0.40
25	0.98	0.02	9.00	0.39	0.06	9.00	0.00	0.02	0.59
26	1.00	0.00	8.00	0.38	0.00	8.00	0.07	0.00	0.00
27	1.00	0.00	7.00	0.38	0.07	7.00	0.00	0.03	0.72
28	1.00	0.00	6.00	0.38	0.00	6.00	0.00	0.00	0.00
29	1.00	0.00	2.90	0.38	0.00	2.90	0.00	0.00	0.00
30	1.00	0.00	3.00	0.38	0.00	3.00	0.00	0.00	0.00
31	1.00	0.00	3.00	0.38	0.00	3.00	0.00	0.00	0.00
32	1.00	0.00	2.00	0.38	0.00	2.00	0.00	0.00	0.00
33	1.00	0.00	2.00	0.38	0.00	2.00	0.00	0.00	0.00
34	0.00	1.00	0.00	0.38	0.00	0.00	0.00	0.00	0.00
35	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Total

Age	p_x	q_x	*Risk* q_x	l_x	m_x	*Risk* m_x	F_x	l_xm_x	$x(l_xm_x)$
0	0.795	0.205	19.6	1	0	Bre	0.00	0.00	0.00
1	1	0	22.6	0.795	0	22.6	0.00	0.00	0.00
2	0.97	0.03	24.8	0.795	0	24.8	0.00	0.00	0.00
3	0.97	0.03	24	0.765	0	24	0.00	0.00	0.00
4	1	0	27.4	0.74	0	27.4	0.05	0.00	0.00
5	0.95	0.05	29.5	0.74	0.045	29.5	0.00	0.03	0.16
6	1	0	25.5	0.705	0	25.5	0.03	0.00	0.00
7	1	0	26.7	0.705	0.03	26.7	0.00	0.02	0.13
8	1	0	28.1	0.705	0	28.1	0.07	0.00	0.00
9	1	0	25.6	0.705	0.065	25.6	0.04	0.05	0.41
10	1	0	21.9	0.705	0.035	21.9	0.02	0.02	0.21
11	1	0	22.2	0.705	0.015	22.2	0.04	0.01	0.13
12	1	0	25.1	0.705	0.04	25.1	0.08	0.03	0.33
13	0.915	0.085	24.7	0.705	0.075	24.7	0.14	0.05	0.59
14	1	0	20.6	0.65	0.15	20.6	0.09	0.10	1.33
15	0.965	0.035	23.2	0.65	0.085	23.2	0.06	0.06	0.89
16	0.96	0.04	24.3	0.625	0.065	24.3	0.07	0.04	0.67
17	1	0	23.1	0.595	0.07	23.1	0.04	0.04	0.74
18	0.835	0.165	22.1	0.595	0.035	22.1	0.00	0.02	0.41
19	0.925	0.075	25.9	0.485	0	25.9	0.01	0.00	0.00
20	0.97	0.03	25.3	0.455	0.015	25.3	0.01	0.01	0.16
21	1	0	24.2	0.44	0.015	24.2	0.05	0.01	0.15
22	0.97	0.03	23.1	0.44	0.05	23.1	0.00	0.02	0.47
23	0.955	0.045	21.3	0.425	0	21.3	0.05	0.00	0.00
24	0.965	0.035	20.4	0.405	0.055	20.4	0.03	0.02	0.53
25	0.99	0.01	14.5	0.39	0.03	14.5	0.00	0.01	0.29
26	1	0	12	0.385	0	12	0.04	0.00	0.00
27	0.835	0.165	9.6	0.385	0.035	9.6	0.00	0.01	0.36
28	1	0	8	0.32	0	8	0.25	0.00	0.00
29	1	0	3.8	0.32	0.25	3.8	0.00	0.07	1.89
30	1	0	4	0.32	0	4	0.00	0.00	0.00
31	1	0	4	0.32	0	4	0.25	0.00	0.00
32	0.765	0.235	3	0.32	0.25	3	0.00	0.07	2.08
33	0.51	0.49	3	0.26	0	3	0.00	0.00	0.00
34	0	1	0	0.19	0	0	0.00	0.00	0.00
35	0	1	0	0	0	0	0.00	0.00	0.00
36	0	1	0	0	0	0	0.00	0.00	0.00

Appendix 2: Life table – *Diceros bicornis michaeli* (*ex situ*)

Males

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	l_xm_x	$x(l_xm_x)$
0	0.87	0.13	49.3	1	0	49.3	0.00	0.00	0.00
1	0.98	0.02	53.5	0.87	0	53.5	0.00	0.00	0.00
2	1	0	49.3	0.85	0	49.3	0.00	0.00	0.00
3	1	0	44.9	0.85	0	44.9	0.00	0.00	0.00
4	1	0	45.6	0.85	0	45.6	0.00	0.00	0.00
5	1	0	42.2	0.85	0	42.2	0.02	0.00	0.00
6	0.95	0.05	41.7	0.85	0.02	41.7	0.03	0.02	0.10
7	0.98	0.03	39.5	0.81	0.03	39.5	0.05	0.02	0.17
8	0.97	0.03	36.8	0.79	0.05	36.8	0.04	0.04	0.32
9	1	0	34.9	0.77	0.04	34.9	0.10	0.03	0.28
10	1	0	36.9	0.77	0.1	36.9	0.10	0.08	0.77
11	1	0	36	0.77	0.1	36	0.06	0.08	0.85
12	0.97	0.03	35.3	0.77	0.06	35.3	0.10	0.05	0.55
13	0.97	0.03	34.7	0.75	0.1	34.7	0.12	0.08	0.98
14	0.97	0.03	34	0.73	0.12	34	0.06	0.09	1.23
15	0.97	0.03	32	0.7	0.06	32	0.12	0.04	0.63
16	0.93	0.07	29.2	0.68	0.12	29.2	0.07	0.08	1.31
17	0.97	0.03	29.5	0.64	0.07	29.5	0.16	0.04	0.76
18	1	0	29.1	0.62	0.17	29.1	0.06	0.11	1.90
19	1	0	27.4	0.62	0.06	27.4	0.24	0.04	0.71
20	1	0	23.4	0.62	0.24	23.4	0.11	0.15	2.98
21	1	0	23.8	0.62	0.11	23.8	0.08	0.07	1.43
22	1	0	23.4	0.62	0.08	23.4	0.16	0.05	1.09
23	0.93	0.07	22.3	0.62	0.16	22.3	0.07	0.10	2.28
24	0.98	0.02	19.2	0.58	0.08	19.2	0.25	0.05	1.11
25	0.94	0.06	16.5	0.56	0.26	16.5	0.09	0.15	3.64
26	0.93	0.07	15.3	0.53	0.1	15.3	0.23	0.05	1.38
27	0.94	0.06	10.4	0.49	0.25	10.4	0.19	0.12	3.31
28	1	0	7.3	0.46	0.2	7.3	0.07	0.09	2.58
29	1	0	7.1	0.46	0.07	7.1	0.00	0.03	0.93
30	1	0	8.2	0.46	0	8.2	0.00	0.00	0.00
31	0.86	0.14	7	0.46	0	7	0.09	0.00	0.00
32	0.71	0.29	6.1	0.4	0.1	6.1	0.09	0.04	1.28
33	1	0	4.4	0.28	0.13	4.4	0.00	0.04	1.20
34	1	0	3.3	0.28	0	3.3	0.00	0.00	0.00
35	0.67	0.33	2.4	0.28	0	2.4	0.00	0.00	0.00
36	1	0	2	0.19	0	2	0.00	0.00	0.00
37	1	0	2	0.19	0	2	0.00	0.00	0.00
38	1	0	2	0.19	0	2	0.00	0.00	0.00
39	1	0	2	0.19	0	2	0.00	0.00	0.00
40	0.78	0.22	2	0.19	0	2	0.00	0.00	0.00
41	0.64	0.36	1.5	0.15	0	1.5	0.00	0.00	0.00
42	1	0	1	0.09	0	1	0.00	0.00	0.00
43	1	0	1	0.09	0	1	0.00	0.00	0.00
44	1	0	1	0.09	0	1	0.00	0.00	0.00
45	1	0	1	0.09	0	1	0.00	0.00	0.00
46	1	0	1	0.09	0	1	0.00	0.00	0.00
47	1	0	1	0.09	0	1	0.00	0.00	0.00
48	1	0	0.5	0.09	0	0.5	0.00	0.00	0.00
49	0	1	0	0.09	0	0	0.00	0.00	0.00

Females

Age	p_x	q_x	*Risk* q_x	l_x	m_x	*Risk* m_x	F_x	l_xm_x	$x(l_xm_x)$
0	0.88	0.12	62.30	1.00	0.00	62.30	0.00	0.00	0.00
1	1.00	0.00	60.90	0.88	0.00	60.90	0.00	0.00	0.00
2	0.98	0.02	60.60	0.88	0.00	60.60	0.00	0.00	0.00
3	1.00	0.00	65.10	0.86	0.00	65.10	0.00	0.00	0.00
4	0.98	0.02	61.70	0.86	0.00	61.70	0.02	0.00	0.00
5	1.00	0.00	57.10	0.85	0.02	57.10	0.05	0.02	0.09
6	1.00	0.00	55.30	0.85	0.05	55.30	0.06	0.04	0.26
7	0.98	0.02	52.00	0.85	0.06	52.00	0.09	0.05	0.36
8	1.00	0.00	52.20	0.83	0.09	52.20	0.06	0.07	0.60
9	0.96	0.04	52.10	0.83	0.06	52.10	0.10	0.05	0.45
10	1.00	0.00	49.30	0.80	0.10	49.30	0.08	0.08	0.80
11	1.00	0.00	48.20	0.80	0.08	48.20	0.06	0.06	0.70
12	0.96	0.04	47.90	0.80	0.06	47.90	0.11	0.05	0.58
13	0.98	0.02	41.90	0.77	0.11	41.90	0.12	0.08	1.10
14	0.97	0.03	38.90	0.75	0.12	38.90	0.07	0.09	1.26
15	0.97	0.03	36.40	0.73	0.07	36.40	0.09	0.05	0.77
16	0.97	0.03	35.40	0.71	0.09	35.40	0.12	0.06	1.02
17	0.94	0.06	32.50	0.69	0.12	32.50	0.11	0.08	1.41
18	1.00	0.00	29.60	0.65	0.12	29.60	0.08	0.08	1.40
19	0.96	0.04	27.30	0.65	0.08	27.30	0.04	0.05	0.99
20	1.00	0.00	23.90	0.62	0.04	23.90	0.12	0.02	0.50
21	1.00	0.00	20.80	0.62	0.12	20.80	0.00	0.07	1.56
22	1.00	0.00	17.70	0.62	0.00	17.70	0.00	0.00	0.00
23	0.93	0.07	14.70	0.62	0.00	14.70	0.04	0.00	0.00
24	0.92	0.08	12.40	0.58	0.04	12.40	0.06	0.02	0.56
25	1.00	0.00	9.70	0.54	0.06	9.70	0.00	0.03	0.81
26	1.00	0.00	8.20	0.54	0.00	8.20	0.06	0.00	0.00
27	0.88	0.13	7.70	0.54	0.06	7.70	0.00	0.03	0.87
28	1.00	0.00	8.60	0.47	0.00	8.60	0.10	0.00	0.00
29	1.00	0.00	10.80	0.47	0.10	10.80	0.09	0.05	1.36
30	0.90	0.10	10.10	0.47	0.09	10.10	0.04	0.04	1.27
31	0.92	0.08	11.70	0.42	0.04	11.70	0.11	0.02	0.52
32	0.86	0.14	13.10	0.39	0.12	13.10	0.07	0.05	1.50
33	1.00	0.00	13.00	0.33	0.08	13.00	0.00	0.03	0.87
34	0.93	0.07	13.00	0.33	0.00	13.00	0.04	0.00	0.00
35	1.00	0.00	12.00	0.31	0.04	12.00	0.05	0.01	0.43
36	0.92	0.08	11.30	0.31	0.05	11.30	0.00	0.02	0.56
37	1.00	0.00	11.00	0.28	0.00	11.00	0.00	0.00	0.00
38	1.00	0.00	9.80	0.28	0.00	9.80	0.00	0.00	0.00
39	0.72	0.28	4.80	0.28	0.00	4.80	0.00	0.00	0.00
40	0.83	0.17	3.10	0.20	0.00	3.10	0.00	0.00	0.00
41	1.00	0.00	2.00	0.17	0.00	2.00	0.00	0.00	0.00
42	1.00	0.00	2.00	0.17	0.00	2.00	0.00	0.00	0.00
43	1.00	0.00	2.00	0.17	0.00	2.00	0.00	0.00	0.00
44	1.00	0.00	2.00	0.17	0.00	2.00	0.00	0.00	0.00
45	1.00	0.00	2.00	0.17	0.00	2.00	0.00	0.00	0.00
46	1.00	0.00	2.00	0.17	0.00	2.00	0.00	0.00	0.00
47	1.00	0.00	2.00	0.17	0.00	2.00	0.00	0.00	0.00
48	0.00	1.00	1.10	0.17	0.00	1.10	0.00	0.00	0.00
49	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Total

Age	p_x	q_x	Risk qx	l_x	m_x	Risk mx	F_x	l_xm_x	$x(l_xm_x)$
0	0.875	0.125	111.6	1	0	111.6	0.00	0.00	0.00
1	0.99	0.01	114.4	0.875	0	114.4	0.00	0.00	0.00
2	0.99	0.01	109.9	0.865	0	109.9	0.00	0.00	0.00
3	1	0	110	0.855	0	110	0.00	0.00	0.00
4	0.99	0.01	107.3	0.855	0	107.3	0.01	0.00	0.00
5	1	0	99.3	0.85	0.01	99.3	0.04	0.01	0.04
6	0.975	0.025	97	0.85	0.035	97	0.04	0.03	0.18
7	0.98	0.025	91.5	0.83	0.045	91.5	0.07	0.04	0.26
8	0.985	0.015	89	0.81	0.07	89	0.05	0.06	0.46
9	0.98	0.02	87	0.8	0.05	87	0.10	0.04	0.36
10	1	0	86.2	0.785	0.1	86.2	0.09	0.08	0.79
11	1	0	84.2	0.785	0.09	84.2	0.06	0.07	0.78
12	0.965	0.035	83.2	0.785	0.06	83.2	0.10	0.05	0.57
13	0.975	0.025	76.6	0.76	0.105	76.6	0.12	0.08	1.04
14	0.97	0.03	72.9	0.74	0.12	72.9	0.06	0.09	1.24
15	0.97	0.03	68.4	0.715	0.065	68.4	0.10	0.05	0.70
16	0.95	0.05	64.6	0.695	0.105	64.6	0.09	0.07	1.16
17	0.955	0.045	62	0.665	0.095	62	0.14	0.06	1.08
18	1	0	58.7	0.635	0.145	58.7	0.07	0.09	1.65
19	0.98	0.02	54.7	0.635	0.07	54.7	0.14	0.04	0.85
20	1	0	47.3	0.62	0.14	47.3	0.12	0.09	1.74
21	1	0	44.6	0.62	0.115	44.6	0.04	0.07	1.50
22	1	0	41.1	0.62	0.04	41.1	0.08	0.02	0.55
23	0.93	0.07	37	0.62	0.08	37	0.06	0.05	1.14
24	0.95	0.05	31.6	0.58	0.06	31.6	0.16	0.03	0.84
25	0.97	0.03	26.2	0.55	0.16	26.2	0.05	0.09	2.23
26	0.965	0.035	23.5	0.535	0.05	23.5	0.15	0.03	0.69
27	0.91	0.095	18.1	0.515	0.155	18.1	0.09	0.08	2.09
28	1	0	15.9	0.465	0.1	15.9	0.09	0.05	1.29
29	1	0	17.9	0.465	0.085	17.9	0.05	0.04	1.15
30	0.95	0.05	18.3	0.465	0.045	18.3	0.02	0.02	0.63
31	0.89	0.11	18.7	0.44	0.02	18.7	0.10	0.01	0.26
32	0.785	0.215	19.2	0.395	0.11	19.2	0.08	0.04	1.39
33	1	0	17.4	0.305	0.105	17.4	0.00	0.03	1.04
34	0.965	0.035	16.3	0.305	0	16.3	0.02	0.00	0.00
35	0.835	0.165	14.4	0.295	0.02	14.4	0.03	0.01	0.22
36	0.96	0.04	13.3	0.25	0.025	13.3	0.00	0.01	0.28
37	1	0	13	0.235	0	13	0.00	0.00	0.00
38	1	0	11.8	0.235	0	11.8	0.00	0.00	0.00
39	0.86	0.14	6.8	0.235	0	6.8	0.00	0.00	0.00
40	0.805	0.195	5.1	0.195	0	5.1	0.00	0.00	0.00
41	0.82	0.18	3.5	0.16	0	3.5	0.00	0.00	0.00
42	1	0	3	0.13	0	3	0.00	0.00	0.00
43	1	0	3	0.13	0	3	0.00	0.00	0.00
44	1	0	3	0.13	0	3	0.00	0.00	0.00
45	1	0	3	0.13	0	3	0.00	0.00	0.00
46	1	0	3	0.13	0	3	0.00	0.00	0.00
47	1	0	3	0.13	0	3	0.00	0.00	0.00
48	0.5	0.5	1.6	0.13	0	1.6	0.00	0.00	0.00
49	0	1	0	0.045	0	0	0.00	0.00	0.00

Appendix 3: Life table – *Ceratotherium simum simum* (*ex situ*)

Males

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	l_xm_x	$x(l_xm_x)$
0	0.83	0.17	97.5	1	0	97.5	0.00	0.00	0.00
1	0.98	0.02	96	0.83	0	96	0.00	0.00	0.00
2	0.97	0.03	90.7	0.82	0	90.7	0.00	0.00	0.00
3	0.94	0.06	86.7	0.79	0	86.7	0.00	0.00	0.00
4	0.99	0.01	86.9	0.75	0	86.9	0.00	0.00	0.00
5	0.99	0.01	85.2	0.74	0	85.2	0.00	0.00	0.00
6	0.99	0.01	81.6	0.73	0	81.6	0.02	0.00	0.00
7	0.99	0.01	80.4	0.72	0.02	80.4	0.00	0.01	0.10
8	0.99	0.01	78.1	0.71	0	78.1	0.04	0.00	0.00
9	1	0	79.8	0.7	0.04	79.8	0.03	0.03	0.25
10	1	0	84.8	0.7	0.03	84.8	0.06	0.02	0.21
11	0.99	0.01	83.7	0.7	0.06	83.7	0.06	0.04	0.46
12	0.99	0.01	83.8	0.69	0.06	83.8	0.08	0.04	0.50
13	1	0	82.9	0.69	0.08	82.9	0.05	0.06	0.72
14	0.98	0.02	79.4	0.69	0.05	79.4	0.10	0.03	0.48
15	0.99	0.01	75	0.67	0.1	75	0.09	0.07	1.01
16	1	0	72.7	0.66	0.09	72.7	0.09	0.06	0.95
17	0.97	0.03	68.3	0.66	0.09	68.3	0.08	0.06	1.01
18	1	0	62.9	0.64	0.08	62.9	0.07	0.05	0.92
19	0.98	0.02	59	0.64	0.07	59	0.10	0.04	0.85
20	1	0	52.8	0.63	0.1	52.8	0.06	0.06	1.26
21	1	0	54.7	0.63	0.06	54.7	0.08	0.04	0.79
22	1	0	53.6	0.63	0.08	53.6	0.06	0.05	1.11
23	1	0	51.3	0.63	0.06	51.3	0.02	0.04	0.87
24	0.96	0.04	49.6	0.63	0.02	49.6	0.07	0.01	0.30
25	0.96	0.04	45.5	0.6	0.07	45.5	0.02	0.04	1.05
26	0.96	0.04	44.1	0.58	0.02	44.1	0.01	0.01	0.30
27	0.98	0.02	41	0.55	0.01	41	0.01	0.01	0.15
28	0.95	0.05	42.7	0.54	0.01	42.7	0.01	0.01	0.15
29	0.96	0.04	43.4	0.51	0.01	43.4	0.02	0.01	0.15
30	1	0	52	0.49	0.02	52	0.05	0.01	0.29
31	0.97	0.03	64.9	0.49	0.05	64.9	0.05	0.02	0.76
32	0.97	0.03	73.4	0.47	0.05	73.4	0.05	0.02	0.75
33	0.95	0.05	83.1	0.46	0.05	83.1	0.03	0.02	0.76
34	0.98	0.02	81.2	0.44	0.03	81.2	0.00	0.01	0.45
35	0.95	0.05	74.1	0.43	0	74.1	0.01	0.00	0.00
36	0.93	0.07	65.6	0.41	0.01	65.6	0.02	0.00	0.15
37	0.95	0.05	62.5	0.38	0.02	62.5	0.01	0.01	0.28
38	0.93	0.07	59.6	0.36	0.01	59.6	0.01	0.00	0.14
39	0.94	0.06	53.8	0.34	0.01	53.8	0.03	0.00	0.13
40	0.78	0.22	36.3	0.32	0.03	36.3	0.00	0.01	0.38
41	0.79	0.21	19.1	0.25	0	19.1	0.00	0.00	0.00
42	0.89	0.11	9.8	0.2	0	9.8	0.00	0.00	0.00
43	0.78	0.22	8.4	0.17	0	8.4	0.00	0.00	0.00
44	0.77	0.23	6.3	0.14	0	6.3	0.00	0.00	0.00
45	0.48	0.52	1.9	0.11	0	1.9	0.00	0.00	0.00
46	0	1	0	0.05	0	0	0.00	0.00	0.00
47	0	1	0	0	0	0	0.00	0.00	0.00

Females

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	l_xm_x	$x(l_xm_x)$
0	0.85	0.15	94.2	1	0	94.2	0.00	0.00	0.00
1	0.98	0.02	100	0.85	0	100	0.00	0.00	0.00
2	0.98	0.02	101.9	0.84	0	101.9	0.00	0.00	0.00
3	0.99	0.01	109.2	0.82	0	109.2	0.01	0.00	0.00
4	0.99	0.01	114.5	0.81	0.01	114.5	0.03	0.01	0.03
5	0.99	0.01	118.4	0.81	0.03	118.4	0.05	0.02	0.12
6	0.99	0.01	118.1	0.8	0.05	118.1	0.06	0.04	0.24
7	0.99	0.01	118.4	0.79	0.06	118.4	0.05	0.05	0.33
8	0.98	0.02	117	0.79	0.05	117	0.08	0.04	0.32
9	0.99	0.01	118.8	0.77	0.08	118.8	0.04	0.06	0.55
10	1	0	114.3	0.77	0.04	114.3	0.08	0.03	0.31
11	0.98	0.02	107	0.77	0.08	107	0.01	0.06	0.68
12	1	0	100.7	0.75	0.01	100.7	0.07	0.01	0.09
13	1	0	97.4	0.75	0.07	97.4	0.05	0.05	0.68
14	0.99	0.01	88.8	0.75	0.05	88.8	0.03	0.04	0.53
15	1	0	83.4	0.74	0.03	83.4	0.04	0.02	0.33
16	1	0	75.1	0.74	0.04	75.1	0.04	0.03	0.47
17	0.97	0.03	72.3	0.74	0.04	72.3	0.03	0.03	0.50
18	0.98	0.02	65.5	0.72	0.03	65.5	0.03	0.02	0.39
19	1	0	57.6	0.71	0.03	57.6	0.03	0.02	0.40
20	0.98	0.02	59	0.71	0.03	59	0.03	0.02	0.43
21	0.98	0.02	62.9	0.7	0.03	62.9	0.02	0.02	0.44
22	0.98	0.02	65.1	0.69	0.02	65.1	0.04	0.01	0.30
23	1	0	60	0.68	0.04	60	0.01	0.03	0.63
24	0.96	0.04	54.1	0.68	0.01	54.1	0.03	0.01	0.16
25	1	0	49.4	0.65	0.03	49.4	0.03	0.02	0.49
26	1	0	51.2	0.65	0.03	51.2	0.02	0.02	0.51
27	1	0	47.2	0.65	0.02	47.2	0.02	0.01	0.35
28	0.96	0.04	45.9	0.65	0.02	45.9	0.02	0.01	0.36
29	1	0	51.9	0.63	0.02	51.9	0.03	0.01	0.37
30	0.95	0.05	62.5	0.63	0.03	62.5	0.03	0.02	0.57
31	0.95	0.05	80.8	0.6	0.03	80.8	0.01	0.02	0.56
32	0.95	0.05	96.1	0.57	0.01	96.1	0.03	0.01	0.18
33	1	0	108.4	0.54	0.03	108.4	0.01	0.02	0.53
34	0.95	0.05	111	0.54	0.01	111	0.00	0.01	0.18
35	0.99	0.01	110.9	0.51	0	110.9	0.02	0.00	0.00
36	0.99	0.01	106.7	0.51	0.02	106.7	0.00	0.01	0.37
37	0.95	0.05	104.6	0.5	0	104.6	0.00	0.00	0.00
38	0.92	0.08	98.3	0.47	0	98.3	0.00	0.00	0.00
39	0.89	0.11	76.7	0.43	0	76.7	0.00	0.00	0.00
40	0.96	0.04	56	0.39	0	56	0.00	0.00	0.00
41	0.83	0.17	32.1	0.37	0	32.1	0.00	0.00	0.00
42	0.9	0.1	19.1	0.31	0	19.1	0.00	0.00	0.00
43	0.82	0.18	6.9	0.28	0	6.9	0.00	0.00	0.00
44	0.97	0.03	3.8	0.23	0	3.8	0.00	0.00	0.00
45	0.38	0.62	1.8	0.22	0	1.8	0.00	0.00	0.00
46	0.87	0.13	0	0.08	0	0	0.00	0.00	0.00
47	0	1	0	0.07	0	0	0.00	0.00	0.00

Total

Age	p_x	q_x	*Risk* q_x	l_x	m_x	*Risk* m_x	F_x	l_xm_x	$x(l_xm_x)$
0	0.84	0.16	191.7	1	0	191.7	0.00	0.00	0.00
1	0.98	0.02	196	0.84	0	196	0.00	0.00	0.00
2	0.975	0.025	192.6	0.83	0	192.6	0.00	0.00	0.00
3	0.965	0.035	195.9	0.805	0	195.9	0.00	0.00	0.00
4	0.99	0.01	201.4	0.78	0.005	201.4	0.01	0.00	0.02
5	0.99	0.01	203.6	0.775	0.015	203.6	0.02	0.01	0.06
6	0.99	0.01	199.7	0.765	0.025	199.7	0.04	0.02	0.12
7	0.99	0.01	198.8	0.755	0.04	198.8	0.02	0.03	0.22
8	0.985	0.015	195.1	0.75	0.025	195.1	0.06	0.02	0.16
9	0.995	0.005	198.6	0.735	0.06	198.6	0.03	0.04	0.40
10	1	0	199.1	0.735	0.035	199.1	0.07	0.03	0.26
11	0.985	0.015	190.7	0.735	0.07	190.7	0.03	0.05	0.57
12	0.995	0.005	184.5	0.72	0.035	184.5	0.07	0.02	0.29
13	1	0	180.3	0.72	0.075	180.3	0.05	0.05	0.70
14	0.985	0.015	168.2	0.72	0.05	168.2	0.06	0.04	0.50
15	0.995	0.005	158.4	0.705	0.065	158.4	0.06	0.04	0.67
16	1	0	147.8	0.7	0.065	147.8	0.07	0.04	0.71
17	0.97	0.03	140.6	0.7	0.065	140.6	0.05	0.04	0.76
18	0.99	0.01	128.4	0.68	0.055	128.4	0.05	0.04	0.66
19	0.99	0.01	116.6	0.675	0.05	116.6	0.06	0.03	0.63
20	0.99	0.01	111.8	0.67	0.065	111.8	0.04	0.04	0.84
21	0.99	0.01	117.6	0.665	0.045	117.6	0.05	0.03	0.62
22	0.99	0.01	118.7	0.66	0.05	118.7	0.05	0.03	0.71
23	1	0	111.3	0.655	0.05	111.3	0.02	0.03	0.75
24	0.96	0.04	103.7	0.655	0.015	103.7	0.05	0.01	0.23
25	0.98	0.02	94.9	0.625	0.05	94.9	0.02	0.03	0.77
26	0.98	0.02	95.3	0.615	0.025	95.3	0.01	0.02	0.40
27	0.99	0.01	88.2	0.6	0.015	88.2	0.01	0.01	0.25
28	0.955	0.045	88.6	0.595	0.015	88.6	0.01	0.01	0.26
29	0.98	0.02	95.3	0.57	0.015	95.3	0.02	0.01	0.26
30	0.975	0.025	114.5	0.56	0.025	114.5	0.04	0.01	0.43
31	0.96	0.04	145.7	0.545	0.04	145.7	0.03	0.02	0.66
32	0.96	0.04	169.5	0.52	0.03	169.5	0.04	0.01	0.47
33	0.975	0.025	191.5	0.5	0.04	191.5	0.02	0.02	0.65
34	0.965	0.035	192.2	0.49	0.02	192.2	0.00	0.01	0.32
35	0.97	0.03	185	0.47	0	185	0.01	0.00	0.00
36	0.96	0.04	172.3	0.46	0.015	172.3	0.01	0.01	0.26
37	0.95	0.05	167.1	0.44	0.01	167.1	0.00	0.00	0.14
38	0.925	0.075	157.9	0.415	0.005	157.9	0.00	0.00	0.07
39	0.915	0.085	130.5	0.385	0.005	130.5	0.01	0.00	0.07
40	0.87	0.13	92.3	0.355	0.015	92.3	0.00	0.00	0.19
41	0.81	0.19	51.2	0.31	0	51.2	0.00	0.00	0.00
42	0.895	0.105	28.9	0.255	0	28.9	0.00	0.00	0.00
43	0.8	0.2	15.3	0.225	0	15.3	0.00	0.00	0.00
44	0.87	0.13	10.1	0.185	0	10.1	0.00	0.00	0.00
45	0.43	0.57	3.7	0.165	0	3.7	0.00	0.00	0.00
46	0.435	0.565	0	0.065	0	0	0.00	0.00	0.00
47	0	1	0	0.035	0	0	0.00	0.00	0.00

Appendix 4: Female life table – *Diceros bicornis minor* and *Diceros bicornis michaeli* (*in situ*)

Females

Age	p_x	q_x	l_x	m_x	F_x	$l_x m_x$	$x(l_x m_x)$
0	0.09	0.91	1.00	0.00	0.00	0.00	0.00
1	0.16	0.84	0.91	0.00	0.00	0.00	0.00
2	0.16	0.84	0.76	0.00	0.00	0.00	0.00
3	0.06	0.94	0.64	0.00	0.00	0.00	0.00
4	0.06	0.94	0.61	0.00	0.00	0.00	0.00
5	0.06	0.94	0.57	0.00	0.00	0.00	0.00
6	0.04	0.96	0.54	0.24	0.45	0.13	0.77
7	0.04	0.96	0.52	0.23	0.45	0.12	0.84
8	0.04	0.96	0.50	0.23	0.44	0.11	0.91
9	0.04	0.96	0.48	0.22	0.43	0.11	0.96
10	0.04	0.96	0.47	0.22	0.42	0.10	1.01
11	0.04	0.96	0.45	0.21	0.41	0.10	1.05
12	0.04	0.96	0.43	0.21	0.40	0.09	1.08
13	0.04	0.96	0.42	0.20	0.39	0.08	1.10
14	0.04	0.96	0.40	0.20	0.38	0.08	1.12
15	0.04	0.96	0.39	0.19	0.37	0.08	1.14
16	0.04	0.96	0.38	0.19	0.37	0.07	1.15
17	0.04	0.96	0.36	0.19	0.36	0.07	1.15
18	0.04	0.96	0.35	0.18	0.35	0.06	1.16
19	0.04	0.96	0.34	0.18	0.35	0.06	1.15
20	0.04	0.96	0.33	0.18	0.34	0.06	1.15
21	0.04	0.96	0.32	0.17	0.33	0.05	1.14
22	0.04	0.96	0.30	0.17	0.33	0.05	1.14
23	0.04	0.96	0.29	0.17	0.32	0.05	1.13
24	0.04	0.96	0.28	0.16	0.32	0.05	1.11
25	0.04	0.96	0.27	0.16	0.31	0.04	1.10
26	0.04	0.96	0.26	0.16	0.31	0.04	1.09
27	0.04	0.96	0.25	0.16	0.30	0.04	1.07
28	0.04	0.96	0.25	0.15	0.30	0.04	1.05
29	0.04	0.96	0.24	0.15	0.29	0.04	1.04
30	0.04	0.96	0.23	0.15	0.29	0.03	1.02
31	0.04	0.96	0.22	0.15	0.28	0.03	1.00
32	0.04	0.96	0.21	0.14	0.28	0.03	0.98
33	0.04	0.96	0.21	0.14	0.27	0.03	0.96
34	0.04	0.96	0.20	0.14	0.27	0.03	0.94
35	0.04	0.96	0.19	0.14	0.27	0.03	0.92
36	0.04	0.96	0.18	0.14	0.26	0.03	0.90
37	0.04	0.96	0.18	0.13	0.26	0.02	0.88
38	0.04	0.96	0.17	0.13	0.25	0.02	0.86
39	0.04	0.96	0.17	0.13	0.25	0.02	0.84
40	0.04	0.96	0.16	0.13	0.25	0.02	0.82

Appendix 5: Female life table – *Ceratotherium simum simum* (*in situ*)

Females

Age	p_x	qx	l_x	m_x	F_x	$l_x m_x$	$x(l_x m_x)$
0	0.92	0.08	1.00	0.00	0.00	0.00	0.00
1	0.97	0.03	0.92	0.00	0.00	0.00	0.00
2	0.97	0.03	0.88	0.00	0.00	0.00	0.00
3	0.94	0.06	0.85	0.00	0.00	0.00	0.00
4	0.94	0.06	0.80	0.00	0.00	0.00	0.00
5	0.94	0.06	0.75	0.00	0.00	0.00	0.00
6	0.94	0.06	0.71	0.00	0.26	0.00	0.00
7	0.99	0.01	0.67	0.28	0.27	0.19	1.30
8	0.99	0.01	0.66	0.27	0.26	0.18	1.43
9	0.99	0.01	0.65	0.26	0.26	0.17	1.56
10	0.99	0.01	0.65	0.26	0.25	0.17	1.68
11	0.99	0.01	0.64	0.25	0.25	0.16	1.78
12	0.99	0.01	0.63	0.25	0.24	0.16	1.89
13	0.99	0.01	0.63	0.24	0.24	0.15	1.98
14	0.99	0.01	0.62	0.24	0.23	0.15	2.07
15	0.99	0.01	0.62	0.23	0.23	0.14	2.15
16	0.99	0.01	0.61	0.23	0.22	0.14	2.22
17	0.99	0.01	0.60	0.22	0.22	0.13	2.29
18	0.99	0.01	0.60	0.22	0.21	0.13	2.36
19	0.99	0.01	0.59	0.22	0.21	0.13	2.42
20	0.99	0.01	0.59	0.21	0.21	0.12	2.47
21	0.99	0.01	0.58	0.21	0.20	0.12	2.53
22	0.99	0.01	0.57	0.20	0.20	0.12	2.57
23	0.99	0.01	0.57	0.20	0.20	0.11	2.62
24	0.99	0.01	0.56	0.20	0.19	0.11	2.66
25	0.99	0.01	0.56	0.19	0.19	0.11	2.69
26	0.99	0.01	0.55	0.19	0.19	0.10	2.73
27	0.99	0.01	0.55	0.19	0.18	0.10	2.76
28	0.99	0.01	0.54	0.18	0.18	0.10	2.79
29	0.99	0.01	0.53	0.18	0.18	0.10	2.81
30	0.99	0.01	0.53	0.18	0.17	0.09	2.84
31	0.99	0.01	0.52	0.18	0.17	0.09	2.86
32	0.99	0.01	0.52	0.17	0.17	0.09	2.88
33	0.99	0.01	0.51	0.17	0.17	0.09	2.89
34	0.99	0.01	0.51	0.17	0.16	0.09	2.91
35	0.99	0.01	0.50	0.17	0.16	0.08	2.92
36	0.99	0.01	0.50	0.16	0.16	0.08	2.93
37	0.99	0.01	0.49	0.16	0.16	0.08	2.94
38	0.99	0.01	0.49	0.16	0.16	0.08	2.95
39	0.99	0.01	0.48	0.16	0.15	0.08	2.96
40	0.99	0.01	0.48	0.15	0.15	0.07	2.96
41	0.99	0.01	0.47	0.15	0.15	0.07	2.96
42	0.99	0.01	0.47	0.15	0.15	0.07	2.97
43	0.99	0.01	0.46	0.15	0.15	0.07	2.97
44	0.99	0.01	0.46	0.15	0.14	0.07	2.97
45	0.99	0.01	0.46	0.14	0.00	0.07	2.97
46	0.00	1.00	0.00	0.00	0.00	0.00	0.00

CHAPTER 3

A COMPARISON BETWEEN FOUNDER *VERSUS* CAPTIVE-BORN FEMALE LIFE TABLES OF THREE AFRICAN RHINOCEROS SUBSPECIES (*DICEROS BICORNIS MINOR, DICEROS BICORNIS MICHAELI* AND *CERATOTHERIUM SIMUM SIMUM*)

3.1 Abstract

Captive-breeding is an integral part of the conservation of threatened species. In the 1999 Status Survey and Conservation Action Plan for African Rhino, captive populations were identified as potential safety nets should field conservation efforts fail. One major concern affecting global population sustainability of *Ceratotherium simum simum* is the poor reproductive performance of the female F_1 generation. No such comparative study seems to be available for the black rhinoceros subspecies. This study compares fecundity as well as mortality rates of founder *versus* captive-born female African rhinoceros found in the global captive population. Three subspecies are assessed, namely, *Diceros bicornis minor*, *Diceros bicornis michaeli* and *Ceratotherium simum simum*. Results for *D. b. minor* indicate that fecundity as well as longevity are lower for the captive-born females *versus* the founder females, but this is likely an artifact of the captive-born cohorts total time in captivity. No significant difference was found between the survivorship curves of the two sub-populations. For *D. b. michaeli*, captive-born female fecundity is higher than of the founder population, although, as with *D. b. minor*, age at last reproduction and longevity are lower than those of their founder counterparts. Once again, no significant differences were found when comparing the survivorship curves. Lastly for *C. s. simum*, both lower fecundity and higher mortality rates cause the lower growth rate observed in the captive-born female population. A significant difference is detected in the founder *versus* captive-born survival curves, largely caused by higher early mortality rates observed in the captive-bred female white rhinoceros. No significant difference could be found between the inter-birth intervals of the $F_{\geq 1}$ versus the F_0 females for any of the three subspecies.

Keywords: Global captive population, fecundity rates, mortality rates, survival curves, life table analysis.

3.2 Introduction

Captive-breeding is an integral part of the conservation of threatened species. In the 1999 Status Survey and Conservation Action Plan for African Rhino, captive populations were identified as potential safety nets should field conservation efforts fail (Emslie & Brooks 1999). Concerns however, have been raised that neither the European nor North American captive populations of the southern white rhinoceros (*Ceratotherium simum simum*) nor black rhinoceros subspecies (*Diceros bicornis minor* and *Diceros bicornis michaeli*) are self-sustaining (Foose & Wiese 2006; Swaisgood 2006). While captive populations can play many supportive roles that serve conservation purposes, ideally the populations should be self-sustaining without having to rely on the wild population for additional founders.

According to Swaisgood *et al.* (2006), one major concern affecting global population sustainability of *Ceratotherium simum simum* is the poor reproductive performance of the female F_1 generation. At a workshop held in San Diego, USA in 1998, the following four factors limiting the breeding of *C. s. simum* were identified: a) acyclicity and varying cycle lengths, b) mating failure, c) conception failure, and d) pregnancy failure (Schwartzenberger *et al.* 1999). At that time it was noted, from data taken from the 1995 International studbook, that over 50% of captive southern white rhinos were over 20 years of age, and that reproductive success of successive generations was varied, with a rate of 30% for founders, 8% for F_1 generation and 0% for F_2 generation animals, respectively (Schwartzenberger *et al.* 1999). Due to this workshop, a huge surge in rhinoceros reproductive research took place and the results were incorporated into the management decisions for the European population of *C. s. simum*, with a few noted successful breeding occurrences (Schwartzenberger *et al.* 1999).

The analysis of life history traits has been used as an important tool for conservation managers across a variety of animal taxa, such as birds (Dennis *et al*. 1991; Heppel *et al*. 2000; Low & Pärt 2009; Mitchell *et al*. 2009; Ortega *et al*. 2009; Schaub *et al*. 2009; Sim *et al*. 2011), eutherian mammals (Dennis *et al*. 1991; Coulson 2005), marsupials (Lachish *et al*. 2009) and reptiles (Heppel 1998; Enneson & Litzgus 2008). Once the life history data have been collated it is possible to construct life tables and survival curves. The data can be used to construct Leslie matrices, the first Eigen value of which equals λ assuming a stable age distribution, and the corresponding right Eigen vector represents the stable age distribution.

Both survivorship and fertility differ greatly across species, and often also differ between sub-populations of the same species. In the case of *C. s. simum*, differences have been observed in the fecundity between the F_0 and F_1 sub-populations of this subspecies, causing concern (Swaisgood *et al.* 2006).

Given the above background, the research questions this chapter attempts to answer are:

- Based on 2010 figures, are the global captive populations of *D. b. minor*, *D. b. michaeli* and *C. s. simum* currently self-sustaining?; and
- Which demographic factors have the most influence on the population growth rate of the three sub-species?

The aims of the present study are therefore to analyse the life tables of F_0 and $F_{\geq 1}$ generations of female *Diceros bicornis minor*, *Diceros bicornis michaeli* and *C. s. simum*, to establish if any difference are observed between the F_0 and $F_{\geq 1}$ generations, not only in terms of fecundity, but also with survivorship which influences lifetime reproductive success. The following hypotheses are tested and discussed:

- *Null (H_0) hypothesis*: Lifetime reproductive success of $F_{\geq 1}$ generation females is not significantly different to that of the founder population;
- *Alternative (H_A) hypothesis*: Lifetime reproductive success of $F_{\geq 1}$ generation females is significantly different to that of the founder population;
- *Null (H_0) hypothesis*: Aging of the F_0 generation will not significantly affect future growth rates of the global captive population;
- *Alternative (H_A) hypothesis*: Aging of the F_0 generation will significantly affect future growth rates of the global captive population;

3.3 Materials and Methods

Life tables were constructed for both the F_0 and $F_{\geq 1}$ female populations of the three subspecies of rhinoceros (*D. b. minor, D. b. michaeli* and *C. s. simum*) under analysis. Global population data were collected from the International Studbook for Rhinoceros (Ochs 2001; 2005) and the Zoological Information Management System (ZIMS) database and entered into the Single Population Animal Record Keeping System version 1.66 (SPARKS) database programme (ISIS 2004). In SPARKS, life tables were constructed to include estimates of age-specific survivorship (l_x), annual survival (p_x) and mortality rates (q_x), age-specific fertility (m_x), and the sample sizes used to calculate these estimates, as described by Lacy *et al.* (Kaplan & Meier 1958; Lacy *et al.* 2012).

Statistica™ (www.statsoft.com) statistical analysis package was used to compare survival curves of founder and captive-born females. Five different (mostly nonparametric) tests for censored data are available for this comparison: Gehan's generalized Wilcoxon test, the Cox-Mantel test, the Cox's *F* test, the log-rank test, and Peto and Peto's generalized Wilcoxon test (Statsoft Inc 2013). Cox's *F* test tends to be more powerful than Gehan's generalized Wilcoxon test when:

- Sample sizes are small (i.e., *n* per group less than 50);
- Samples are from an exponential or Weibull distribution;
- There are no censored observations (Statsoft Inc 2013).

As the data currently under analyses contains censored data points, Cox's *F* test was therefore omitted. There is also little difference between the Cox-Mantel test and the log-rank test when the samples are drawn from a population that follows an exponential or Weibull distribution, therefore the log-rank test was also omitted (Statsoft Inc 2013). The three statistical tests performed were therefore:

1. Gehan's Wilcoxon Test (Gehan 1965)
2. Cox-Mantel Test (Cox 1959; Mantel 1966; Mantel & Haenszel 1959)
3. Peto & Peto Wilcoxon Test (Peto & Peto 1972)

For all tests a difference between curves was deemed to be significantly different when $P < 0.05$.

To improve accuracy of the statistical analysis, l_x rates in the first age class for $F_{\geq 1}$ were excluded to compensate for lack of early neonate mortality data of founder rhinoceros entered into the studbook. This is due to founders only entering the captive population from age class 1.

F_x and R_o were calculated from the SPARKS estimates of p_x, m_x and l_x (Lacy *et al.* 2012) as follows:

- F_x – number of female offspring produced in the next age class weighted by the probability of the dam reaching that age class after surviving to age *x*. $F_x = p_x m_{x+1}$ (Rockwood 2006); and
- R_o – lifetime reproductive success or average number of same sex offspring produced by an individual per lifetime.

  $R_o = \sum l_x m_x$ (Begon *et al.* 2006; Rockwood 2006).

The data calculated for the life table analysis were transferred into Mathematica 8 in the form of a Leslie matrix, with the realized fecundity (F_x) forming the first row of the Leslie matrix, and the p_x values entered in the sub-diagonal. The Eigen value of the Leslie matrix was calculated to determine λ, the finite population growth rate parameter (Rockwood 2006).

In order to achieve sufficiently large samples in this chapter, all available life history data for the three subspecies were assessed as opposed to the ten-year sample of Chapter 2. Sample size for this analysis are summarised in Table 11 below. Age classes with sample sizes below 30 should be viewed with caution as results may be affected by small sample size (Traylor-Holzer 2011). More detailed on the sample sizes used in the life table analyses can be viewed in Appendixes 6 to 11, where sample sizes are reflected under the risk columns for both q_x and m_x, and risk is defined as the number of animals alive during that age class (Lacy *et al.* 2012). In total, 37, 163 and 457 F_0 female rhinoceros were assessed for *D. b. minor*, *D. b. michaeli* and *C. s. simum* respectively, while $F_{\geq 1}$ sample sizes were 34, 260 and 404.

Table 11: Sample size used for female F_0 *versus* $F_{\geq 1}$ analysis

Subspecies		Age class with sample size > 30	Age class with sample size < 30
D. b. minor	F_0	1 - 7	0; 8 - 34
	$F_{\geq 1}$	0	1 - 22
D. b. michaeli	F_0	0 - 31	32 - 46
	$F_{\geq 1}$	0 - 21	22 - 39
C. s. simum	F_0	0 - 41	42 - 45
	$F_{\geq 1}$	0 - 25	26 - 36

Founder and $F_{\geq 1}$ female reproductive performance of the three subspecies were analysed using studbook data on all births recorded in captivity. First, analyses were conducted on the female data to determine the proportion of the F_0 *versus* $F_{\geq 1}$ population to have bred once they have reached breeding age. While this gives an indication of the breeding success, this calculation may underestimate the breeding potential, as some of the females that have not bred may still do so. Secondly, average number of offspring was calculated for the F_0 *versus* $F_{\geq 1}$ females from all dams that had produced one or more offspring. Lastly, analyses were conducted on the inter-birth intervals observed in wild-born females in comparison to captive-born females to obtain a figure of potential lifetime reproductive rate. In order to calculate the inter-birth intervals, all records of captive births in the global database were assessed where dams gave birth to two or more offspring. Inter-birth intervals were calculated from the dams' age at parturition. These data were further divided into founder dams and captive-born dams. For these data, the mean, median, minimum and maximum figures were calculated, as well as the standard deviation and skewness of the data. Due to the skewness observed in the data, a log transformation was performed to normalise the data before performing a *t*-test to determine if any difference in the inter-birth intervals observed were statistically significant. Differences observed were deemed to be statistically significant where $P < 0.05$.

3.4 Results

Diceros bicornis minor

Fecundity analysis reveals that captive-born females are reported to start breeding earlier than their founder counterparts, with first births reported at age 4 for captive-born dams and around the age of 5 for wild-born dams. While a slightly slower start is noted, founders have been reported to breed for a much longer time period, up until the age of 27. No captive-born females have so far bred over the age of 16 years, although a maximum age of 22 has been recorded for the captive-born females. Studbook analysis reveals that 23 out of 34 (68%) founders of breeding age have produced offspring, whereas only 8 out of 19 (42%) captive-born females of breeding age have produced offspring. Observed average number of offspring is calculated to be 3 offspring per dam in founder females, and 1.7 per dam in captive-born females.

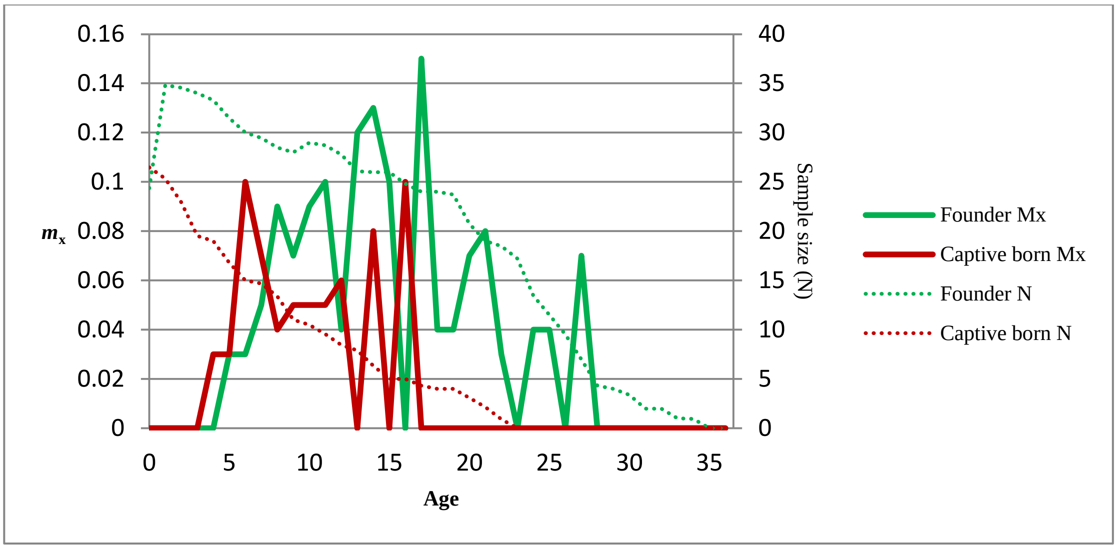

Figure 46: Female fecundity (m_x) - Founder *versus* captive-born *Diceros bicornis minor*

A mean inter-birth interval of 3.5 years for captive-born dams is recorded, compared to 3.3 years for founder females. However, cognizance needs to be taken of the captive-born data being based on a very small sample size as only four captive-born dams were recorded as having given birth two or more times. Numbers for mean, median, maximum and minimum calculations in Table 12 below are recorded in days. *T*-test analysis performed on the inter-birth intervals of founder *versus* captive-born dams shows no significant difference between the two ($t_{(21)} = 0.62$; $n = 23$; $P = 0.55$).

Table 12: Inter-birth interval analysis: Founder *versus* captive-born dams - *Diceros bicornis minor*.

Variable	Valid N	Mean (Days)	Median (Days)	Minimum (Days)	Maximum (Days)	Std. Dev	Skewness
Captive-born	4	1284	1269	1060	1538	199.99	0.41
Founder	19	1203	1197	540	1973	420.24	0.10

The first founder mortality is recorded in age class 1. Zero mortality for founders is to be expected in the first age class, as founders generally only enter the population once they have been weaned from their mothers in the wild. Neonatal mortality in the female captive-born population is 22%, with spikes in mortality seen at age classes 5, 7 and 8. No mortalities have been recorded from the age of 8, but of concern is that captive-born female longevity is only 22 years, compared to founder longevity of 32 years of age. However, this is probably a result of significant numbers of captive births only being recorded from 1990 onwards, therefore the captive born animal have not yet had enough time to reach the longevity recorded for the wild-born females.

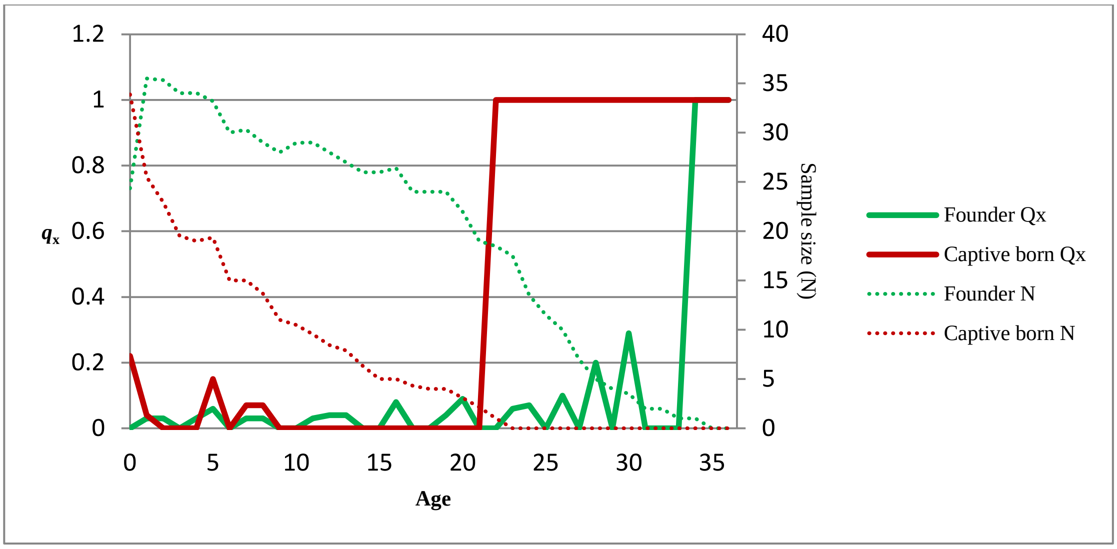

Figure 47: Female mortality (q_x) - Founder *versus* captive-born *Diceros bicornis minor*.

After adjustment for the absence of information about founder neonate mortality, captive-born animals show an initial higher survival rate than the founder population. However, a dip at age 6 brings the captive-born survival rate below that of the founder curve, until the age of 16 where the curves cross once more. The founder curve shows a linear decline until the age of 35, unlike the captive-born curve which plunges to 0 at the age of 23, a result of the longevity differences noted above due to the amount of time to date of the subpopulation in captivity. Assessment of the original survivorship curve indicates that there is a 55% survival rate up until the age of 22 for the captive-born females (Figure 48).

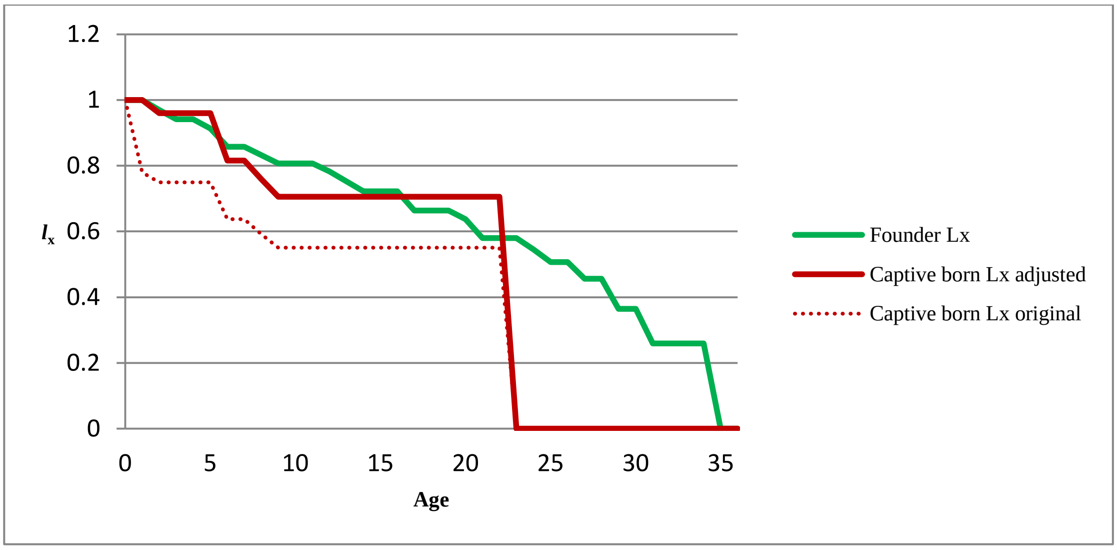

Figure 48: Female Kaplan-Meier survivorship (l_x) - founders *versus* captive-born *Diceros bicornis minor.*

Differences seen in the survivorship curves between the two groups from age class 1 onwards were not found to be statistically different in all three statistical tests performed (Gehan's Wilcoxon, Peto & Peto Wilcoxan and Cox-Mantel; Table 13). These results may be influenced by: a) a small sample size (*n* = 37 wild-born; 25 captive-born), and b) the proportion of censored data between the two sub-populations (wild-born = 41% censored data; captive born = 52% censored data).

Table 13: Survivorship curve statistical analyses: Founder *versus* captive-born female *Diceros bicornis minor.*

	Test statistic	Probability (*P*)
Gehan's Wilcoxon	1.59	0.11
Peto & Peto Wilcoxan	-1.52	0.13
Cox-Mantel	1.55	0.12

Population growth rate (λ) is 0.999 for the founder population, compared to 0.971 for the captive-born population and this is reflected in an R_0 of 0.383 for captive-born females compared to 0.997 of the F_0 generation.

Diceros bicornis michaeli

Founder females are recorded as having given birth from the age of 3 up until 37, while captive-born individuals breed from the age of 5 up until 35 years (Figure 49). Studbook analysis indicates that percentage wise, more captive-born females have bred than their founder counterparts. 87 out of 151 (58%) captive females have produced offspring compared to 73 out of 142 (51%) wild-caught females. While more captive-born females of breeding age have produced offspring than wild-caught females, average number of offspring per dam is much lower, with captive-born dams producing 2.6 offspring on average compared to 3.8 offspring per founder dam.

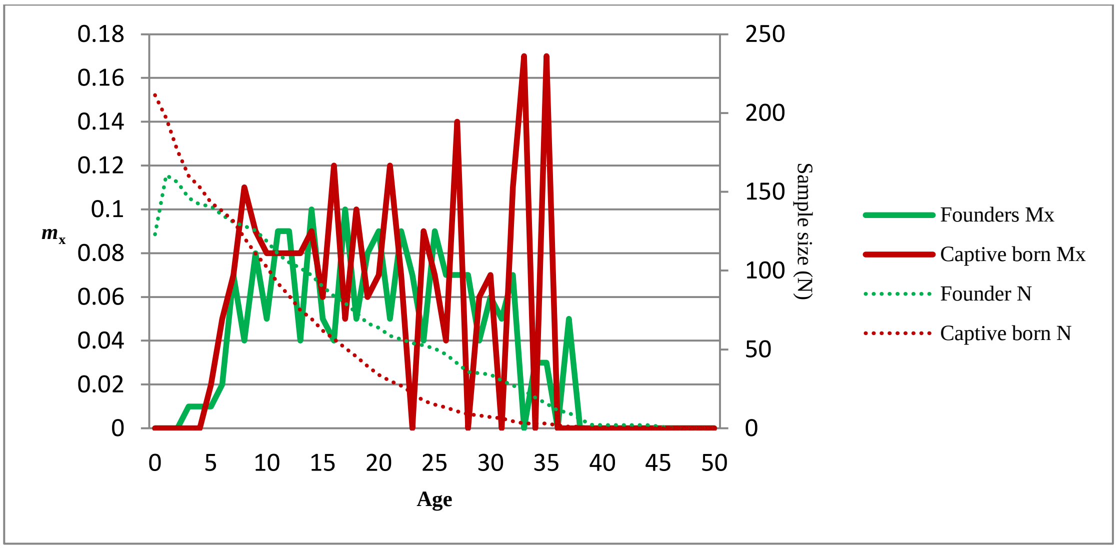

Figure 49: Female fecundity (m_x) - founder *versus* captive-born *Diceros bicornis michaeli.*

Statistical analyses of captive-born *versus* founder inter-birth intervals showed no statistically significant difference between the two ($t_{(112)} = 0.47$; $n = 114$; $P = 0.64$). With very similar sample sizes, mean inter-birth intervals were calculated to be 3.19 and 3.20 years for captive-born and founder dams, respectively. The minimum inter-birth interval for a captive-born dam is below the normal gestation period, only 13.5 months. Minimum inter-birth interval for wild-born dams is more consistent with reported gestation periods, and is 18 months, although this is still less than the normal inter-birth interval. Maximum inter-birth intervals recorded are 7.6 years for captive-born dams, and 8 years for wild-born dams.

Table 14: Inter-birth interval analysis: Founder *versus* captive-born dams - *Diceros bicornis michaeli*.

Variable	Valid N	Mean (Days)	Median (Days)	Minimum (Days)	Maximum (Days)	Std. Dev	Skewness
Captive-born	59	1163	980	413	2763	524.03	1.41
Founder	55	1168	1108	554	2920	420.72	1.58

Neonate mortality for *D. b. michaeli* females is very similar to that of *D. b. minor*, with a mortality rate recorded of 21%. Maximum longevity is recorded at 39 years of age for a captive-born female, while longevity of 45 years is recorded for a wild-born female (Figure 50).

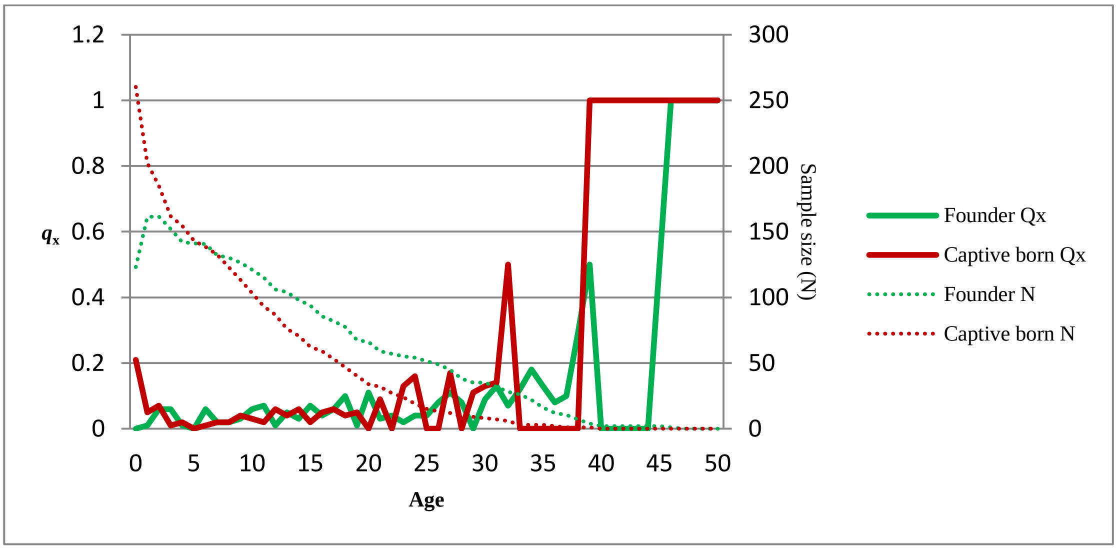

Figure 50: Female mortality (q_x) - founder *versus* captive-born *Diceros bicornis michaeli*

After exclusion of neonate deaths (≤ 1 year), both founder and captive-born female survivorship curves show linear declines very close to each other. A higher degree of survivorship is seen for captive-born females up until around the age of 29, where the curve then dips below that of the founders (Figure 51).

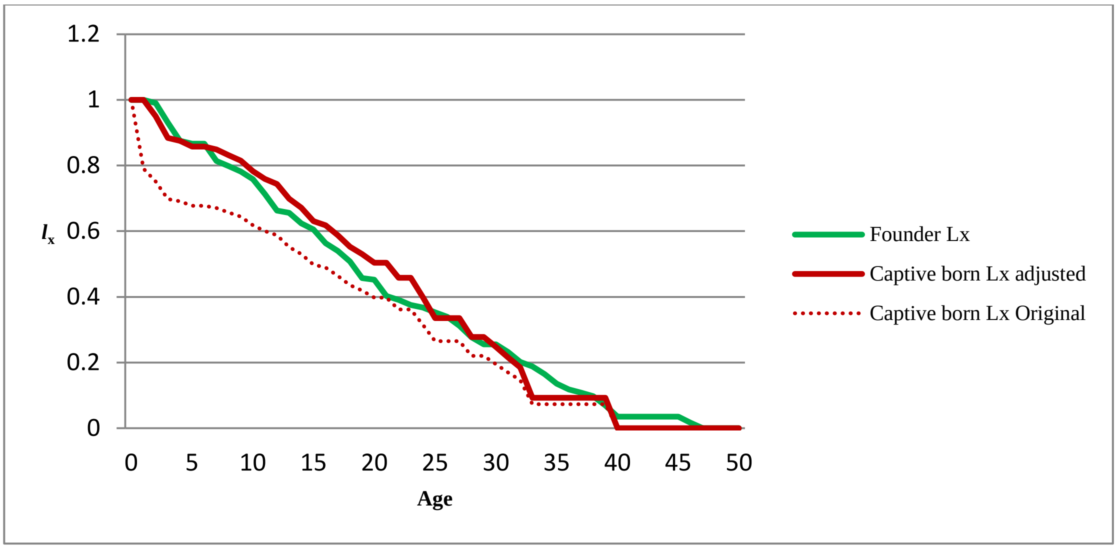

Figure 51: Female Kaplan-Meier survivorship (l_x) - founders *versus* captive-born *Diceros bicornis michaeli.*

Statistical analyses show that there is no significant difference in all three statistical tests between founder and captive-born survivorship (Gehan's Wilcoxon, Peto & Peto Wilcoxan and Cox-Mantel; Table 15). For the analysis, the censored samples make up 8% of the total data samples assessed for the wild-born population, while for the captive-born data, censored samples make up 55% of the data points (wild-born *n* = 163, censored sample *n* = 13, uncensored sample *n* = 150; captive-born sample *n* = 208, censored sample *n* = 115, uncensored sample *n* = 93).

Table 15: Survivorship curve statistical analyses: Founder *versus* captive-born female *Diceros bicornis michaeli.*

	Test statistic	Probability (*P*)
Gehan's Wilcoxon	-0.54	0.59
Peto & Peto Wilcoxan	0.64	0.52
Cox-Mantel	0.69	0.49

Population growth rates calculated from the Leslie matrix for both the captive-born population and the founder population were very similar, with λ rates of 0.995 and 0.994, respectively. R_0 figures are also very similar, with a slightly higher R_0 of 0.89 calculated for the $F_{\geq 1}$ generations compared to 0.88 for the F_0 group.

Ceratotherium simum simum

Proportionally fewer females of white rhinoceros have bred in captivity than either of the black rhinoceros subspecies. 74 out of 232 (32%) captive-born females have produced offspring compared to 162 out of 441 (37%) of the founder population. Animals have been bred down to the F_4 generation. The first female m_x values are recorded at 4 and 5 years for captive-born females and wild-born females, respectively. Oldest dams recorded to have given birth are age 31 for captive-born animals and age 36 for wild-born individuals (Figure 52). Average number of offspring born to breeding dams is 3.9 for founder dams and 2.4 for captive-born dams.

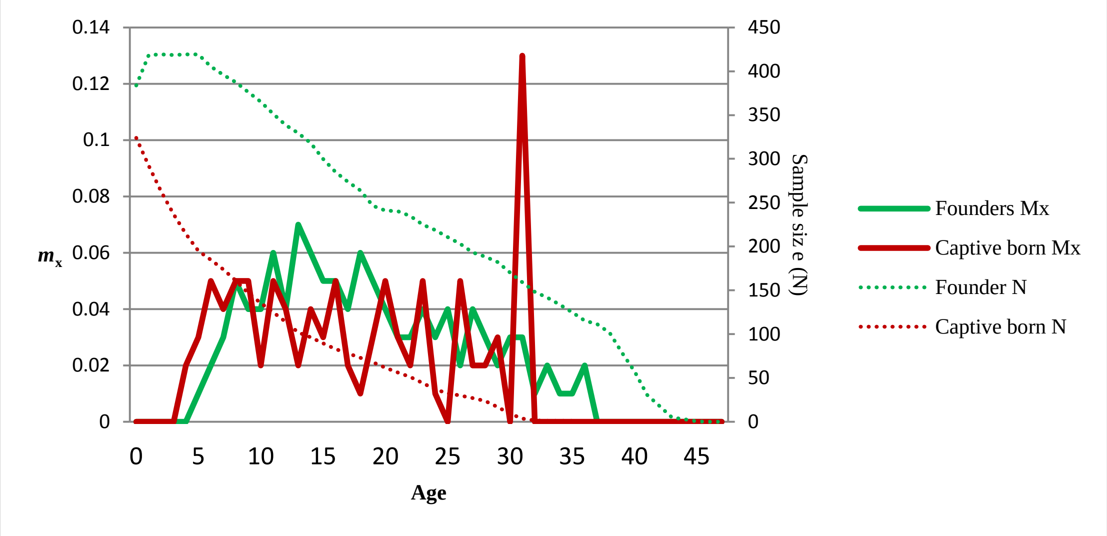

Figure 52: Female fecundity (m_x) - founder *versus* captive-born *Ceratotherium simum simum.*

As with the analyses for the two black rhinoceros subspecies, *t*-test analyses for *C. s. simum* show no significant difference between founder and captive-born dam inter-birth intervals ($t_{(103)} = 0.71$; $n = 105$; $p = 0.48$). Mean inter-birth intervals were 1020 (2.8 years) for captive-born dams, while wild-born dams experienced an inter-birth interval of 954 days (2.6 years). Minimum inter-birth intervals calculated are 17 months for the captive-born dams, and 18 months for wild-born dams, while a maximum of 4.9 years is recorded for captive-born dams, and 5.5 years for offspring born to the founder dams.

Table 16: Inter-birth interval analysis: Founder *versus* captive-born dams - *Ceratotherium simum simum.*

Variable	Valid N	Mean (Days)	Median (Days)	Minimum (Days)	Maximum (Days)	Std. Dev	Skewness
Captive-born	36	1020	942	518	1799	372.88	0.78
Founder	69	954	886	552	2002	286.22	1.42

.

In the captive-born population, after initial neonate mortality, death rates are low throughout the life table except for a very high spike seen at age 31. Longevity is less in the captive-born population, with the oldest recorded female being 37 years old compared to 45 years seen in the founder population. As with the black rhinoceros subspecies in this study, sample size of the captive-born population near longevity is very low, therefore the lower longevity recorded is likely to be a result of the recent origin of the cohort, and not of earlier mortality. This first captive born female is recorded in 1971, making the oldest possible female 39 years of age at the end of the study.

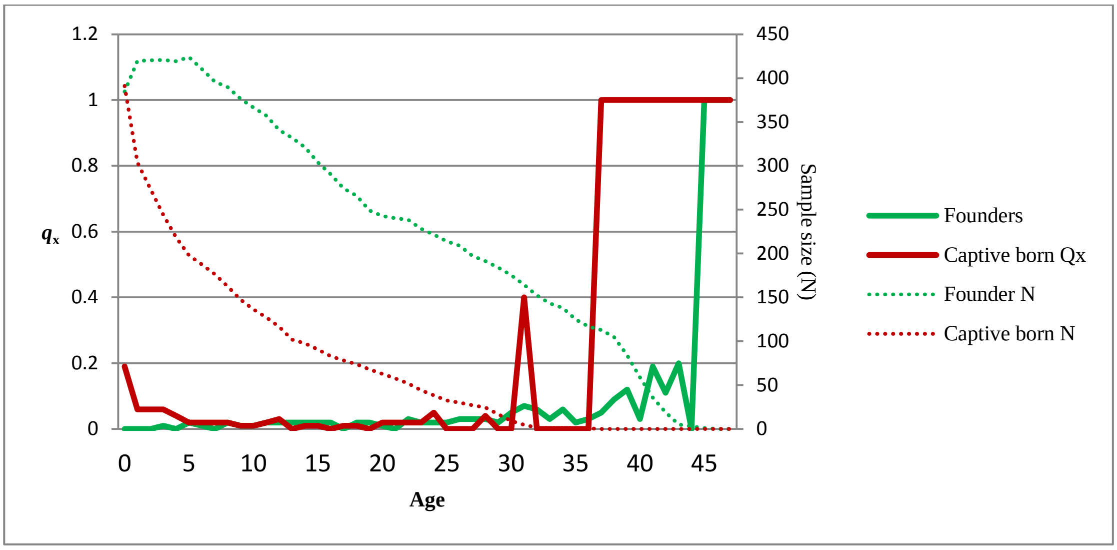

Figure 53: Female mortality (q_x) - founder *versus* captive-born *Ceratotherium simum simum.*

After adjustment of the neonate survival rate, the captive-born survivorship curve is still consistently below that of the founder curve. This is due to low levels of mortality being recorded for the captive-born individuals between the age of one and four years, whereas almost no mortality is recorded for founder animals in these age classes (Figure 54).

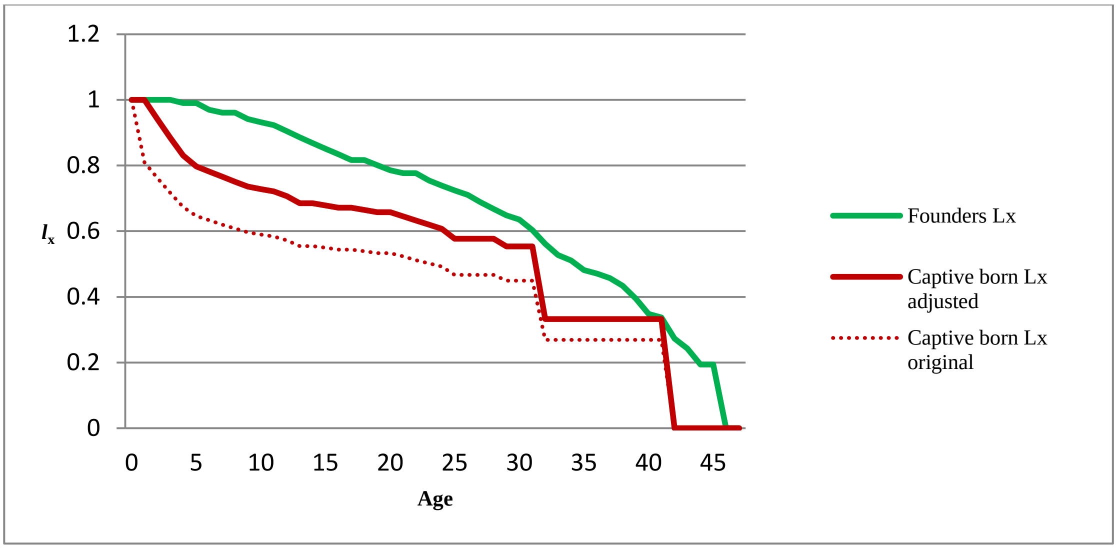

Figure 54: Female Kaplan-Meier survivorship (l_x) - Founder *versus* captive-born *Ceratotherium simum simum.*

Statistical tests show that there is a highly significant difference between the two survivorship curves in all three statistical tests as $P < 0.05$ for all three (Gehan's Wilcoxon, Peto & Peto Wilcoxan and Cox-Mantel; Table 17). This is mostly an effect of comparatively high mortality in the $F_{\geq 1}$ group between ages 1 and 5.

Table 17: Survivorship curve statistical analyses: Founder *versus* captive-born female *Ceratotherium simum simum.*

	Test statistic	Probability (*P*)
Gehan's Wilcoxon	5.56	0.00
Peto & Peto Wilcoxan	-4.76	0.00
Cox-Mantel	4.37	0.00

The captive-born population is not managing to achieve the same growth rate as the founder population, with a life table λ of 0.971 compared to 0.994 calculated for the founder population. R_o for the captive population was calculated to be 0.49 compared to 0.88 of the founder population.

Summary of key demographic life parameters for founder females *versus* captive-born females

Some of the key demographic parameters for the founder *versus* the captive-born females for each subspecies are presented in Table 18. In all three subspecies, age at first reproduction is recorded around the age of four (± one year), with both *D. b. minor* and *C. s. simum* data indicating the possibility of captive-born females giving birth earlier than founder females. When comparisons are made for the age of last reproduction however, of concern is that captive-born *D. b. minor* have a far lower age of last reproduction than their founder counterparts, and so far have not been able to reproduce beyond 16 years of age. Both *D. b. michaeli* and *C. s. simum* captive-born females are far more on par with the founder females, with an age gap of two and five years seen between the two sub-populations, respectively. Captive-born female longevity is also lower in all three subspecies than the founder females, but may be a result of the captive-born females being a far younger population, and this may change once the captive-born females have been given more opportunity to age.

Mean inter-birth interval show very similar values when comparing the founder *versus* captive-born female sub-populations for all three subspecies. *Ceratotherium simum simum* shows the lowest inter-birth intervals, with intervals under three years recorded. Both black rhinoceros subspecies have inter-birth intervals of over three years. The proportion of captive-born adult females to breed in the case of *D. b. minor* is very low compared to the founder females. While *C. s. simum* also shows a comparatively low proportion of captive-born to wild-born females to breed (31.9% *versus* 36.7%), *D. b. michaeli* shows the opposite, with 57.6% of the captive-born females having bred *versus* 51.4% of the wild-born females.

Median survival time is very low in both captive-born and wild-born female populations of *D. b. minor* and *D. b. michaeli* indicating that early mortality may play a higher role in these subspecies than for *C. s. simum*. Both *D. b. minor* and *C. s. simum* show lower median survival times in their captive-born female populations than the founder females, while *D. b. michaeli* has a higher captive-born median survival time.

Overall population growth rates are higher in the founder females, except for *D. b. michaeli*, where the population growth rate for the captive-born population is higher than that of the founder population.

The latter population is therefore no longer reliant on the founder population for its growth. The stability of this population can also be seen in the lifetime reproduction success values, where both founder and captive-born females have similar values. Both *D. b. minor* and *C. s. simum* however, show lifetime reproductive success for their captive-born females far lower than those produced by the founder females. The values calculated here however, are not directly comparable as total time in captivity for the two subpopulations is not equal, with the captive-born female having less time to breed. Generation lengths in all three subspecies are slightly lower in the captive-born females than the founder females, with *D. b. minor* showing the greatest difference between the subpopulations.

Table 18: Summary of demographic parameters for founder females *versus* captive-born females

	D. b. minor		*D. b. michaeli*		*C. s. simum*	
Parameter	F_0	$F_{\geq 1}$	F_0	$F_{\geq 1}$	F_0	$F_{\geq 1}$
Age at 1st reproduction	5	4	3	5	5	4
Highest age of reproduction	32	16	37	35	36	31
Oldest recorded female	34	22	46	39	45	37
Oldest living female	33	21	42	38	44	37
Mean inter-birth interval (years)	3.3	3.52	3.2	3.19	2.61	2.79
Female neonate mortality	N/A	0.22	N/A	0.21	N/A	0.19
Proportion of adult ♀♀ to breed (%)	67.6	42.1	51.4	57.6	36.7	31.9
Median survival time	26	22	18	20	34	31
Age at which $l_x = 0.25$	34	22	30	27	42	41
Age at which $l_x = 0.1$	34	22	37	32	45	41
λ	0.999	0.971	0.994	0.995	0.994	0.971
R_o	0.977	0.383	0.88	0.89	0.88	0.49
T	13.9	9.7	16.3	15.5	17.2	16.2

3.5 Discussion

Diceros bicornis minor

Population growth rate calculated for the $F_{\geq 1}$ generation of female *D. b. minor* is considerably lower than the rate of growth currently seen for the founder female population. Current founder population growth rate appears to be stationary with a calculated life table λ of 0.999, whereas the captive-born population is displaying a negative growth rate of -3% ($\lambda = 0.971$) per annum. A concern needs to be noted here. Due to small sample sizes, the dataset used to calculate life tables for this chapter included the entire studbook dataset. Female λ in Chapter 2, which was calculated using data from the last 10 years in order to reflect current management practices, shows a female population growth rate much lower than that calculated for this chapter. This would indicate a recent decrease in population viability.

Another concern is that female captive-born *D. b. minor* have up until now not survived in captivity beyond the age of 22, this despite captive births having been recorded since 1965. However, this is likely because during the first two decades, numbers of captive births remained very low resulting in a very low sample size. Since 1987 the number of captive births has improved considerably. Survivorship curve analysis indicates no statistically significant difference in the survival rates of the two populations. It is therefore feasible that new longevity records will be set in the next decade or so as individuals born after 1987, age, and therefore that lifetime reproductive success will also increase for the captive-born females.

Currently, 96% of the founders are above the age of 20 and it is this population that has up until now carried the subspecies population in captivity. The data indicate that while mean inter-birth intervals of the founder *versus* captive-born females are approximately the same, the number of captive-born females of breeding age that have produced young and average number of young produced, is far lower than the numbers seen in founder females. It remains to be seen in the next decade if the results observed in the present study are therefore related to the time that the captive population has been present in captivity. If so, longevity for captive-born individuals will increase and, hopefully age at last reproduction along with it. If this happens, lifetime reproductive success, which for the captive-born females is currently very low and not self-sustainable at 0.383, should improve. Current analyses therefore indicates that the captive-born population is not reproducing as well as the founder population may be age-related, but if this does not show signs of improvement over the next few years, this subspecies is unlikely to survive without additional founders being brought into the population. The null (H_0) hypothesis that lifetime reproductive success of the $F_{\geq 1}$ females is not significantly different to that of the founder population is therefore rejected. The second null (H_0) hypothesis, that aging of the F_0 generation will not significantly affect future growth rates of the global captive population, is rejected as it appears that the effect of the aging F_0 population can already be observed, with lower growth rate of the female population over the last ten years compared to previously calculated growth rates.

Diceros bicornis michaeli

Diceros bicornis michaeli is the most stable population out of all of the three rhinoceros subspecies under investigation. Not only have more captive-born females reproduced proportionally to their founder counterparts, but the female population growth rate is higher than that of the founders. Age at last reproduction as well as longevity are however, lower than the wild-caught animals, but like in *D. b. minor*, this may be a result of the $F_{\geq 1}$ generation being a much younger population than the founders, without the opportunity as yet to achieve maximum longevity seen in the founder population. Survivorship curves between the founders and captive-born generations are not significantly different, which supports this assumption.

While the captive-born female generation does appear to be performing relatively better than the founder population, lifetime reproductive rate and female population growth rate both indicate that the population is at risk of declining. However, the ten-year dataset analysed in Chapter 2 indicates a positive change to the female population growth rate. Using the ten-year dataset, a female life table λ of 1.02 is calculated compared to female λ of 0.99 calculated using the entire studbook. This provides further evidence that *D. b. michaeli* captive population is indeed capable of sustaining itself without the need for additional founders. As the 50 and 100 years target population sizes set at the GCAP workshop in 1992 are lower than the current population size, there should be no problem with maintaining the target sizes.

Both null (H_0) hypotheses proposed for this chapter are therefore accepted for the *D. b. michaeli* population. As so few founders still exist in the population, aging of the few that do exist should not have any detrimental effect on the current population growth rate.

Ceratotherium simum simum

Based on 1995 International studbook data, both Schwartzenberger *et al.* (1999) and Swaisgood *et al.* (2006), raised concern that reproductive performance of the F_1 generation of *C. s. simum* was not as good as the F_0 generation thereby affecting global population sustainability. They pointed out that a number of pre-copulatory as well as post-copulatory factors may play a role in the reproductive success of the F_1 generation, and investigated a number of hypotheses in an attempt to explain the F_1 failure. Their results pointed to development in captivity as the root cause of post-copulatory reproductive failure in F_1 females. The present study indicates that the *C. s. simum* captive-born female population is still not achieving the population growth rates achieved by the founder population, with a life table λ of 0.971 for the $F_{\geq 1}$ opposed to 0.994 achieved by the founder females. Female λ from the ten-year dataset is exactly the same as the λ seen in the dataset used for these analyses, so no additional considerations need to be deliberated.

Indications are that the mortality rates seen in the first 5 years of life in captive-born females may play a large role in this negative population growth rate. Statistical analyses of the survivorship curves show a highly significant difference between the founder and captive-born populations, and while 99% of female founders survive until breeding age, only 88% of captive-born females do.

Reproductive factors may also influence the $F_{\geq 1}$ population growth rate observed. Although reproductive success of successive generations is not as dire as reported by Schwartzenberger *et al.* (1999) where only 8% of F_1 females had bred, the current study shows that 32% of breeding age F_1 females have now bred, only slightly below the reproductive success of 37% for founder females. Founder females are reported to have bred in captivity up until the age of 40, 6 years longer than captive bred females. Lower average numbers of offspring are also seen for $F_{\geq 1}$ dams compared to founder dams. As no statistically significant differences are observed between founder and $F_{\geq 1}$ inter-birth intervals, low lifetime reproductive success for the $F_{\geq 1}$ generation (55% lower than that recorded for the founder population) is likely to be caused by the compounding effect of lower $F_{\geq 1}$ fecundity observed between the ages 10 and 18 and less total time of the sub-population in captivity.

Based on the results seen in this study, the null (H_0) hypothesis that lifetime reproductive success of $F_{\geq 1}$ generation females is not significantly different to that of the founder population is rejected. It remains to be seen if the lower reproductive success currently observed for the $F_{\geq 1}$ females is indeed an artifact of time in captivity. The second null (H_0) hypothesis, that ageing of the F_0 generation will not significantly affect future growth rates of the global captive population, is accepted. A large proportion of the females currently found in the population are founders under the age of 35. As these founders are fairly well distributed in the age pyramid, the effects of the aging of these founders may be less perceptible than for *D. b. minor* for a number of years.

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Appendix 6: F_0 Female life table – *Diceros bicornis minor*

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	l_xm_x	$x(l_xm_x)$
0	1.00	0.00	24.35	1.00	0.00	24.35	0.00	0.00	0.00
1	0.97	0.03	35.50	1.00	0.00	34.82	0.00	0.00	0.00
2	0.97	0.03	35.35	0.97	0.00	34.57	0.00	0.00	0.00
3	1.00	0.00	34.00	0.94	0.00	34.00	0.00	0.00	0.00
4	0.97	0.03	34.04	0.94	0.00	33.28	0.00	0.00	0.00
5	0.94	0.06	33.21	0.91	0.03	31.46	0.03	0.03	0.14
6	1.00	0.00	30.00	0.86	0.03	30.00	0.03	0.03	0.15
7	0.97	0.03	30.31	0.86	0.05	29.45	0.05	0.04	0.30
8	0.97	0.03	29.00	0.83	0.09	28.50	0.09	0.07	0.60
9	1.00	0.00	28.00	0.81	0.07	28.00	0.07	0.06	0.51
10	1.00	0.00	28.98	0.81	0.09	28.98	0.09	0.07	0.73
11	0.97	0.03	29.00	0.81	0.10	28.72	0.10	0.08	0.89
12	0.96	0.04	28.00	0.78	0.04	27.78	0.04	0.03	0.38
13	0.96	0.04	27.00	0.75	0.12	26.07	0.12	0.09	1.17
14	1.00	0.00	26.00	0.72	0.13	26.00	0.13	0.09	1.31
15	1.00	0.00	26.00	0.72	0.10	26.00	0.10	0.07	1.08
16	0.92	0.08	26.42	0.72	0.00	24.83	0.00	0.00	0.00
17	1.00	0.00	24.00	0.66	0.15	24.00	0.15	0.10	1.69
18	1.00	0.00	24.00	0.66	0.04	24.00	0.04	0.03	0.48
19	0.96	0.04	24.00	0.66	0.04	23.72	0.04	0.03	0.50
20	0.91	0.09	22.00	0.64	0.07	20.77	0.06	0.04	0.89
21	1.00	0.00	19.00	0.58	0.08	19.00	0.08	0.05	0.97
22	1.00	0.00	18.50	0.58	0.03	18.50	0.03	0.02	0.38
23	0.94	0.06	17.50	0.58	0.00	17.23	0.00	0.00	0.00
24	0.93	0.07	13.50	0.55	0.04	13.44	0.04	0.02	0.52
25	1.00	0.00	11.50	0.51	0.04	11.50	0.04	0.02	0.51
26	0.90	0.10	10.00	0.51	0.00	9.52	0.00	0.00	0.00
27	1.00	0.00	7.00	0.46	0.07	7.00	0.07	0.03	0.86
28	0.80	0.20	5.00	0.46	0.00	4.31	0.00	0.00	0.00
29	1.00	0.00	4.00	0.37	0.00	4.00	0.00	0.00	0.00
30	0.71	0.29	3.50	0.37	0.00	3.37	0.00	0.00	0.00
31	1.00	0.00	2.00	0.26	0.00	2.00	0.00	0.00	0.00
32	1.00	0.00	2.00	0.26	0.00	2.00	0.00	0.00	0.00
33	1.00	0.00	1.00	0.26	0.00	1.00	0.00	0.00	0.00
34	0.00	1.00	1.00	0.26	0.00	0.95	0.00	0.00	0.00
35	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 7: $F_{\geq 1}$ Female life table – *Diceros bicornis minor*

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	l_xm_x	$x(l_xm_x)$
0	0.78	0.22	33.87	1.00	0.00	26.46	0.00	0.00	0.00
1	0.96	0.04	25.50	0.78	0.00	25.33	0.00	0.00	0.00
2	1.00	0.00	22.93	0.75	0.00	22.93	0.00	0.00	0.00
3	1.00	0.00	19.51	0.75	0.00	19.51	0.03	0.00	0.00
4	1.00	0.00	19.00	0.75	0.03	19.00	0.03	0.02	0.09
5	0.85	0.15	19.36	0.75	0.03	16.78	0.09	0.02	0.11
6	1.00	0.00	15.00	0.64	0.10	15.00	0.07	0.06	0.38
7	0.93	0.07	15.00	0.64	0.07	14.67	0.04	0.04	0.31
8	0.93	0.07	13.69	0.59	0.04	13.38	0.05	0.02	0.19
9	1.00	0.00	11.00	0.55	0.05	11.00	0.05	0.03	0.25
10	1.00	0.00	10.50	0.55	0.05	10.50	0.05	0.03	0.28
11	1.00	0.00	9.56	0.55	0.05	9.56	0.06	0.03	0.30
12	1.00	0.00	8.46	0.55	0.06	8.46	0.00	0.03	0.40
13	1.00	0.00	7.91	0.55	0.00	7.91	0.08	0.00	0.00
14	1.00	0.00	6.35	0.55	0.08	6.35	0.00	0.04	0.62
15	1.00	0.00	5.00	0.55	0.00	5.00	0.10	0.00	0.00
16	1.00	0.00	5.00	0.55	0.10	5.00	0.00	0.06	0.88
17	1.00	0.00	4.34	0.55	0.00	4.34	0.00	0.00	0.00
18	1.00	0.00	4.00	0.55	0.00	4.00	0.00	0.00	0.00
19	1.00	0.00	4.00	0.55	0.00	4.00	0.00	0.00	0.00
20	1.00	0.00	3.08	0.55	0.00	3.08	0.00	0.00	0.00
21	1.00	0.00	2.14	0.55	0.00	2.14	0.00	0.00	0.00
22	0.00	1.00	1.00	0.55	0.00	0.91	0.00	0.00	0.00
23	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
26	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
28	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
31	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
32	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
33	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
34	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
35	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 8: F_0 Female life table – *Diceros bicornis michaeli*

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	l_xm_x	$x(l_xm_x)$
0	1.00	0.00	122.96	1.00	0.00	122.96	0.00	0.00	0.00
1	0.99	0.01	161.32	1.00	0.00	160.52	0.00	0.00	0.00
2	0.94	0.06	161.53	0.99	0.00	156.08	0.01	0.00	0.00
3	0.94	0.06	152.06	0.93	0.01	146.23	0.01	0.01	0.03
4	0.99	0.01	142.00	0.88	0.01	141.86	0.01	0.01	0.04
5	1.00	0.00	141.00	0.87	0.01	141.00	0.02	0.01	0.04
6	0.94	0.06	140.68	0.87	0.02	135.26	0.07	0.02	0.10
7	0.98	0.02	132.00	0.81	0.07	130.66	0.04	0.06	0.40
8	0.98	0.02	130.00	0.80	0.04	128.28	0.08	0.03	0.26
9	0.97	0.03	126.49	0.78	0.08	125.48	0.05	0.06	0.56
10	0.94	0.06	121.00	0.76	0.05	118.87	0.08	0.04	0.38
11	0.93	0.07	114.91	0.71	0.09	110.70	0.08	0.06	0.71
12	0.99	0.01	106.00	0.66	0.09	105.17	0.04	0.06	0.72
13	0.95	0.05	104.00	0.66	0.04	101.68	0.10	0.03	0.34
14	0.97	0.03	98.00	0.62	0.10	97.00	0.05	0.06	0.87
15	0.93	0.07	93.88	0.61	0.05	90.00	0.04	0.03	0.45
16	0.96	0.04	85.50	0.56	0.04	83.92	0.10	0.02	0.36
17	0.94	0.06	82.00	0.54	0.10	79.41	0.05	0.05	0.92
18	0.90	0.10	77.44	0.51	0.05	73.27	0.07	0.03	0.46
19	0.99	0.01	67.50	0.46	0.08	66.53	0.09	0.04	0.69
20	0.89	0.11	66.00	0.45	0.09	63.82	0.04	0.04	0.81
21	0.97	0.03	59.00	0.40	0.05	58.72	0.09	0.02	0.42
22	0.96	0.04	57.00	0.39	0.09	56.45	0.07	0.04	0.77
23	0.98	0.02	55.00	0.38	0.07	54.03	0.04	0.03	0.60
24	0.96	0.04	54.00	0.37	0.04	52.52	0.09	0.01	0.35
25	0.96	0.04	51.50	0.35	0.09	50.57	0.07	0.03	0.79
26	0.92	0.08	49.00	0.34	0.07	47.01	0.06	0.02	0.62
27	0.89	0.11	44.77	0.31	0.07	41.31	0.06	0.02	0.59
28	0.92	0.08	38.00	0.28	0.07	35.66	0.04	0.02	0.54
29	1.00	0.00	35.00	0.26	0.04	35.00	0.06	0.01	0.30
30	0.91	0.09	35.00	0.26	0.06	34.06	0.05	0.02	0.46
31	0.87	0.13	32.00	0.23	0.05	30.21	0.06	0.01	0.36
32	0.93	0.07	28.00	0.20	0.07	27.21	0.00	0.01	0.45
33	0.88	0.12	26.00	0.19	0.00	23.80	0.03	0.00	0.00
34	0.82	0.18	21.99	0.17	0.03	19.42	0.02	0.00	0.17
35	0.87	0.13	16.00	0.14	0.03	15.73	0.00	0.00	0.14
36	0.92	0.08	12.00	0.12	0.00	11.36	0.05	0.00	0.00
37	0.90	0.10	10.50	0.11	0.05	9.74	0.00	0.01	0.20
38	0.71	0.29	7.00	0.10	0.00	5.87	0.00	0.00	0.00
39	0.50	0.50	4.00	0.07	0.00	2.17	0.00	0.00	0.00
40	1.00	0.00	2.00	0.04	0.00	2.00	0.00	0.00	0.00
41	1.00	0.00	2.00	0.04	0.00	2.00	0.00	0.00	0.00
42	1.00	0.00	2.00	0.04	0.00	2.00	0.00	0.00	0.00
43	1.00	0.00	2.00	0.04	0.00	2.00	0.00	0.00	0.00
44	1.00	0.00	2.00	0.04	0.00	2.00	0.00	0.00	0.00
45	0.50	0.50	2.00	0.04	0.00	1.34	0.00	0.00	0.00
46	0.00	1.00	1.00	0.02	0.00	0.21	0.00	0.00	0.00
47	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
48	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
49	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
50	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 9: $F_{\geq 1}$ Female life table – *Diceros bicornis michaeli*

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	l_xm_x	$x(l_xm_x)$
0	0.79	0.21	260.09	1.00	0.00	211.38	0.00	0.00	0.00
1	0.95	0.05	202.31	0.79	0.00	196.70	0.00	0.00	0.00
2	0.93	0.07	184.83	0.75	0.00	176.17	0.00	0.00	0.00
3	0.99	0.01	161.76	0.70	0.00	160.09	0.00	0.00	0.00
4	0.98	0.02	154.47	0.69	0.00	152.91	0.02	0.00	0.00
5	1.00	0.00	143.12	0.68	0.02	143.12	0.05	0.01	0.07
6	0.99	0.01	138.35	0.68	0.05	137.80	0.07	0.03	0.20
7	0.98	0.02	132.56	0.67	0.07	131.32	0.11	0.05	0.33
8	0.98	0.02	122.74	0.66	0.11	120.87	0.09	0.07	0.58
9	0.96	0.04	113.28	0.64	0.09	110.88	0.08	0.06	0.52
10	0.97	0.03	103.24	0.62	0.08	102.24	0.08	0.05	0.49
11	0.98	0.02	92.99	0.60	0.08	92.00	0.08	0.05	0.53
12	0.94	0.06	86.67	0.59	0.08	83.98	0.08	0.05	0.56
13	0.96	0.04	75.95	0.55	0.08	75.00	0.09	0.04	0.57
14	0.94	0.06	70.61	0.53	0.09	69.43	0.06	0.05	0.67
15	0.98	0.02	62.51	0.50	0.06	61.90	0.12	0.03	0.45
16	0.95	0.05	58.91	0.49	0.12	56.62	0.05	0.06	0.94
17	0.94	0.06	53.08	0.46	0.05	51.03	0.09	0.02	0.39
18	0.96	0.04	46.77	0.44	0.10	45.56	0.06	0.04	0.78
19	0.95	0.05	40.20	0.42	0.06	39.43	0.07	0.03	0.48
20	1.00	0.00	33.97	0.40	0.07	33.97	0.12	0.03	0.56
21	0.91	0.09	32.00	0.40	0.12	30.15	0.06	0.05	1.00
22	1.00	0.00	26.97	0.36	0.07	26.97	0.00	0.03	0.56
23	0.87	0.13	23.96	0.36	0.00	22.38	0.08	0.00	0.00
24	0.84	0.16	19.06	0.32	0.09	17.49	0.06	0.03	0.68
25	1.00	0.00	15.14	0.27	0.07	15.14	0.04	0.02	0.46
26	1.00	0.00	13.31	0.27	0.04	13.31	0.14	0.01	0.28
27	0.83	0.17	11.91	0.27	0.14	10.70	0.00	0.04	1.00
28	1.00	0.00	9.00	0.22	0.00	9.00	0.06	0.00	0.00
29	0.89	0.11	9.00	0.22	0.06	8.23	0.06	0.01	0.38
30	0.87	0.13	8.00	0.20	0.07	7.17	0.00	0.01	0.41
31	0.86	0.14	7.00	0.17	0.00	6.32	0.09	0.00	0.00
32	0.50	0.50	6.00	0.15	0.11	4.46	0.09	0.02	0.51
33	1.00	0.00	3.00	0.07	0.17	3.00	0.00	0.01	0.41
34	1.00	0.00	3.00	0.07	0.00	3.00	0.17	0.00	0.00
35	1.00	0.00	3.00	0.07	0.17	3.00	0.00	0.01	0.43
36	1.00	0.00	1.91	0.07	0.00	1.91	0.00	0.00	0.00
37	1.00	0.00	1.00	0.07	0.00	1.00	0.00	0.00	0.00
38	1.00	0.00	1.00	0.07	0.00	1.00	0.00	0.00	0.00
39	0.00	1.00	1.00	0.07	0.00	0.05	0.00	0.00	0.00
40	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
41	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
42	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
43	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
44	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
45	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
46	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
47	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
48	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
49	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
50	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 10: F_0 Female life table – *Ceratotherium simum simum*

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	l_xm_x	$x(l_xm_x)$
0	1.00	0.00	384.58	1.00	0.00	383.64	0.00	0.00	0.00
1	1.00	0.00	419.41	1.00	0.00	418.43	0.00	0.00	0.00
2	1.00	0.00	420.26	1.00	0.00	419.14	0.00	0.00	0.00
3	0.99	0.01	420.65	1.00	0.00	418.52	0.00	0.00	0.00
4	1.00	0.00	419.08	0.99	0.00	419.03	0.01	0.00	0.00
5	0.98	0.02	423.91	0.99	0.01	419.31	0.02	0.01	0.05
6	0.99	0.01	409.94	0.97	0.02	405.41	0.03	0.02	0.12
7	1.00	0.00	395.99	0.96	0.03	395.99	0.05	0.03	0.20
8	0.98	0.02	389.51	0.96	0.05	387.57	0.04	0.05	0.38
9	0.99	0.01	376.62	0.94	0.04	375.99	0.04	0.04	0.34
10	0.99	0.01	366.16	0.93	0.04	365.12	0.06	0.04	0.37
11	0.98	0.02	357.23	0.92	0.06	351.37	0.04	0.06	0.61
12	0.98	0.02	340.83	0.90	0.04	338.40	0.07	0.04	0.43
13	0.98	0.02	331.81	0.89	0.07	329.49	0.06	0.06	0.81
14	0.98	0.02	321.09	0.87	0.06	318.15	0.05	0.05	0.73
15	0.98	0.02	303.80	0.85	0.05	299.81	0.05	0.04	0.64
16	0.98	0.02	290.39	0.83	0.05	284.83	0.04	0.04	0.67
17	1.00	0.00	274.40	0.82	0.04	274.07	0.06	0.03	0.56
18	0.98	0.02	265.96	0.82	0.06	264.10	0.05	0.05	0.88
19	0.98	0.02	248.99	0.80	0.05	246.36	0.04	0.04	0.76
20	0.99	0.01	243.00	0.79	0.04	240.91	0.03	0.03	0.63
21	1.00	0.00	240.41	0.78	0.03	240.41	0.03	0.02	0.49
22	0.97	0.03	238.57	0.78	0.03	234.68	0.04	0.02	0.51
23	0.98	0.02	228.31	0.75	0.04	224.94	0.03	0.03	0.69
24	0.98	0.02	221.77	0.74	0.03	218.72	0.04	0.02	0.53
25	0.98	0.02	214.00	0.72	0.04	210.59	0.02	0.03	0.72
26	0.97	0.03	208.83	0.71	0.02	202.99	0.04	0.01	0.37
27	0.97	0.03	197.24	0.69	0.04	193.06	0.03	0.03	0.74
28	0.97	0.03	191.38	0.67	0.03	188.42	0.02	0.02	0.56
29	0.98	0.02	184.20	0.65	0.02	182.07	0.03	0.01	0.38
30	0.95	0.05	175.19	0.64	0.03	170.27	0.03	0.02	0.57
31	0.93	0.07	164.42	0.60	0.03	159.28	0.01	0.02	0.56
32	0.94	0.06	152.42	0.56	0.01	148.26	0.02	0.01	0.18
33	0.97	0.03	143.00	0.53	0.02	141.72	0.01	0.01	0.35
34	0.94	0.06	138.25	0.51	0.01	133.61	0.01	0.01	0.17
35	0.98	0.02	124.99	0.48	0.01	124.85	0.02	0.00	0.17
36	0.97	0.03	117.00	0.47	0.02	115.34	0.00	0.01	0.34
37	0.95	0.05	112.99	0.46	0.00	111.35	0.00	0.00	0.00
38	0.91	0.09	104.98	0.43	0.00	101.63	0.00	0.00	0.00
39	0.88	0.12	83.96	0.40	0.00	78.61	0.00	0.00	0.00
40	0.97	0.03	58.94	0.35	0.00	57.35	0.00	0.00	0.00
41	0.81	0.19	35.96	0.34	0.00	30.86	0.00	0.00	0.00
42	0.89	0.11	18.98	0.27	0.00	17.89	0.00	0.00	0.00
43	0.80	0.20	5.00	0.24	0.00	4.79	0.00	0.00	0.00
44	1.00	0.00	2.99	0.19	0.00	2.99	0.00	0.00	0.00
45	0.00	1.00	1.00	0.19	0.00	0.41	0.00	0.00	0.00
46	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
47	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 11: $F_{\geq 1}$ Female life table – *Ceratotherium simum simum*

Age	p_x	q_x	Risk q_x	l_x	m_x	Risk m_x	F_x	$l_x m_x$	$x(l_x m_x)$
0	0.81	0.19	391.00	1.00	0.00	323.75	0.00	0.00	0.00
1	0.94	0.06	303.87	0.81	0.00	292.15	0.00	0.00	0.00
2	0.94	0.06	273.46	0.76	0.00	262.69	0.00	0.00	0.00
3	0.94	0.06	243.95	0.72	0.00	236.77	0.02	0.00	0.00
4	0.96	0.04	218.25	0.67	0.02	214.48	0.03	0.01	0.05
5	0.98	0.02	197.83	0.65	0.03	194.97	0.05	0.02	0.10
6	0.98	0.02	187.26	0.63	0.05	184.87	0.04	0.03	0.19
7	0.98	0.02	176.34	0.62	0.04	173.89	0.05	0.02	0.17
8	0.98	0.02	162.53	0.61	0.05	160.93	0.05	0.03	0.24
9	0.99	0.01	147.65	0.60	0.05	146.71	0.02	0.03	0.27
10	0.99	0.01	136.38	0.59	0.02	135.69	0.05	0.01	0.12
11	0.98	0.02	126.99	0.58	0.05	125.00	0.04	0.03	0.32
12	0.97	0.03	116.41	0.57	0.04	114.10	0.02	0.02	0.27
13	1.00	0.00	101.79	0.56	0.02	101.79	0.04	0.01	0.14
14	0.99	0.01	97.47	0.56	0.04	96.52	0.03	0.02	0.31
15	0.99	0.01	90.54	0.55	0.03	89.57	0.05	0.02	0.25
16	1.00	0.00	82.85	0.54	0.05	82.85	0.02	0.03	0.44
17	0.99	0.01	78.25	0.54	0.02	78.09	0.01	0.01	0.18
18	0.99	0.01	73.99	0.54	0.01	73.06	0.03	0.01	0.10
19	1.00	0.00	67.84	0.53	0.03	67.84	0.05	0.02	0.30
20	0.98	0.02	62.84	0.53	0.05	61.85	0.03	0.03	0.53
21	0.98	0.02	57.62	0.52	0.03	56.38	0.02	0.02	0.33
22	0.98	0.02	51.82	0.51	0.02	51.34	0.05	0.01	0.23
23	0.98	0.02	44.32	0.50	0.05	44.12	0.01	0.03	0.58
24	0.95	0.05	38.28	0.49	0.01	36.95	0.00	0.00	0.12
25	1.00	0.00	32.40	0.47	0.00	32.40	0.05	0.00	0.00
26	1.00	0.00	29.83	0.47	0.05	29.83	0.02	0.02	0.61
27	1.00	0.00	27.20	0.47	0.02	27.20	0.02	0.01	0.25
28	0.96	0.04	24.35	0.47	0.02	23.94	0.03	0.01	0.26
29	1.00	0.00	16.88	0.45	0.03	16.88	0.00	0.01	0.39
30	1.00	0.00	9.07	0.45	0.00	9.07	0.13	0.00	0.00
31	0.60	0.40	4.97	0.45	0.13	3.77	0.00	0.06	1.81
32	1.00	0.00	1.37	0.27	0.00	1.37	0.00	0.00	0.00
33	1.00	0.00	1.00	0.27	0.00	1.00	0.00	0.00	0.00
34	1.00	0.00	1.00	0.27	0.00	1.00	0.00	0.00	0.00
35	1.00	0.00	1.00	0.27	0.00	1.00	0.00	0.00	0.00
36	1.00	0.00	0.71	0.27	0.00	0.71	0.00	0.00	0.00
37	1.00	1.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00
38	1.00	1.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00
39	1.00	1.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00
40	1.00	1.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00
41	0.00	1.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00
42	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
43	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
44	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
45	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
46	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
47	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

CHAPTER 4

BIRTH SEX RATIO ANALYSIS IN CAPTIVE-BORN *DICEROS BICORNIS MINOR, DICEROS BICORNIS MICHAELI* AND *CERATOTHERIUM SIMUM SIMUM*.

4.1 Abstract

It has been reported that the birth sex ratio of captive black rhinoceros (*Diceros bicornis*) in North America is male-biased causing a problem of major concern. Unbalanced sex ratios which are male-biased can compromise the use of limited space in zoos and have a negative effect on population growth rates as well as predicted population extinction rates. This chapter investigates the birth sex ratio of three captive African rhinoceros subspecies, *Diceros bicornis minor*, *Diceros bicornis michaeli* and *Ceratotherium simum simum*, to determine if a male birth sex-bias exists in the populations on a global scale. One possible determinant of birth sex ratio, maternal age, is also examined to access if a correlation exists between the age of the dam and the sex of her offspring. Both *D. b minor* and *D. b. michaeli* data indicate that the birth sex ratios in the global populations are unbiased from an expected 1:1 (male:female) ratio. Global birth sex ratio in captive births to date show a ratio of 1.44:1 (n = 83) for *D. b. minor*; 0.91:1 (n = 444) exists for *D. b. michaeli*, and *C. s. simum* shows a birth sex ratio of 1.14:1 (n = 866). In both black rhinoceros subspecies, statistical tests show no significant difference from parity. However, logistic regression conducted on the white rhinoceros data indicates a statistically significant male bias. In all three subspecies, no significant link was found between maternal age and the sex of the offspring.

Keywords: Birth sex ratio bias, maternal age, global captive population.

4.2 Introduction

It has been recognized by the IUCN that with the increasing number of threatened taxa, it will not be possible to ensure the survival of most species without the utilization of complementary conservation approaches, including for some taxa, the practical use of *ex situ* techniques (IUCN 2002). While it is possible to maintain captive populations of threatened species as a form of insurance population, the captive population need be able to hold populations large enough to be both demographically and genetically self-sustaining (Foose *et al*. 1995)

The 2002 Rhinoceros Species Survival Plan (SSP) Masterplan (AZA 2002) prepared by the American Association of Zoos and Aquariums Rhino Advisory Group, states that the skew toward males in the sex ratio of calves is a problem of increasing concern for the captive population of black rhinoceroses in North America. In a polygamous species such as rhinoceros, a skewed sex ratio favoring males creates difficulties in managing these large, solitary animals in captivity, as only one male is needed to breed with several females. Excess males can therefore add to an institutions logistical and financial constraint (Berkeley 2011). Unbalanced sex ratios which are male-biased can compromise limited space found in the zoos and have a negative effect on population growth rates as well as predicted population extinction rates (Robertson *et al.* 2006; Ferrer *et al.* 2009; Berkeley 2011).

Fisher (1930) first described a theory on the mechanism for vertebrate sex ratio equilibrium, where he predicted that sex ratios will always return to equilibrium because the reproductive advantage is always enjoyed by the rarer sex (Hardy 1997). He proposed that once the sex ratios in a population become imbalanced, offspring of the rarer sex have the advantage of reproduction, as prospects of mating have subsequently increased. This results in a genetic tendency for parents to produce more of the rarer sex in order to take advantage of this imbalance and ensuring maximum genetic contribution. Eventually this brings the sex ratio back to equilibrium. This is known as Fisher’s theory of equal investment (Hardy 1997). Since then, various authors have tried to explain deviations from this basic theory, but adaptive explanations for deviations from this equilibrium are still a subject of much debate and uncertainty (Hamilton 1967; Hardy 1997). Multiple hypotheses have been proposed to try and explain the skewing of natal sex ratios and the mechanisms that determine an offspring’s sex. Strictly, Fisher’s model applies to the ratio of maternal investment, not necessarily to the number of offspring, i.e., if one sex requires twice the amount of maternal investment, that sex would be produced half as frequently.

Trivers and Willard (1973) proposed that when one sex gains more than the other from extra maternal investment, when parents are in good condition they will be biased towards the sex that requires the additional investment (Trivers & Willard 1973; Hardy 1997). The theory was developed for polygynous species (as is the case with rhinoceros), where one male dominates a harem. The additional effort of producing a male offspring will therefore be offset by the male's potential to produce multiple offspring. For polygynous species therefore, the Trivers and Willard's (1973) theory is that females in good condition are more likely to produce male offspring as these require greater investment i.e., better males beat their competitors later in life. The condition of female offspring does not really make much difference – they can most often only produce one offspring per cycle. Therefore dams in prime condition should produce more male offspring, while dams in poor condition should produce more female offspring.

In contrast to the Trivers and Willard's (1973) theory, Clark's (1978) local resource competition hypothesis suggests that where parents compete with their offspring for a local resource, a parent will invest in the sex more likely to disperse when resources are limited, or the sex less likely to disperse when resources are favourable (Silk 1983; Hjernquist *et al.* 2009). Therefore, if food resources are limited and therefore dam condition is poor, Clark's (1978) hypothesis predicts that more male offspring will be produced, with the converse of more female offspring for dams in good condition (Clark 1978).

As additions to the two alternative theories proposed by Trivers and Willard (1973), and Clark (1978), several other factors have been investigated as influencing birth sex ratio in different mammalian species. These include timing of insemination (Pratt *et al*. 1987), amount of previous investment (Drickamer 1990; Robert *et al*. 2010), and maternal age (Reubinoff & Schenker 1996; Saltz 2001). Recent research specific to rhinoceros, have assessed the possible links of the effects of corticoadrenal stress during translocation (Linklater 2007), maternal age and time spent in captivity (Dennis *et al.* 2007), and maternal condition (Berkely & Linklater 2010).

Recent research on rhinoceros species has assessed several possible links to birth sex allocation. Linklater (2007) assessed multiple sex-allocation mechanisms from time of conception to birth of both black and white rhinoceros translocated from the wild into captivity. Four mechanisms were investigated: 1) hormone-induced conception bias; 2) sex-differential embryo death from excess glucose metabolism; 3) sex-differential embryo death from embryo–uterine developmental asynchrony;

and 4) pregnancy hormone suppression and resource deprivation; all linked to corticoadrenal stress response. Linklater (2007) found that translocation induced a statistically significant birth sex ratio reversal between translocations that took place during early gestation (86% male births) and mid-gestation (38% male). Captivity also induced a strongly male-biased (67% male) birth sex ratio for conceptions after arrival in captivity. Linklater's (2007) results suggest that at least two sex-allocation mechanisms operate in sequence; and indicate that sex-differential embryo death around implantation, sex-differential glucose metabolism by the pre-implantation embryo and stress, all likely play a role in birth sex ratio.

Dennis *et al.* (2007), in a case study of Black rhinoceros in North America, described a number of factors associated with birth sex ratio bias in captive populations. In this study, no association was found in sex ratio of offspring born to captive-born dams of any age. However, with wild-born dams, increased time in captivity increased likelihood of a male calf until the age of 12 – after which the likelihood of a male calf once again decreased until the age of 19. Dennis *et al*.'s (2007) data supported the hypothesis that dams of prime breeding age would produce more of one sex, while early and late breeders would result in a tendency towards the opposite sex. However, in opposition to Trivers and Willard's (1973) theory, more female offspring were born to dams of prime breeding age, and more male offspring to females that bred very early or later in life.

Birth sex ratio analysis of black rhinoceros in the wild show a male bias of 1.46:1 (n = 86), however, statistical tests show that this ratio is not significantly different from parity (Owen-Smith 1988). This was calculated from data collected before 1988 in Hluhluwe Game Reserve (Owen-Smith 1988). In white rhinoceros, however, a statistically significant male-biased ratio of 1.73:1 was observed (n = 139; Owen-Smith 1988). Berkeley and Linklater (2010) further investigated the male birth sex bias in HiP between 1989 and 2004. They found a link between male-biased sex ratios and wet or dry season when conception took place. Dams were more likely to be seen with male calves if they conceived during the wet season (57.3% male), compared to those that conceived during the dry season (42.2% male). Berkeley and Linklater (2010) linked this to maternal condition at the time just after conception, further supporting the Trivers and Willard's (1973) theory that females in good condition are more likely to produce male offspring. They suggest therefore that the male-bias in the offspring of captive black rhinoceros populations might be reduced by restricting food intake in pregnant females, to get them into a neutral or negative energy balance just after time of conception (Berkeley & Linklater 2010). Assessing maternal condition during pregnancy is unfortunately beyond the scope of this study. However, it was possible to assess overall birth sex ratios and whether birth sex is linked to specific age classes.

This chapter provides a retrospective study to determine if a birth sex ratio bias is observed in the global populations of three subspecies of rhinoceros currently held in captivity, namely *Diceros bicornis minor*, *Diceros bicornis michaeli* and *Ceratotherium simum simum.* Further investigations are then carried out to determine if any bias can be correlated with the age of the dam at parturition, linking this to the theory that young and old females are of inferior reproductive condition and therefore more likely to give birth to female offspring, while middle aged dams in their prime are more likely to give birth to male offspring (Trivers & Willard 1973; Saltz 2001).

The aim of this chapter is therefore:

- To examine if the birth sex ratios in *D. b. minor, D. b. michaeli* and *C. s. simum* differ significantly from the expected 1:1 norm; and
- To examine if the birth sex ratio is male-biased and if the bias is dependent on the age of the dam.

This investigation is therefore testing the following hypotheses:

- *Null (H_0) hypothesis*: Birth sex ratios do not differ from the theoretical 1:1 sex ratio;
- *Alternative (H_A) hypothesis*: Birth sex ratios differ from the theoretical 1:1 sex ratio;
- *Null (H_0) hypothesis*: Females of prime breeding age produce equal numbers of male and female offspring;
- *Alternative (H_{A1}) hypothesis*: Females of prime breeding age produce more male than female offspring; and
- *Alternative (H_{A2}) hypothesis*: Females of prime breeding age give birth to more female than male offspring.

4.3 Materials and Methods

Population data were collated from two sources, the International Studbook for Rhinoceros (Ochs 2001, 2005) and the Zoological Information Management System database (ZIMS), and entered into the Single Population Animal Record Keeping System version 1.66 (SPARKS) database programme (ISIS 2004; 2011). The three subspecies (*D. b. minor*, *D. b. michaeli* and *C. s. simum*) were assessed separately using records from the first births in captivity, which were in 1965 for *D. b. minor*, 1941 for *D. b. michaeli* and 1967 for *C. s. simum*. All records of captive births in the global database, where the sex of the offspring was known, were assessed. Regional and a global assessment were conducted, to determine if the North American population is alone in experiencing a male-bias, and how this affects the global population. Chi-square goodness-of-fit analyses were conducted on the regional data to determine statistically significant deviation from a 1:1 ratio, however, sample sizes are extremely small for some regions, and therefore the results should be viewed with caution. Any bias was deemed to be statistically significant where $P > 0.05$. Zoological regions were assigned as per ISIS recommendations, and are as follows (Traylor-Holzer 2011):

- North America (Canada, Greenland, US, Bermuda)
- Latin America (from Mexico south through the Caribbean Islands, Central America and South America)
- Europe (including Russia, Armenia, Azerbaijan, Belarus, Estonia, Georgia, Kazakhstan, Kyrgyzstan, Latvia, Lithuania, Moldova, Tajikistan, Turkmenistan, Ukraine, Uzbekistan)
- Africa (all of Africa)
- Middle East (Bahrain, Iran, Iraq, Israel, Jordan, Kuwait, Lebanon, Oman, Qatar, Saudi, Syria, UAE, Yemen)
- South Asia (Afghanistan, Bangladesh, Bhutan, BIOT, India, Maldives, Nepal, Pakistan, Sri Lanka)
- South East Asia (Myanmar, Laos, Vietnam, Cambodia, Thailand, Malaysia, Singapore, Indonesia, Philippines)
- East Asia (China, Hong Kong, Macao, Taiwan, Japan, North Korea, South Korea, Mongolia)
- Australasia (Australia, New Zealand, Papua New Guinea, Fiji, New Caledonia, plus nearby island groups)

Sample sizes of captive births used for analyses are given in Table 19 below:

Table 19: Sample sizes of captive births per region.

	D. b. minor	*D. b. michaeli*	*C. s. simum*
	N	N	N
Africa	18	12	68
Australasia	11	9	46
East Asia	0	59	78
Europe	8	151	261
India	0	15	0
Latin America	0	7	42
Middle East	0	5	23
North America	18	186	346
Total	55	444	864

In order to assess if maternal age has any influence on any deviation from a 1:1 birth sex ratio in the global populations, age at parturition was determined for all dams that were identifiable and that had given birth to a known sex offspring. The following analyses were then conducted on the data:

a) Percentage male offspring for each age class were calculated and plotted on a line graph to determine any discernible pattern of male bias. Where no offspring were recorded as being born to an age class, a 50% male probability was entered;

b) Male offspring were assigned a binary digit of 1, and female offspring a binary digit of 0. The results were then plotted on a scatter graph to see if a pattern emerged according to the dam's age; and

c) Linear and quadratic logistic regression analyses as described in Ter Braak & Looman (1987) were performed on the data using Statistica 8.0. Values with $P < 0.05$ were deemed to be statistically significant.

4.4 Results

Diceros bicornis minor

The overall birth sex ratio distribution shows a male-bias with 49 male births compared to 34 female births (1.44:1) over the time period from a total sample size of 83 births. As Figure 55 indicates, the youngest dam to give birth in age class 4 produced a male offspring, but this is from a single sample. Dams of 5 and 6 years produced offspring that were female-biased, whereas the trend for offspring sex ratio for dams from the age of 7 to 12 appears to be more male-biased. Birth sex ratio in the age classes that follow seem to swing more in favour of females once again until the maternal age of 17. Dams of age 18 have only produced female offspring. Above the age of 20, there is once again a male-bias except for age 25. The results for these later age classes, however, are based once again on single samples. No births were recorded at the age classes of 23 and 26, so 50% values were assigned to these age classes.

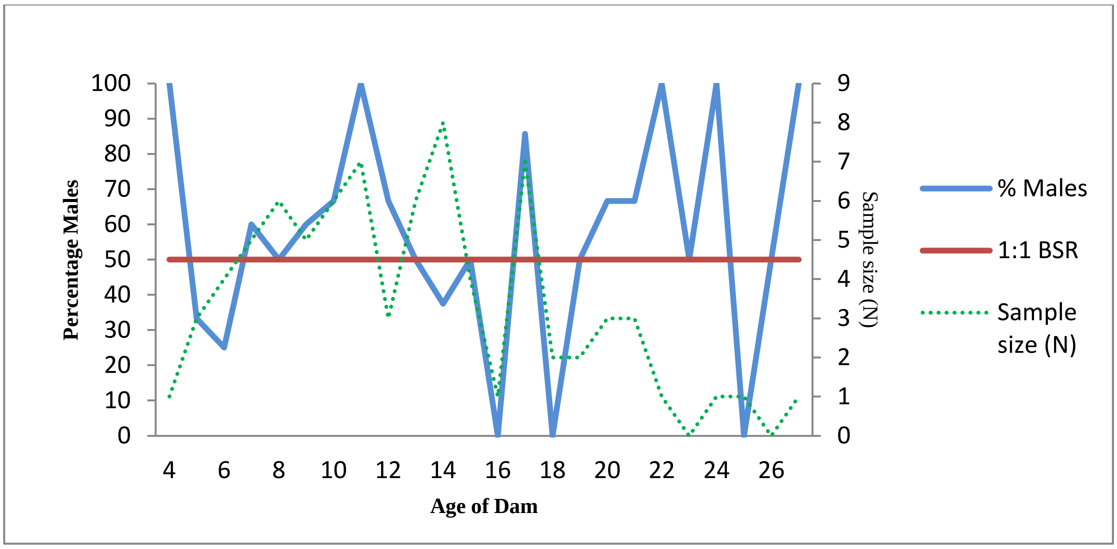

Figure 55: Birth sex ratio analysis - *Diceros bicornis minor*.

Dams' age at parturition ranged from 4.8 to 27 years. The binary scatter graph shows no clear pattern of preferred birth sex allocation for various age classes (Figure 56). It appears from the graph, however, that there is an overall preponderance towards male offspring.

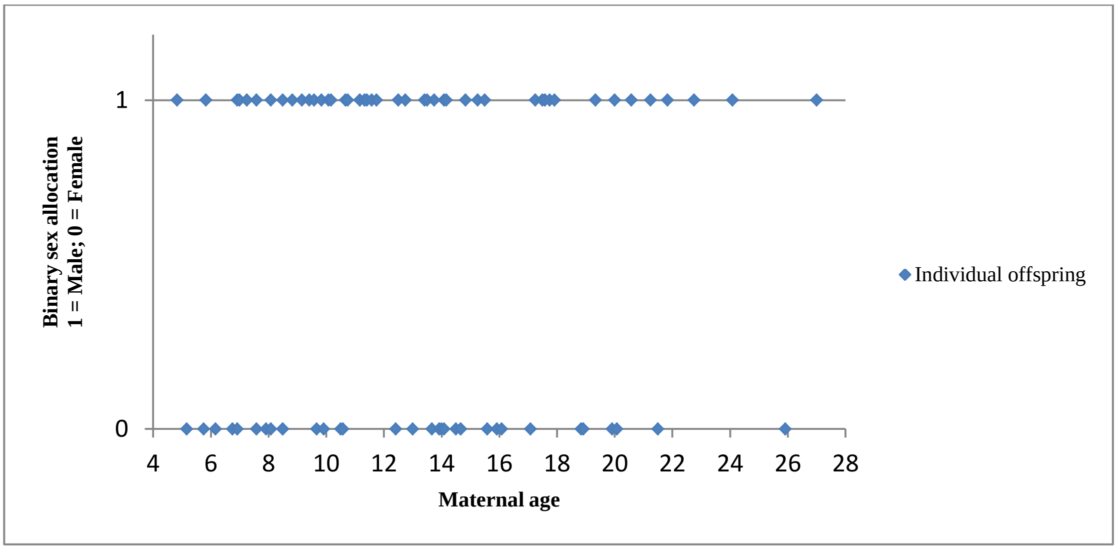

Figure 56: Binary birth sex ratio analysis - *Diceros bicornis minor*

Four global regions are currently holding *D. b. minor* in captivity. Regional differences in birth sex ratio bias are presented below in Table 20. Three of the regions show a male birth sex ratio bias, with Australasia being the most prominent, with a ratio of 1.75:1. Europe shows a 1:1 birth sex ratio. Neither the regional nor the global analyses showed a statistically significant difference from the expected 1:1 birth sex ratio.

Table 20: Regional birth sex ratio analysis - *Diceros bicornis minor*

	Total N	Male	Female	Birth sex ratio	χ^2	Probability (*P*)
Africa	18	10	8	1.22:1	0.25	> 0.05
Australasia	11	7	4	1.75:1	0.82	> 0.05
Europe	8	4	4	1:1	0.00	> 0.05
North America	46	28	18	1.56:1	2.20	> 0.05
Total	83	49	34	1.44:1	2.71	> 0.05

Neither Linear nor Quadratic Logit regression conducted on *D. b. minor* data show any statistical significance linked to birth sex ratio and age of the dam as seen in

Table 21 and Table 22. Overall birth sex ratio observed was also not statistically significant in both the analyses. *P* values for all analyses conducted were > 0.05.

Table 21: Birth sex ratio analysis: Linear Logit regression - *Diceros bicornis minor*

	Column	Estimate	Standard error	Wald Stat	Probability (*P*)
Intercept	1	0.10	0.06	0.02	0.87
Age_Days	2	0.00	0.00	0.22	0.64
Scale		1.00	0.00		

Table 22: Birth sex ratio analysis: Quadratic Logit regression - *Diceros bicornis minor*

	Column	Estimate	Standard error	Wald Stat	Probability (*P*)
Intercept	1	0.12	1.51	0.00	0.94
Age_Days	2	0.00	0.00	0.06	0.08
Age_Days^2	3	0.00	0.00	0.02	0.88
Scale		1.00	0.00		

Diceros bicornis michaeli

Diceros bicornis michaeli overall birth sex ratio distribution from a total of 444 captive births shows a female-bias, with 212 male births compared to 232 female (0.91:1) births over the time period. As with *D. b. minor*, youngest dams to give birth have produced more male offspring, and in the case of *D. b. michaeli,* for both age classes 4 and 5. The trend thereafter, between ages 6 and 29, appear to be more female-biased, with a few exceptions where male-bias is observed at age classes 9, 16, 19, 21 and 25. Age classes above 29 show erratic trends, probably caused by an increase in stochasticity, due to the small sample sizes at this end of the age spectrum. No births were reported in the age classes of 33 and 36, so a 1:1 ratio was assumed and 50% assigned to these age classes (Figure 57).

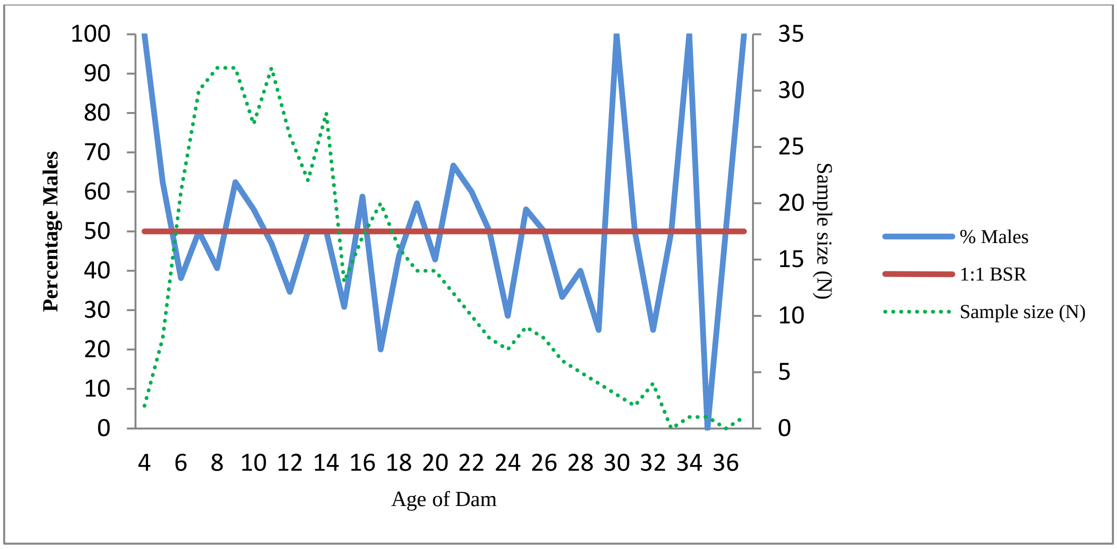

Figure 57: Birth sex ratio analysis - *Diceros bicornis michaeli.*

Maternal age at parturition ranged from 4.8 to 37.3 years. No discernible pattern of sex ratio bias dependent on age of dam can be detected from the binary scatter graph (1 = male offspring, 0 = females offspring; Figure 58).

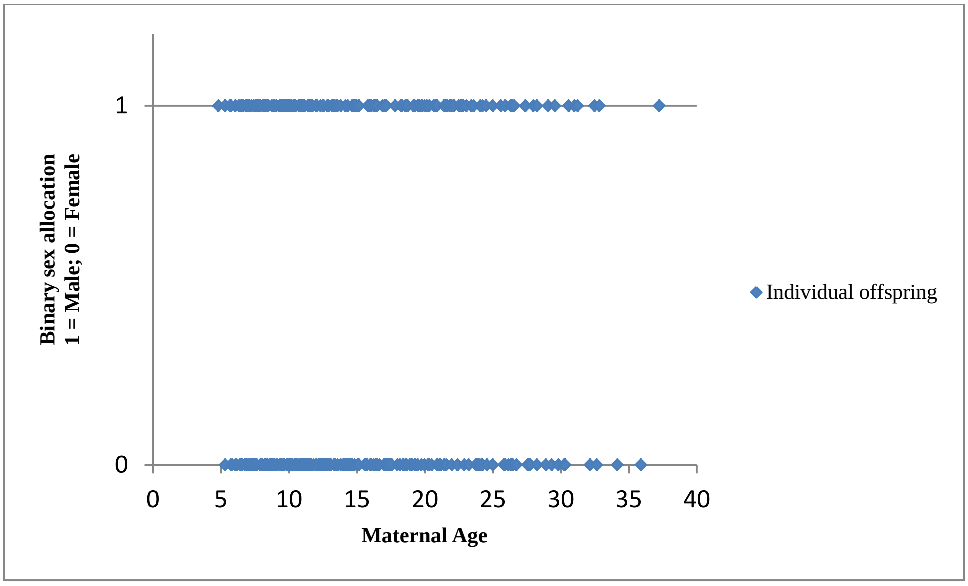

Figure 58: Binary birth sex ratio analysis - *Diceros bicornis michaeli.*

Eight zoological regions are currently holding *D. b. michaeli.* The majority show a female sex ratio bias, the highest bias seen in Australasia, where double the amount of female offspring have been born than male offspring. Only North America and Africa show male biases, but these are not statistically significant. Only the European population shows a statistically significant difference from parity, experiencing a female bias of 0.66:1 (Table 23).

Table 23: Regional birth sex ratio analysis – *Diceros bicornis michaeli*

	Total	Males	Female	Birth sex ratio	X^2	Probability (*P*)
Africa	12	8	4	2.00:1	1.30	> 0.05
Australasia	9	3	6	0.50:1	1.00	> 0.05
East Asia	59	26	33	0.79:1	0.83	> 0.05
Europe	151	60	91	0.66:1	6.36	< 0.05
India	15	6	9	0.67:1	0.60	> 0.05
Latin America	7	3	4	0.75:1	0.14	> 0.05
Middle East	5	2	3	0.67:1	0.20	> 0.05
North America	186	104	82	1.26:1	2.60	> 0.05
Total	444	212	232	0.91:1	0.90	> 0.05

As with *D. b. minor*, linear (Table 24) and quadratic (Table 25) Logit regression shows no statistically significant link between age of dam and sex of offspring. There is also no statistical significance to the overall female birth sex ratio bias observed.

Table 24: Birth sex ratio analysis: Linear Logit regression - *Diceros bicornis michaeli*.

	Column	Estimate	Standard error	Wald Stat	Probability (*P*)
Intercept	1	-0.02	0.23	0.01	0.94
Age_Days	2	0.00	0.00	0.13	0.72
Scale		1.00	0.00		

Table 25: Birth sex ratio analysis: Quadratic Logit regression - *Diceros bicornis michaeli*.

	Column	Estimate	Standard error	Wald Stat	Probability (*P*)
Intercept	1	0.36	0.52	0.05	0.49
Age_Days	2	0.00	0.00	0.75	0.39
Age_Days^2	3	0.00	0.00	0.65	0.42
Scale		1.00	0.00		

Ceratotherium simum simum

In the case of *C. s. simum*, a total of 786 captive births were assessed. Overall birth sex ratio distribution shows a male-bias with 426 male births compared to 360 female births (1.18:1) over the time period. Data points appear to be more consistent around a 1:1 ratio throughout the age range, until the age of 35, where more male births are observed. As with the black rhinoceros subspecies, the youngest age class produced offspring with a birth sex ratio that is male-biased (Figure 59).

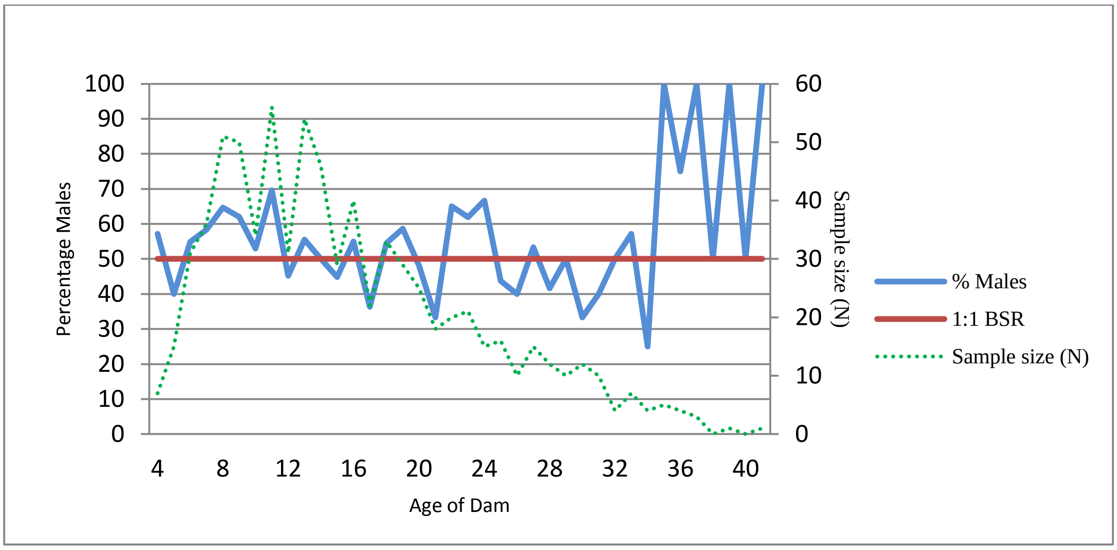

Figure 59: Birth sex ratio analysis - *Ceratotherium simum simum.*

Maternal age at birth ranges from 4.1 years to 41.3 years. A similar pattern is seen in the binary scatter graph as with the previous graph, with no discernible birth sex ratio bias until the age of around 35 after which a male bias is prevalent (1 = male offspring, 0 = female offspring; Figure 60).

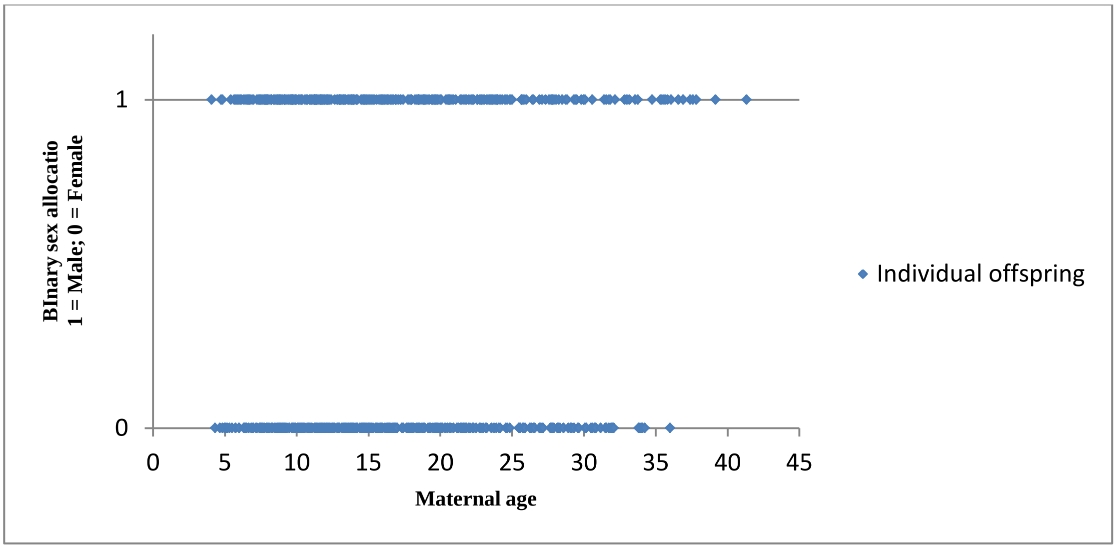

Figure 60: Binary birth sex ratio analysis - *Ceratotherium simum simum*.

Eight zoological regions provide captive space for *C. s. simum*, with only East Asia and Latin America showing higher numbers of female offspring compared to male offspring. The only region that displays a significant bias from parity, however, is the Middle East countries, where a strong male-bias is observed ($\chi^2 = 5.26$; d.f. = 1; $n = 23$; $P < 0.025$). There is no significant bias observed in the overall global population at $P = 0.05$, although there have been more male than female births with a birth sex ratio of 1.14:1 observed and this ratio does become significant at $P = 0.1$ (Table 26).

Table 26: Regional birth sex ratio analyses - *Ceratotherium simum simum*

	Total	Males	Female	Birth sex ratio	X^2	Probability (*P*)
Africa	68	35	33	1.06:1	0.06	>0.05
Australasia	46	27	19	1.42:1	1.39	>0.05
East Asia	78	39	39	1:1	0.00	>0.05
Europe	261	135	126	1.07:1	0.31	>0.05
India	2	1	1	1:1	0.00	>0.05
Latin America	42	21	21	1:1	0.00	>0.05
Middle east	23	17	6	2.83:1	5.26	<0.05
North America	346	186	160	1.16:1	1.95	>0.05
Total	866	461	405	1.14:1	3.63	>0.05

Linear Logit regression analysis indicates that dam age does not affect the likelihood of producing a male or female offspring (Table 27). However, Quadratic Logit analysis results indicated a significant overall birth sex ratio bias towards males with a *P* value = 0.02 (Table 28).

Table 27: Birth sex ratio analysis: Linear Logit regression – *Ceratotherium simum simum*

	Column	Estimate	Standard error	Wald Stat	Probability (*P*)
Intercept	1	0.28	0.17	2.72	0.10
Age_Days	2	0.00	0.00	0.52	0.47
Scale		1.00	0.00		

Table 28: Birth sex ratio analysis: Quadratic Logit regression - *Ceratotherium simum simum*

	Column	Estimate	Standard error	Wald Stat	Probability (*P*)
Intercept	1	0.87	0.37	5.45	0.02
Age_Days	2	0.00	0.00	3.60	0.06
Age_Days^2		0.00	0.00	3.17	0.07
Scale		1.00	0.00		

4.5 Discussion

Neither *D. b. minor* nor *D. b. michaeli* global captive populations show statistically significant different birth sex ratios from a 1:1 norm, although *D. b. minor* populations did have a higher overall number of male births, and *D. b. michaeli* a higher overall number of female births. *Ceratotherium simum simum* however, did show a statistically significant male sex ratio bias in one statistical test. For all three sub-species, no statistically significant relationship was found between the age of the dam and the sex of the offspring.

Diceros bicornis minor

The *D. b. minor* captive population currently shows a male to female sex ratio of 1.1:1. As the birth sex ratio calculated from all captive births recorded in the population is 1.44:1, the current population's sex ratio is likely to be a result of higher female immigration or lower female mortality. Census data analysis supports the latter, as total numbers of founders entering the population were 35 and 36 males and females, respectively. The global birth sex ratio is close to that reported in the wild population in Hluhluwe-iMfolozi Park of 1.46:1 (Owen-Smith 1988).

A retrospective study by Dennis *et al.* (2007) reported a male birth sex ratio bias of 1.41:1 for the North American *D. b. minor* population. The present study found that this ratio has risen even further for the North American population to 1.56:1 from a sample of 46 captive births. *Diceros bicornis minor* populations in Africa and Australasia both show an inclination towards more male offspring with birth sex ratios of 1.22:1 ($n = 18$) and 1.75:1 ($n = 11$), respectively, while Europe currently shows a birth sex ratio of 1:1 but with the smallest sample size of eight births assessed. However, total birth sex ratio in this current study was found not to be significantly different from the expected 1:1 ratio when compared statistically, therefore the null (H_o) hypothesis is accepted. This is likely to be influenced by the low statistical power due to the small sample size. While it appears from the graphs that birth sex ratio is likely to become more male-biased as the dam's age, no statistical significant relationship was found between the age of the dam and the sex of the offspring, therefore the null (H_o) hypothesis that "Females of prime breeding age produce equal numbers of male and female offspring" is also accepted.

Diceros bicornis michaeli

A statistically significant overall female bias is currently observed in the *D. b. michaeli* population, with a male to female ratio calculation of 0.72:1. The present study showed that this is partly as a result of the global birth sex ratio of 0.91:1, as well as the addition of more female founders than male founders. The female sex ratio bias seen in the global data is in contrast to what has been reported for the North American *D. b. michaeli* population. In the study conducted by Dennis *et al.* (2007), a male birth sex ratio bias of 1.29:1 was reported, thus indicating that there must be a strong female-bias in one or more of the other global populations. This is indeed the case, as the regional assessment of the studbook data shows that only two out of the eight regions holding *D. b. michaeli*, experience a male birth sex ratio bias. The other region experiencing a male bias is Africa, with 8 male births compared to 4 female births. The European region, which reaches a sample size closest to that of North America, has a birth sex ratio which is significantly biased towards female offspring. Reasons for this may warrant further investigation into husbandry practises between the North American and European regions, which is beyond the scope of the present study.

In the case of *D. b. michaeli*, the current birth sex ratio observed was not statistically biased, therefore the null (H_0) hypothesis that "Birth sex ratios do not differ from the theoretical 1:1 sex ratio", is accepted. As with *D. b. minor*, the null (H_0) hypothesis that "Females of prime breeding age produce equal numbers of male and female offspring" is also accepted as no sex ratio bias was statistically detected in any particular age class.

Ceratotherium simum simum

As seen with *D. b. michaeli*, a female sex ratio bias is currently observed in the total captive population of *C. s. simum,* with a male to female ratio of 0.76:1 recorded. The female bias currently observed in the population is likely to be the result of the higher number of female founders entering the population than males – 362 compared to 245. Overall birth sex ratio, however, shows a trend towards a male bias (overall 1.14:1), but this is not statistically significant. No correlation of the sex of the offspring to the age of the dam could be found. This indicates that without additional founders entering the population and with the current higher male birth sex ratio noted, overall population sex ratio may move more toward a 1:1 sex ratio as new offspring are born. Out of 8 regions assessed, five showed higher male births and three produced equal birth sex ratios. The trend towards higher male births observed in captivity is far lower than that reported in the wild, where a birth sex ratio of 1.73:1 was reported.

No statistically significant birth sex ratio bias is observed in *C. s. simum* with linear logit analysis, however, quadratic analysis does indicate a significant male biased birth sex ratio. This may therefore be a limiting factor in the overall growth of this population, but is not likely to be a high concern, as this subspecies currently exceeds its target population size set out in the GCAP (1972) meeting. Excess males may at this time be managed by removing them from the population without significant risk to the global target population numbers. The null (H_0) hypothesis that "Birth sex ratios do not differ from the theoretical 1:1 sex ratio" is therefore rejected. Once again, the null (H_0) hypothesis that "Females of prime breeding age will produce equal numbers of male and female offspring" is accepted, as no statistically significant correlation could be found between a females' age and the sex of her offspring.

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CHAPTER 5

GENERAL DISCUSSION AND RECOMMENDATIONS

The present study assessed demographic parameters for all three subspecies of managed African rhinoceros captive populations found in zoological gardens at a global level. Data collated between 2001 and 2010 were assessed for comparable average population growth rates. This study showed that the global populations of *Diceros bicornis minor* and *Ceratotherium simum simum* are currently in decline, with an average population growth rate per annum over the past ten years of 0.98 and 0.99, respectively. *Diceros bicornis michaeli* is faring better, with a global population growth rate of 1.02. While the two black rhinoceros subspecies have not had any additional founder supplementation since 1989 and 1993 for *D. b. minor* and *D. b. michaeli*, respectively, *C. s. simum* has had continual, albeit minimal founder supplementation since 1997.

Sensitivity analysis and benchmarking to *in situ* populations clearly shows that fecundity, rather than mortality, is the main factor limiting the growth rate with fecundity rates well below those reported for the *in situ* population. While several studies have highlighted physiological reasons for low fecundity in captive rhinoceros (Patton *et al*. 1999; Hermes *et al*. 2002, 2004, 2005, 2006), it is unclear if basic management practices, e.g. under which circumstances success has been achieved, have been fully documented on a global level. Compounding the risk of extinction in both *D. b. minor* and *C. s. simum* is that neither subspecies have stable age distributions, further contributing to demographic instability. Factors that make the situation for *C. s. simum* less precarious than for *D. b. minor* are: a) large population size, b) the cause for the age distribution not to be stable is a large aging founder population that is making very little contribution to recruitment, and c) current total population size is far larger than the target population size set out for the captive population.

Based on 1995 International studbook data, both Schwartzenberger *et al.* (1999) and Swaisgood *et al.* (2006), raised concern that reproductive performance of the F_1 generation of *C. s. simum* was not as good as the F_0 generation thereby affecting global population sustainability. This study indicates that the *C. s. simum* female captive-born population is still not achieving the population growth rates achieved by the founder population, with a life table λ of 0.971 for the $F_{\geq 1}$ as opposed to 0.994 achieved by the founder females. Indications are that the mortality rates seen in the first 5 years of life in captive-born females may play a large role in this negative population growth rate. However, on a positive side, the current study shows that 32% of breeding age F_1 females have now bred compared to 37% of founder females, a stark improvement on the 8% of F_1 females to breed reported by Schwartzenberger *et al.* (1999). *Diceros bicornis minor* is the main population of concern, as while the current founder population growth rate appears to be stationary with a calculated life table λ of 0.999, the captive-born population is displaying a negative growth rate of -3% ($\lambda = 0.971$) per annum and lifetime reproduction rate for the $F_{\geq 1}$ is 38% less than that observed for the founder population. Analyses conducted on *D. b. minor* indicated that an 80% increase in current fecundity rate is needed before a positive growth rate will be observed; and in order to reach the 50-year target population size set out in the 1992 GCAP meeting (Foose & Wiese 2006), the fecundity rate would need to increase by 170%. This is theoretically possible, as changing m_x rates to rates calculated by the median figure of inter-birth intervals currently seen in the captive population resulted in a 276% increase in fecundity. While no difference was found between the inter-birth intervals of the founder *versus* the captive-born females for all three sub-species, the data for both *D. b. minor* and *C. s. simum* indicate that the number of captive-born females of breeding age that have produced young and average number of young produced, is far lower than the numbers seen in founder females. *Diceros bicornis michaeli* is the most stable population out of all of the three rhinoceros subspecies under investigation. Not only have more captive-born females reproduced proportionally to their founder counterparts, but the female population growth rate is higher than that of the founders.

Birth sex ratios were shown not to be significantly different from parity for either *D. b. minor* and *D. b. michaeli*, although a ♂♂:♀♀ global birth sex ratio of 1.44:1 for *D. b. minor* and 0.91:1 for *D. b. michaeli* are observed. However, with a birth sex ratio of 1.14:1, a quadratic logit regression statistical test used to analyse the *C. s. simum* data does indicate a statistically significant male bias. No significant link between maternal age and sex of offspring could be found in all three subspecies**.** Other important results to note are that the North American *D. b. michaeli* population is the only population with a reasonable sample size that is experiencing a male birth sex ratio bias.

The results of this study show that the 50-year and 100-year targets set at the GCAP workshop in 1992 are achievable (Foose & Wiese 2006). *Diceros bicornis michaeli* has in fact exceeded these targets, and the challenge now will be to keep reproduction in check if no alternative accommodation can be found for surplus animals. *Ceratotherium simum simum* is in a similar situation, with current numbers exceeding global targets set, but with the current decline, numbers are reducing fast to the required population size. Care will have to be taken, however, to increase fecundity once the population target is reached by approximately 30% to achieve a stationary population. Lastly, *D. b. minor* will only be able to achieve the target population sizes with a significant increase in fecundity rate. While this is theoretically possible, strategic management plans will have to be put into practice that maximise fecundity by allowing as many females as possible to breed with minimal inter-birth intervals. This may require that an evaluation be carried out on all potential breeders to check for reproductive viability. If an increase in female fecundity of around 170% is not possible, the target population size will not be met in time without supplementation.

While this study focussed on a global overview of the captive populations of *D. b. minor, D. b. michaeli* and *C. s. simum,* in depth comparisons of individual regional populations will provide insights into how different management systems impact on demographic factors, as is seen in the differing birth sex ratios for *D. b. michaeli.* While husbandry techniques often differ not only between regions, but between institutions, it would be good practice for the regional associations to identify institutions with the highest breeding success rate, and to try and mimic the conditions in these in the rest of their member institutions.

Based on the outcomes of this study, the following actions are recommended:

- Prioritized research and knowledge sharing of breeding management practices across individual institutions, particularly where breeding success has been achieved.
- In depth inter-regional comparison of management systems to determine how these impact on demographic factors.
- In the case of *D. b. minor*, strategic management plans to be put into practice that maximise fecundity by allowing as many females as possible to breed with minimal inter-birth intervals.

- Further investigation for *D. b. michaeli* and *C. s. simum* populations to determine if lower $F_{\geq 1}$ than F_0 fecundity is an effect of: a) less time of the global captive population spent to date in captivity than the founder population thereby skewing lifetime reproductive success, b) less opportunity provided by holding institutions for $F_{\geq 1}$ generations to breed, possibly because of inbreeding or space concerns, or c) as Swaigood *et al*. (2006) suggested, a negative causal factor during early development of captive-born individuals.
- Research into the husbandry practice of *D. b. michaeli* in the North American population compared to the other regional populations to provide insight into possible causes for male birth sex ratio bias in this region compared to other regions.
- A global population management plan for *D. b. minor.* This subspecies is currently the subspecies most at risk, and therefore a formalized Global Species Management Plan (GSMP) under the auspices of WAZA will ensure a unified approach to this populations' management, and therefore an improved chance of captive population survival (WAZA 2013).

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