






Historical development of the survivorship of zoo rhinoceroses—A comparative historical analysis

Anita Wittwer¹ | Marco Roller²  | Dennis W. H. Müller³  |
Mads F. Bertelsen⁴  | Laurie Bingaman Lackey⁵  | Beatrice Steck⁶ |
Rebecca Biddle⁷ | Lars Versteeg⁸ | Marcus Clauss¹ 

¹Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich, Switzerland

²Zoological Garden Karlsruhe, Karlsruhe, Germany

³Zoological Garden Halle (Saale), Halle, Germany

⁴Copenhagen Zoo, Frederiksberg, Denmark

⁵1230 Oakland Street, Hendersonville, North Carolina, USA

⁶Zoological Garden of Basel, Basel, Switzerland

⁷Twycross Zoo—East Midland Zoological Society, Norton Grange, Warwickshire, UK

⁸Safaripark Beekse Bergen, Hilvarenbeek, The Netherlands

Correspondence

Marcus Clauss, Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland.
Email: mclauss@vetclinics.uzh.ch

Abstract

Zoo animal husbandry is a skill that should be developing constantly. In theory, this should lead to an improvement of zoo animal survivorship over time. Additionally, it has been suggested that species that are at a comparatively higher risk of extinction in their natural habitats (in situ) might also be more difficult to keep under zoo conditions (ex situ). Here, we assessed these questions for three zoo-managed rhinoceros species with different extinction risk status allocated by the IUCN: the “critically endangered” black rhino (*Diceros bicornis*), the “vulnerable” greater one-horned (GOH) rhino (*Rhinoceros unicornis*), and the “near threatened” white rhino (*Ceratotherium simum*). Comparing zoo animals ≥ 1 year of age, the black rhino had the lowest and the white rhino the highest survivorship, in congruence with their extinction risk status. Historically, the survivorship of both black and white rhino in zoos improved significantly over time, whereas that of GOH rhino stagnated. Juvenile mortality was generally low and decreased even further in black and white rhinos over time. Together with the development of population pyramids, this shows increasing competence of the global zoo community to sustain all three species. Compared to the continuously expanding zoo population of GOH and white rhinos, the zoo-managed black rhino population has stagnated in numbers in recent years. Zoos do not only contribute to conservation by propagating ex situ populations, but also by increasing species-specific husbandry skills. We recommend detailed research to understand specific factors responsible for the stagnation but also the general improvement of survivorship of zoo-managed rhinos.

KEYWORDS

husbandry, Perissodactyla, progress, survival, zoo

1 | INTRODUCTION

Historically, rhinoceroses (“rhinos”) were a speciose group, with more than 50 genera recognized in the fossil record (Geraads, 2011; Prothero, 2005; Wang et al., 2013). Currently, the group comprises only four genera (*Ceratotherium*, *Dicerorhinus*, *Diceros*, *Rhinoceros*) with five species, which show a generally low level of genetic diversity that has been exacerbated recently, most likely due to man-made declines of available habitat and population sizes (Liu et al., 2021). The five species range in terms of conservation status from “critically endangered” (Javan rhino *Rhinoceros sondaicus*, Sumatran rhino *Dicerorhinus sumatrensis*, black rhino *Diceros bicornis*) over “vulnerable” (greater one-horned [GOH] rhino *Rhinoceros unicornis*) to “near threatened” (white rhino *Ceratotherium simum*) (IUCN, 2021).

The main threats are poaching and habitat loss; additionally, comparatively slow reproduction and long gestation length for their body size (Clauss et al., 2019) is a biological constraint for the recovery of populations. Reduced habitats may particularly affect solitary species, and the social nature of the white rhino (Owen-Smith, 1974)—in contrast to the solitary nature of the other species (Hubback, 1939; Kandel & Jhala, 2008; Mukinya, 1973; Sody, 1959)—may be a contributing factor to their least threatened status; on the other hand, a higher degree of sociality may make a species more vulnerable to poaching.

Rhinos are a prime example for conservation efforts. Highly professionally operating NGOs dedicated to rhino conservation exist, such as the International Rhino Foundation (www.rhinos.org) and Save the Rhino International (www.savetherhino.org). Conservation efforts range from attempts to rescue a basically extinct (sub)species, the Northern white rhino (*Ceratotherium simum cottoni*), via cryopreservation and in vitro reproduction (Biasseti et al., 2022; Callender, 2021; Ryder et al., 2020), to in situ breeding centers for the Sumatran rhino (*Dicerorhinus sumatrensis*) (Zafir et al., 2011), and, more generally, in situ protection programs for all species. Zoos, while maintaining these animals, generate awareness for the situation of rhinos and finances donated to in situ protection efforts, and also act as locations where rhino husbandry knowledge and skills are maintained and increased.

Black, GOH and white rhinos are kept in zoos around the world today. Managing rhinos in human care is challenging from a logistical point of view, especially due to the substantial amounts of space and infrastructure required (Miller & Buss, 2003). In the European Association of Zoos and Aquaria, for example, for black rhino individuals, outside enclosures of at least 1000 m² per animals (with an option to connect the enclosures for a male and a female) and additional inside enclosures of at least 60 m² are recommended in climates that prohibit year-round access to the outside (Pilgrim & Biddle, 2020). For GOH rhinos, indoor pools are considered mandatory (von Houwald, 2015). For white rhinos, a minimum group of one male and three females is recommended

with at least 10,000 m² of outside enclosure and facilities to ensure that the male is not in constant contact with the females, and 45 m² indoor enclosures for a mother and calf (Versteegen, 2018). Hence, expanding the number of institutions that sustain a managed rhino population is not easily achieved.

The three rhino species differ in several aspects of zoo husbandry. Whereas white and GOH rhinos are considered grazers and are thus comparatively easy to manage in terms of feeding, the black rhino is a strict browser (Clauss & Hatt, 2006). Due to the logistical challenges of providing non-grass forage in large quantities (Clauss & Dierenfeld, 2008), this alone makes their husbandry more complex; for example, the deviation in dental wear in zoos from the typical state in the wild is most pronounced in black rhinos (Taylor et al., 2014). Aggression towards conspecifics, e.g., during mating, can occur in all species, but is particularly dangerous in GOH, because in contrast to white and black rhinos, GOH have incisors and can inflict serious wounds (Miller & Buss, 2003). Even though difficult to quantify objectively, black rhinos appear, as a species, more nervous and more easily stressed than GOH or white rhinos (Pilgrim & Biddle, 2020). Finally, while no particular diseases appear typical for white rhinos (Versteegen, 2018), and for GOH rhinos only foot problems appear as a major concern across facilities (von Houwald, 2016), there is a suite of specific diseases affecting only black rhinos (Dennis et al., 2007; Miller & Buss, 2003; Schook et al., 2015) that make their management even more challenging, such as Idiopathic Haemorrhagic Vasculopathy Syndrome, Haemolytic Anaemia, Leucoencephalomalacia, and Iron Overload Disorder.

Here, we evaluate birth and death data for zoo-kept black, GOH and white rhinos to test whether there is a difference in age-related mortality between the species (that would indicate greater husbandry challenges in BR), and to test whether there is directional development in the juvenile mortality (reduction) and adult longevity (increase) in zoos over time. Because similar data for wild populations are not available for rhinos (Tidière et al., 2016), we use reports on rhino populations in natural habitats to compare their age structure with that of the zoo populations, discussing the effect of changes in husbandry success on these structures.

2 | MATERIALS AND METHODS

Our evaluation followed the principles outlined by Roller et al., (2021) and Scherer et al., (2022). We obtained global records for three zoo-kept rhino species from Species360 (ZIMS for Husbandry), an online database platform in current use by more than 1200 zoos worldwide (and also including historic data from a further 600 zoos) to manage their animal data, with known dates of birth and death, from which the subsequent data were calculated (Species360 Research Data Agreement # 2019-Q3-RR3). The reporting of animal data into this repository is

mandatory for zoos accredited by the European Association of Zoos and Aquaria (EAZA) but not for others such as members of the American Association of Zoos and Aquaria (AZA), and providing historical data in the database is not required for any region. It must be noted that while it is very unlikely that adult animals alive at member zoos are not entered into the system due to their visibility, there is no independent control of whether newborns are consistently entered. In the experience of one of the co-authors (LBL), the practice of not entering newborn animals until they survived to about 1 month of age was more common in earlier decades of the last century than it is now, especially when entering historical data into the database. This would result in an underestimation of positive developments in neonate mortality. The dataset that we worked with did not contain indications of the cause of death or the location of zoological institutions, but did include information on the sex and whether the animal was born in the wild or at a zoo. We did not know ages at which wildborn animals were imported; therefore, these animals were excluded from the assessment of juvenile mortality (up to 1 year of age). Note that birth dates given in the dataset for wildborn animals were typically estimated at the time of import, and their reliability cannot be ascertained.

For all three rhino species investigated, we assumed 50 years to be the maximum lifespan (de Magalhães & Costa, 2009); thus, no corrections for species-specific maximum lifespans were necessary. Data were available from 1905 onwards. The final dataset included 716 black rhinos, 433 GOH rhinos, and 1422 white rhinos.

The dataset was used to depict population pyramids as of the 31st of December for 1969, 1979, 1989, 1999, 2009, and 2019. For comparison, data for free-ranging populations was extracted to also depict population pyramids (Ferreira et al., 2011; Hitchins & Anderson, 1983; Mukinya, 1973; Owen-Smith, 1988; Pienaar, 1994; Subedi et al., 2017). Due to the lesser age resolution in studies on free-ranging populations, where e.g., an age range of 5–10 years is summarized by a single number of animals, these pyramids were constructed by distributing such a number of animals equally across the yearly age classes. To indicate this uncertainty of the final shape, and to prevent that these graphs are taken as robust data, these construed pyramids are marked by a question mark. For each population pyramid, we also calculated the ratio of animals ≥ 7 years of age to younger animals.

For statistical analyses, the dataset was pruned in different ways to yield only animals born from 1960 onwards, animals that survived to at least 1 year or at least 5 years of age, or only zoo-born animals. The endpoint of survival was set to the end of March 2022. Analyses were performed in R (R Core Team, 2017) in the survival package (Therneau, 2022), using the Cox proportional hazard analysis, with the age of an individual and “event” (death or living; the latter is treated as right-censored). In these analyses, a coefficient < 1 (i.e., the 95% confidence interval excludes 1) indicates that the group in question has a lower overall mortality

risk than the reference group, or that there is a mortality-reducing effect of a continuous variable. Proportionality of hazards was tested either by comparing birth cohorts (for the periods of 1960–1979, 1980–1999, 2000–2020) as discrete categories or the year of birth as a continuous variable. The approach using discrete categories is considered less informative and was mainly chosen to facilitate visualization. The approach using the year of birth as a continuous variable is considered the most appropriate. The significance level was set to 0.05, and p values between .05 and .09 were considered trends. The proportional hazards are reported with their 95% confidence interval.

Because the interpretation of these statistical results is, in our own experience, not intuitive, we provide example narrative interpretations of these tables under each table in a footnote. It must be noted that the statistical approach we chose does not allow the extrapolation of “longevity” for different cohorts (such as cohorts of which a large part of the animals are still alive). Such extrapolations would require other methods (e.g., Aburto et al., 2020; Colchero et al., 2016). Survivorship analyses can generate data such as the “median life expectancy” if, of the cohort included in the analysis, 50% of animals have already died. For a description of the shape of the survivorship curves, we follow Pearl & Miner, (1935) and Deevey, (1947): Survivorship curves for large precocial mammals with reduced exposure to predation (such as rhinos in zoos) should have a convex or “type I” shape; a straight-line pattern in survivorship is called “type II,” whereas a concave or “type III” shape would be representative for animals with a high early-life mortality, which would not be expected for large precocial mammals.

3 | RESULTS

At the early onset of rhino zoo husbandry, the population pyramids (Figure 1) did not have the typical shape, with the large number of newborn and juvenile animals typical of free-ranging populations (Figure 2). In the black rhino, such a pattern was achieved in the 1990s, but the most current pyramid shows a relatively even distribution of animals across age classes. For the GOH rhino, a pyramid shape has emerged in more recent times. The data for the white rhinos bespeaks the lack of breeding in this species, with a high number of (imported) adults in prime breeding age in the 1970s, yet very few offspring. Subsequently, breeding increased, and currently the white rhino is the species with the clearest pyramid shape with a larger number of juvenile animals (Figure 1). Between 1969 and 2019, the number of zoo-kept black rhinos increased from 109 to 209 (192%), that of GOH rhinos from 33 to 178 (539%), and that of white rhinos from 204 to 657 (322%); these increases were due to both, reproduction and import of animals. Between 1999 and 2019, there was a stagnation in zoo-kept black rhino numbers (from 194 to 202, 104%) in contrast to GOH rhinos (from 112 to 178, 159%) and white rhinos (490 to 657, 134%). When also counting the minimum of 21 black rhinos that were sent

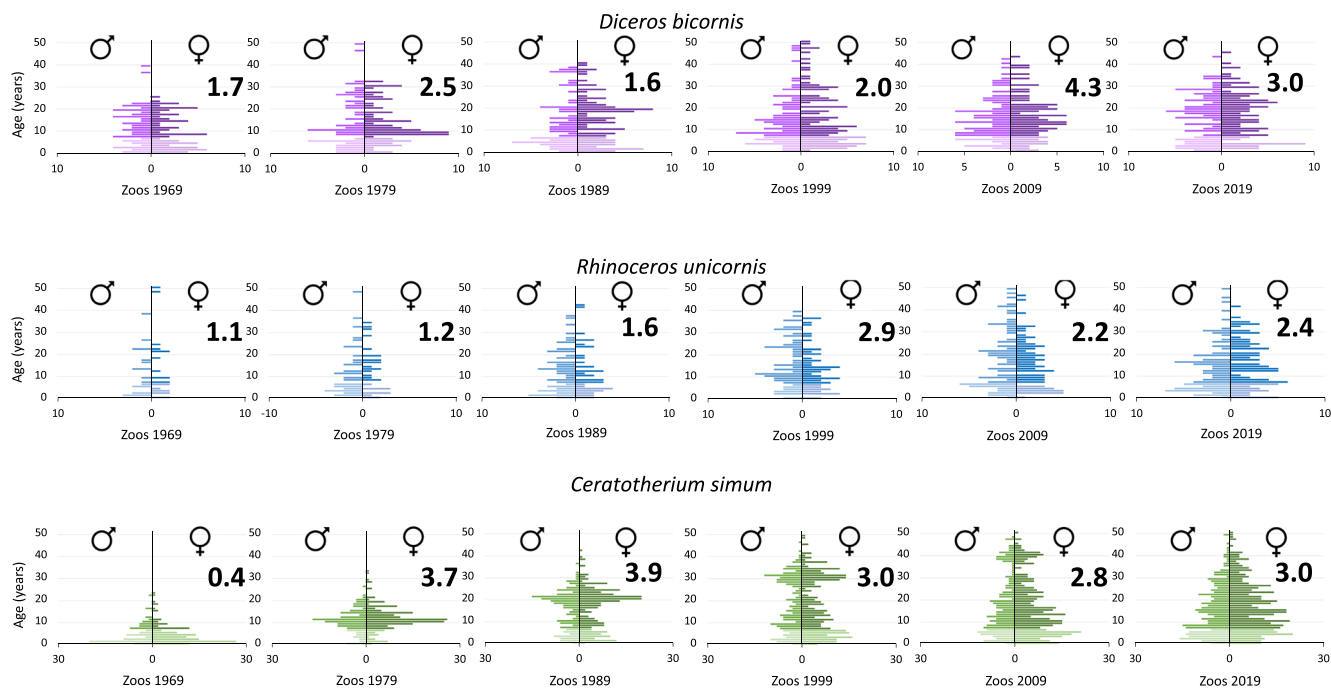


FIGURE 1 Global population “pyramids” for zoo-managed rhinoceros species in different decades. The data represent the number of animals alive on December 31 of the respective year. Males on the left side, females on the right side. The large bold number represents the ratio of adult (≥ 7 years) to subadult and juvenile animals (< 7 years). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/zoo.21793)]

from EEP zoos to African countries during this period (R. Biddle, pers. comm.), the global black rhino zoo population increased by 115%. The current adult-to-young ratios in all three species are comparatively high in zoos (Figure 1) as compared to values described for free-ranging populations (Figure 2).

By comparison, population pyramids reconstructed for free-ranging populations indicated a distinct decrease from juvenile to adult animals, although the uncertainty how the number of adult animals was distributed across ages in years of life does not rule out a more gradual decrease (Figure 2).

When comparing the survivorship of the three rhino species, the black rhino has the least survivorship with a relatively straight, type II pattern; the GOH rhino has an intermediate position but a concave, type I pattern; and the white rhino has the best survivorship with a concave, type I pattern (Figure 3 and Table 1). For the whole cohort from 1905 until 2020, this translates into a median life expectancy of about 21 years for black rhinos, 30 years for GOH rhinos and 35 years for white rhinos that reached their first year of life. It should be noted that this median life expectancy does not apply for most recent cohorts. The general difference between the species is statistically significant, irrespective of whether animals born since 1905 or only animals since 1960 are included in the analysis, or whether the analysis includes all animals or only those that reached their first year of life (Table 1). However, whether all animals or only those ≥ 1 year of age were included had an effect on whether a general improvement in survivorship was detected in this comparative analysis: Whereas no such improvement was evident for the dataset including all animals, birth year had a significant, negative effect in

the analysis including only animals ≥ 1 year of age, indicating that with advancing birth year, survivorship improved (Table 1). When assessing the survivorship of only zoo-born animals up to their first year of life, there was also an improvement over time; for the period of 1960–today, no difference between the species was evident, but for 1980–today, the white rhino had an increased juvenile survivorship compared to the black rhino (Table 1).

When assessing the black rhino alone, there was a distinct improvement in survivorship between 1960 and today, irrespective of whether this was assessed using birth year as a continuous variable, or by splitting the data into three 20-year-cohorts (Table 2 and Figure 4a). In particular, the survivorship curve changed from a rather straight, type II pattern in the 1960–79 cohort to a convex, type I pattern in the most recent cohort (Figure 4a). Survivorship was lower in males compared to females (Figure 5a), and lower in zoo-born than in wild-born individuals (Figure 6a). However, the effect of zoo- versus wild-born was less distinct when analysing only animals ≥ 5 years of age, indicating that this effect could possibly be an artefact due to the importation of comparatively old wild-born individuals (Figure 6d). Among zoo-born animals, 1st year survivorship did not differ between the sexes, and did not change over time when assessed from 1960 till today, but showed a significant increase from 1980 till today (Table 2). The day 0, day 30 and first year mortality was 8.9%, 13.6%, and 17% for animals born between 1980 and 1999, and 11%, 14.1%, and 16.9% for animals born between 2000 and 2021.

When assessing the GOH rhino alone, there was no change in survivorship over time (Figure 4b), and no difference in survivorship

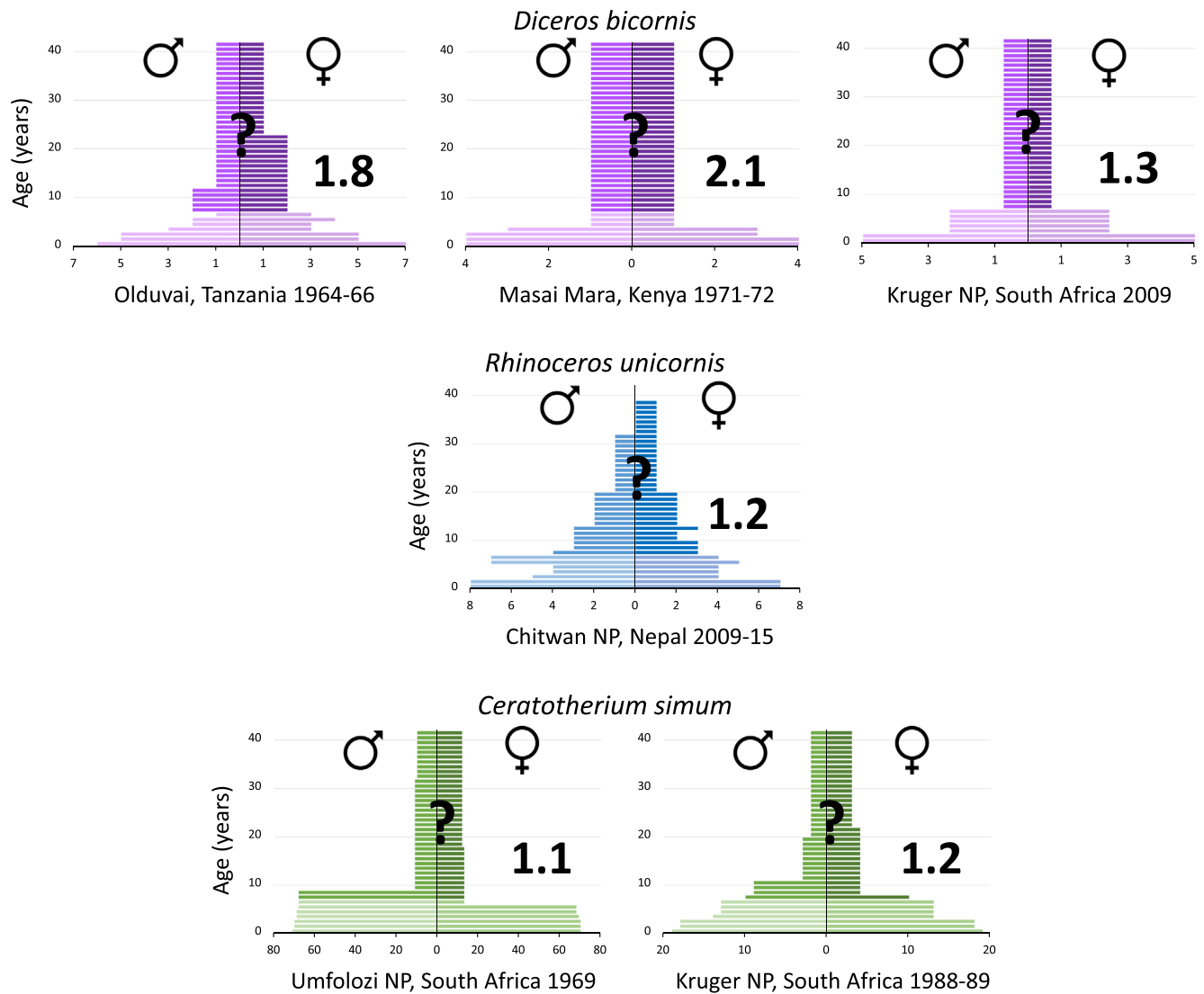


FIGURE 2 Population “pyramids” for free-ranging rhinoceros populations from the literature. Black rhino: Olduvai, Tanzania (Goddard, 1967), Masai Mara, Kenya (Mukinya, 1973), Kruger NP, South Africa (Ferreira et al., 2011); greater one-horned rhino: Chitwan NP, Nepal (Subedi et al., 2017); white rhino: Umfolozi NP, South Africa (Owen-Smith, 1988), Kruger NP, South Africa (Pienaar, 1994). The question mark reminds that data from the literature that referred to age groups that spanned several years of age were distributed equally between the years covered; therefore, the uncertainty of the distribution. The large bold number represents the ratio of adult (≥ 7 years) to subadult and juvenile animals (< 7 years), which is subject to the uncertainty in the original data around this cutoff. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

between the sexes (Figure 5b) or between zoo-born and wild-born animals (Figure 6b and 6e, Table 3). In the animals ≥ 5 years of age, there was a trend for a higher survivorship in females. Among zoo-born animals, 1st year survivorship did not differ between the sexes, and did not change over time, although there was a statistical trend for a peak in the 1980–1999 period (Table 3). The day 0, day 30 and first year mortality was 17.5%, 21.9%, and 30.7% for animals born between 1980 and 1999, and 13.5%, 17.4%, and 19.6% for animals born between 2000 and 2021.

When assessing the white rhino alone, there was a distinct improvement in survivorship between 1960 and today (Figure 4c), irrespective of whether this was assessed using birth year as a continuous variable, or by splitting the data into three 20-year-

cohorts (Table 4). Survivorship did not differ between the sexes (Figure 5c). Survivorship was significantly lower in zoo-born than in wild-born individuals for all animals ≥ 1 year of age (Figure 6c). However, this latter effect of zoo- versus wild-born was no longer significant when analysing only animals ≥ 5 years of age (Figure 6f), indicating that this effect could possibly be an artefact due to the importation of comparatively old wild-born individuals of an age group between 1 and 5 years. Among zoo-born animals, 1st year survivorship did not differ between the sexes, but improved significantly over time, especially in the 2000–2021 period (Table 4). The day 0, day 30 and first year mortality was 7.7%, 13.5%, and 16.5% for animals born between 1980 and 1999, and 8.9%, 11.25%, and 12.9% for animals born between 2000 and 2021.

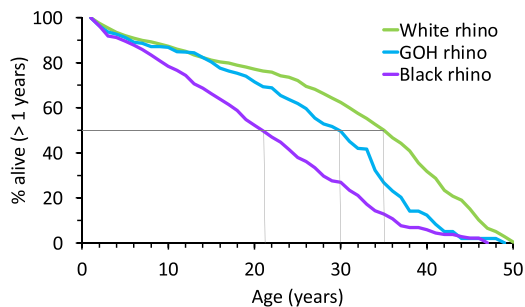


FIGURE 3 Survivorship of zoo-kept black (*Diceros bicornis*, critically endangered), greater one-horned (*Rhinoceros unicornis*, vulnerable) and white (*Ceratotherium simum*, near threatened) rhinos from 1905 until 2020 in animals ≥ 1 year of age. The thin gray line notes the median life expectancy (black rhino: 21.2 years, GOH rhino 30 years, white rhino 35 years). Note that survivorship decreases in correspondence to the IUCN threat categories. For statistics, see Table 1. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

4 | DISCUSSION

The results of this study demonstrate distinct differences in survivorship between the main three rhino species managed in those zoos that contribute data to Species360. Mason et al., (2013) suggested that species more threatened by extinction in their natural habitats might also be more difficult to maintain under managed care. Thus, zoo-kept rhinos might be an example illustrating the theory that extinction risk level in the wild and ease of management in human care may share a common biological background (Mason et al., 2013), with the most difficult of the three zoo-kept species being the most vulnerable in terms of natural populations. The most threatened species, the black rhino, has the lowest zoo survivorship, and the least threatened species, the white rhino, has the highest zoo survivorship. Evidently, to ascertain this relationship as a rule, a larger number of species would have to be tested, and it needs to be remembered that the hypothesis does not claim that all species difficult to maintain in zoos are also threatened in the wild. Whether the trend that the number of black rhinos kept in zoos increased distinctively less than that of the other species is due to deliberate decisions by zoos to focus on the easier-to-keep rhino species remains to be investigated. Regardless of whether the hypothesis of Mason et al., (2013) is considered a general rule or not, the example of the black rhino points out a dilemma, where zoos might have to choose between keeping species of higher conservation value or species easier to maintain.

The results demonstrate an improvement in survivorship over time, particularly in animals ≥ 1 year of age, suggesting a certain degree of improvement of husbandry success. The black and the white rhino thus join the list of species for which a historical improvement of husbandry success is detectable (Haverkamp et al., 2019; Jaakkola & Willis, 2019; Jett & Ventre, 2015; Roller et al., 2021; Scherer et al., 2022; Wich et al., 2009). As stated previously, this development is to be expected and should not induce complacency (Scherer et al., 2022).

Some limitations of the present study need to be mentioned. While the demographic data available allows survivorship calculations, it does not contain information on the causes of death, and hence reasons for the improvement of black and white rhino husbandry success and the stagnation in GOH rhinos must remain speculative. For the black rhino, a comparison of the evaluation of different sets of necropsy reports over the years suggests that several diseases, such as hemolytic anemia, that were once considered important in the species, have recently occurred less frequently (Radeke-Auer et al., 2023). This might indicate a higher success in the management of particularly longevity-reducing diseases.

Another limitation is that the reliability of data on newborn mortality cannot be estimated; as mentioned in the Methods section, not all zoos have followed the practice of reporting every birth, especially if the neonate died on the same day. Notably, the same uncertainty must be assumed for observations of free-ranging populations (see below). The difference in survivorship between zoo-born and wild-born white rhinos, evident when assessing all animals ≥ 1 year of age but no longer discernible when assessing animals ≥ 5 years of age (Figure 6c and 6f), suggests that animals older than 1 year of age were imported from the wild. For example, an animal imported at the age of 4 will automatically be counted as “alive” at 0–4 years of age due to its reconstructed birth date, but its cohort mates that died at these ages in the wild were evidently not imported, not known, and are therefore not considered in survivorship analyses. Because information on the age of importation was not available to us, this effect could not be controlled for but only gauged by assessing survivorship repeatedly, using different age cut-offs.

Neonate mortality in zoos can be considered moderate. Owen-Smith (1988) summarizes the literature as neonatal losses for black rhinos at two locations of 9%–16% (with a substantially higher mortality due to hyena predation at another location), those for white rhinos at 3.5%–8.3%, and those for GOH rhinos at 5.6%. For free-ranging black rhinos, first-year mortalities of 20% have been reported (Brodie et al., 2011). For GOH rhinos, Subedi et al., (2017) reported a mortality of dependent young of 13%. Owen-Smith, (1988) discusses the problems of quantifying neonate mortality because detecting each birth reliably is a prerogative, even if the resulting neonate died on the same day. Given this difficulty, the neonate mortality derived from the data used in the present study—with the exception of the peak for GOH rhinos in 1980–1999—does not appear excessive or remarkable.

The historical population pyramids of zoo-managed rhinos indicate first a development from a barrel-shape (most likely consisting of animals imported from the wild) towards a structure typical for a breeding population with a broader basis of juvenile animals (Figure 1). It must be kept in mind that especially at the beginning of zoo husbandry, reproduction need not have automatically been an aim. Over the initial decades, breeding increased, also supported by increased husbandry skills. Nevertheless, low reproductive rates have more recently been mentioned as an issue of concern for the black rhino (Edwards et al., 2015). Assuming a

TABLE 1 Comparative survivorship analyses (Cox proportional hazards) for black rhino (*Diceros bicornis*), greater one-horned rhino (*Rhinoceros unicornis*) and white rhino (*Ceratotherium simum*) in zoos worldwide.

Model		Coef (95% CI)	z	p
All animals				
Born 1905–2021				
Reference: <i>D. bicornis</i> (n = 716)	<i>R. unicornis</i> (n = 433)	0.86 (0.74, 1.00)	−3.47	.047
	<i>C. simum</i> (n = 1422)	0.49 (0.44, 0.55)	−12.18	<.001
	Birth year	0.998 (0.995, 1.001)	−1.25	.211
Born 1960–2021				
Reference: <i>D. bicornis</i> (n = 612)	<i>R. unicornis</i> (n = 411)	0.87 (0.74, 1.02)	−1.74	.083
	<i>C. simum</i> (n = 1400)	0.49 (0.43, 0.56)	−11.12	<.001
	Birth year	0.997 (0.993, 1.001)	−1.62	.106
All animals ≥1 year of age				
Born 1905–2020				
Reference: <i>D. bicornis</i> (n = 602)	<i>R. unicornis</i> (n = 332) ^a	0.72 (0.60, 0.87)	−3.47	<.001
	<i>C. simum</i> (n = 1210) ^a	0.43 (0.38, 0.49)	−12.18	<.001
	Birth year ^a	0.990 (0.987, 0.994)	−5.11	<.001
Born 1960–2020				
Reference: <i>D. bicornis</i> (n = 503)	<i>R. unicornis</i> (n = 310)	0.71 (0.58, 0.87)	−3.35	<.001
	<i>C. simum</i> (n = 1188)	0.41 (0.35, 0.47)	−11.94	<.001
	Birth year	0.988 (0.983, 0.993)	−4.47	<.001
Zooborn animals: survival till the first year				
Born 1960–2021				
Reference: <i>D. bicornis</i> (n = 492)	<i>R. unicornis</i> (n = 340)	1.24 (0.92, 1.69)	1.41	.159
	<i>C. simum</i> (n = 934)	1.02 (0.79, 1.32)	0.17	.866
	Birth year	0.988 (0.981, 0.995)	−3.51	<.001
Born 1980–2021				
Reference: <i>D. bicornis</i> (n = 391)	<i>R. unicornis</i> (n = 300)	1.05 (0.84, 1.31)	0.42	.672
	<i>C. simum</i> (n = 834)	0.73 (0.60, 0.87)	−3.44	<.001
	Birth year	0.981 (0.973, 0.988)	−4.99	<.001

Abbreviation: CI, confidence interval.

^aExample interpretation: compared to the reference species *D. bicornis*, both *R. unicornis* and *C. simum* have a significantly ($p < .001$) lower (both 0.72 and 0.43 are <1, and the confidence intervals do not include 1) mortality, i.e. a higher survivorship; because “birth year” has a significant ($p < .001$) factor that is lower than 1 (0.990, and the confidence interval does not include 1), there is a significantly lower mortality (=higher survivorship) for animals of higher birth year (=more recently born).

saturation of available holding space, and longer occupation of this space by individual animals due to the documented improvements in survivorship, one might expect a gradual shift again to comparatively barrel-shaped population pyramids. This is because in the absence of more holding space, studbook coordinators may impose breeding restrictions. In recent years, a deviation is thus evident from the pattern typical of free-ranging populations—a larger basis of neonate and juvenile animals—, also evident in different ratios of adult-to-subadult/juvenile animals (Figures 1 and 2). The pyramids in Figure 1

provide some evidence of the attempts to keep the numbers of newborns at a comparatively low level.

Whereas a careful prolongation of inter-birth intervals, as specifically recommended for the GOH rhino for this reason, does not appear problematic (Pluháček et al., 2017), there is evidence that a longer cessation of breeding activity can be detrimental to female health (Hermes et al., 2006, 2014). The “use it or lose it” adage (Penfold et al., 2014), suggesting that reproductive potential must be used relatively consistently in order not to be lost, applies to rhinos as

TABLE 2 Survivorship analyses (Cox proportional hazards) for black rhino (*Diceros bicornis*) in zoos worldwide for different age groups and cohorts.

Model		Coef (95% CI)	z	p
Diceros bicornis ≥1 year of age (n = 503)				
Born 1960–2020 reference:				
Females (n = 262)	Males (n = 241)	1.24 (0.99, 1.56)	1.88	.061
Wildborn (n = 115)	Zooborn (n = 388)	1.53 (1.16, 2.02)	3.01	.003
	Birth year	0.968 (0.958, 0.978)	-6.31	<.001
Born 1960–2020 reference:				
Females (n = 262)	Males (n = 241)	1.22 (0.97, 1.53)	1.72	.086
Wildborn (n = 115)	Zooborn (n = 388)	1.33 (1.02, 1.75)	2.12	.034
Born 1960–1979 (n = 155)	Born 1980–1999 (n = 195)	0.64 (0.50, 0.83)	-3.38	<.001
	Born 2000–2020 (n = 153)	0.25 (0.15, 0.41)	-5.31	<.001
Diceros bicornis ≥5 years of age (n = 422)				
Born 1960–2020 reference:				
Females (n = 220)	Males (n = 202) ^a	1.38 (1.08, 1.76)	2.54	.011
Wildborn (n = 106)	Zooborn (n = 316) ^a	1.42 (1.05, 1.92)	2.30	.021
	Birth year ^a	0.967 (0.955, 0.978)	-5.58	<.001
Born 1960–2020 reference:				
Females (n = 220)	Males (n = 202)	1.34 (1.05, 1.72)	2.35	.019
Wildborn (n = 106)	Zooborn (n = 316)	1.24 (0.93, 1.66)	1.47	.141
Born 1960–1979 (n = 136)	Born 1980–1999 (n = 171) ^a	0.61 (0.46, 0.81)	-3.39	<.001
	Born 2000–2020 (n = 115) ^a	0.25 (0.13, 0.47)	-4.33	<.001
Diceros bicornis up to 1 year of age, zooborn (n = 492)^b				
Born 1960–2021 reference:				
Females (n = 246)	males (n = 241)	1.08 (0.72, 1.63)	0.38	.706
	Birth year	0.991 (0.978, 1.003)	-1.46	.144
Born 1960–2021 reference:				
Females (n = 246)	Males (n = 241)	1.08 (0.72, 1.62)	0.35	.727
Born 1960–1979 (n = 101)	Born 1980–1999 (n = 201)	0.79 (0.48, 1.29)	-0.95	.342
	Born 2000–2021 (n = 190)	0.70 (0.41, 1.18)	-1.34	.181
Diceros bicornis up to 1 year of age, zooborn (n = 391)^b				
Born 1980–2021 reference:				
Females (n = 194)	Males (n = 194)	1.11 (0.84, 1.47)	0.75	.451
	Birth year	0.975 (0.960, 0.990)	-3.17	.002
Born 1980–2021 reference:				
Females (n = 194)	Males (n = 194)	1.11 (0.84, 1.47)	0.76	.449
Born 1980–1999 (n = 201)	Born 2000–2021 (n = 190)	0.62 (0.44, 0.88)	-2.71	.007

Abbreviation: CI, confidence interval.

^aExample interpretation: compared to the reference females and wildborn, males and zooborn have a significantly ($p = .011$ and $.021$) higher (both 1.38 and $1.42 > 1$, and the confidence interval does not include 1) mortality, i.e. a lower survivorship; because "birth year" has a significant ($p < .001$) factor that is lower than 1 (0.967 , and the confidence interval does not include 1), there is a significantly lower mortality (=higher survivorship) for animals of higher birth year (=more recently born); this is also evident when comparing the two cohorts (1980–1999 and 2000–2021) against the reference cohort of 1960–1979.

^bThe difference between the total and the sum of females and males is due to animals of unknown sex.

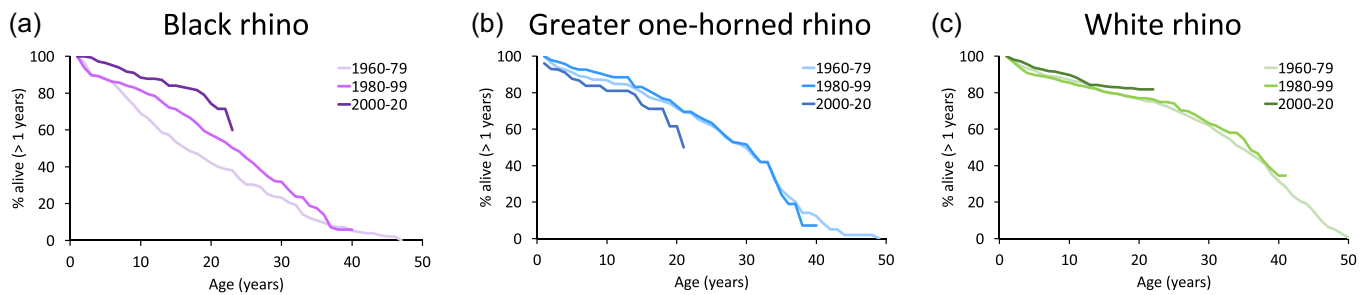


FIGURE 4 Survivorship of the three zoo-managed rhino species over time in animals ≥ 1 year of age. For statistics, see Tables 2–4. Note that statistics were also done using year of birth as a continuous variable rather than the arbitrary 20-year-cohorts. [Color figure can be viewed at wileyonlinelibrary.com]

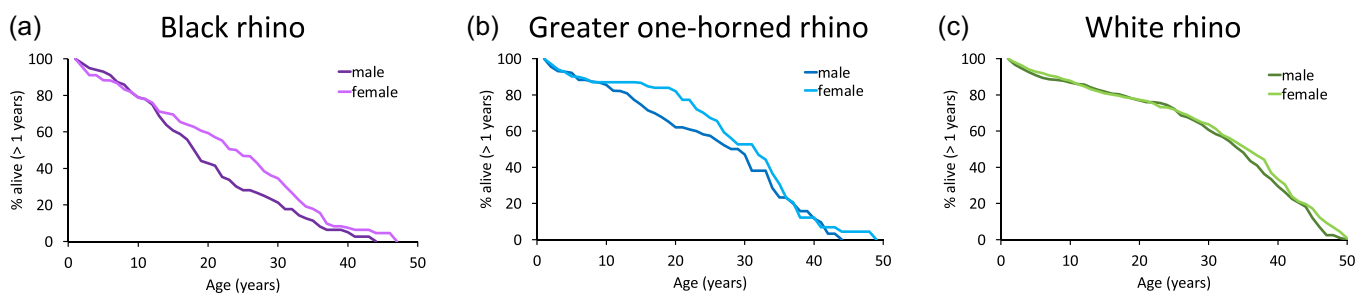


FIGURE 5 Survivorship of the three zoo-managed rhino species since 1960, compared between the sexes in animals ≥ 1 year of age. For statistics, see Tables 2–4. [Color figure can be viewed at wileyonlinelibrary.com]

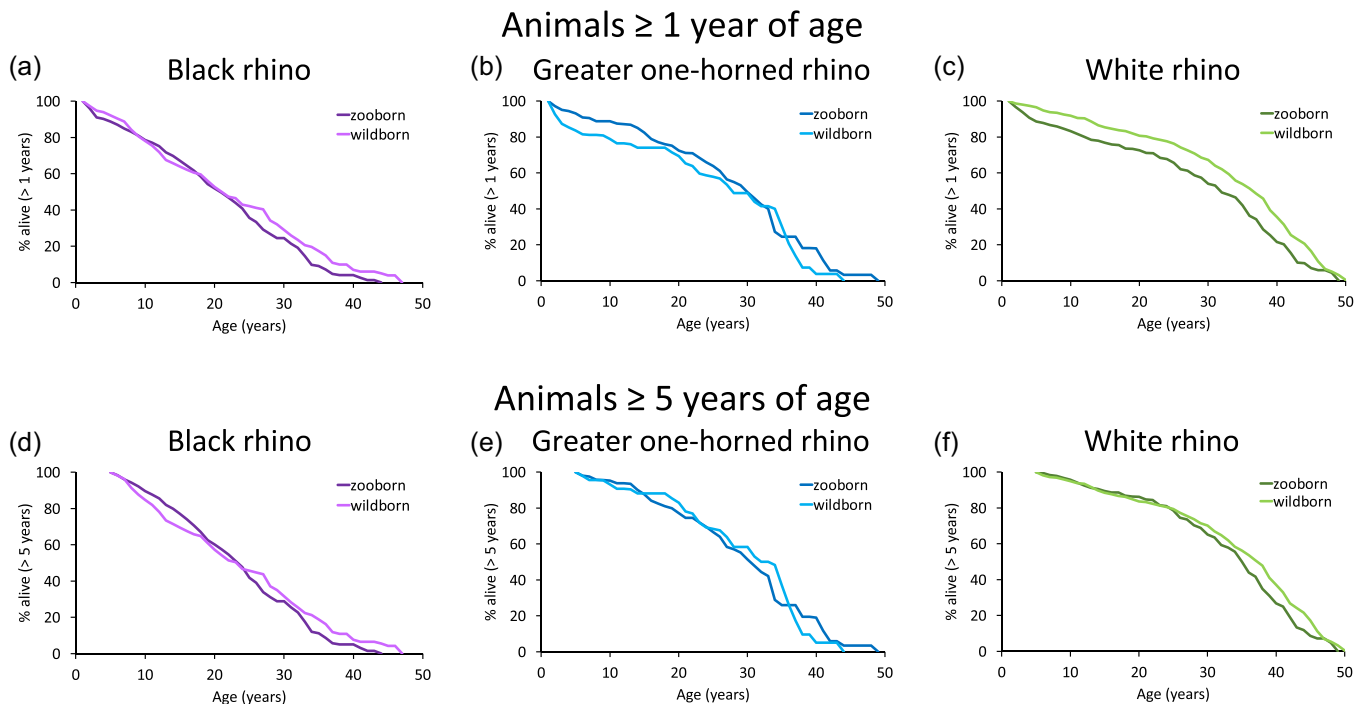


FIGURE 6 Survivorship of the three zoo-managed rhino species since 1960, compared between zoo-born and wild-born animals ≥ 1 year of age (a–c) or ≥ 5 years of age (d–f). For statistics, see Tables 2–4. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Survivorship analyses (Cox proportional hazards) for greater one-horned rhino (*Rhinoceros unicornis*) in zoos worldwide for different age groups and cohorts.

Model		Coef (95% CI)	z	p
Rhinoceros unicornis ≥1 year of age (n = 310)				
Born 1960–2020 reference:				
Females (n = 146)	Males (n = 164)	1.32 (0.94, 1.86)	1.62	.106
Wildborn (n = 55)	Zooborn (n = 255)	0.91 (0.62, 1.34)	-0.49	.628
	Birth year	1.000 (0.986, 1.015)	0.04	.968
Born 1960–2020 reference:				
Females (n = 146)	Males (n = 164)	1.32 (0.94, 1.86)	1.62	.106
Wildborn (n = 55)	Zooborn (n = 255)	0.89 (0.60, 1.31)	-0.62	.539
Born 1960–1979 (n = 57)	Born 1980–1999 (n = 95)	0.91 (0.61, 1.36)	-0.47	.636
	Born 2000–2020 (n = 158)	1.21 (0.69, 2.11)	0.68	.499
Rhinoceros unicornis ≥5 years of age (n = 261)				
Born 1960–2020 reference:				
Females (n = 121)	Males (n = 140) ^a	1.42 (0.97, 2.07)	1.79	.073
Wildborn (n = 46)	Zooborn (n = 215) ^a	1.09 (0.71, 1.69)	0.42	.673
	Birth year ^a	0.998 (0.980, 1.016)	0.04	.812
Born 1960–2020 reference:				
Females (n = 121)	Males (n = 140)	1.42 (0.97, 2.08)	1.80	.072
Wildborn (n = 46)	Zooborn (n = 215)	1.07 (0.69, 1.65)	0.30	.763
Born 1960–1979 (n = 50)	Born 1980–1999 (n = 89) ^a	0.99 (0.64, 1.52)	-0.06	.951
	Born 2000–2020 (n = 122) ^a	1.28 (0.63, 2.58)	0.69	.492
Rhinoceros unicornis up to 1 year of age, zooborn (n = 340)				
Born 1960–2021 reference:				
Females (n = 154)	Males (n = 186)	0.99 (0.63, 1.56)	-0.06	.956
	Birth year	0.997 (0.983, 1.012)	-0.40	.687
Born 1960–2021 reference:				
Females (n = 154)	Males (n = 186)	0.97 (0.61, 1.53)	-0.14	.886
Born 1960–1979 (n = 40)	Born 1980–1999 (n = 101)	2.24 (0.93, 5.38)	1.80	.072
	Born 2000–2021 (n = 199)	1.36 (0.58, 3.22)	0.71	.480
Rhinoceros unicornis up to 1 year of age, zooborn (n = 300)				
Born 1980–2021 reference:				
Females (n = 135)	Males (n = 166)	1.22 (0.87, 1.74)	1.17	.241
	Birth year	0.990 (0.974, 1.007)	-1.14	.254
Born 1980–2021 reference:				
Females (n = 135)	Males (n = 166)	1.23 (0.88, 1.75)	1.21	.225
Born 1980–1999 (n = 101)	Born 2000–2021 (n = 199)	0.86 (0.59, 1.25)	0.71	.426

Abbreviation: CI, confidence interval.

^aExample interpretation: compared to the reference females and wildborn, males and zooborn do not have a significantly ($p > .05$) different mortality, i.e. no difference in survivorship (note that the confidence interval of the coefficient includes 1); because “birth year” is also not significant ($p > .05$), there is no change in mortality (survivorship) over time; this is also evident when comparing the two cohorts (1980–1999 and 2000–2021) against the reference cohort of 1960–1979 (no significance; coefficient confidence intervals include 1).

TABLE 4 Survivorship analyses (Cox proportional hazards) for white rhino (*Ceratotherium simum*) in zoos worldwide for different age groups and cohorts.

Model		Coef (95% CI)	z	p
Ceratotherium simum ≥1 year of age (n = 1187)				
Born 1960–2020 reference:				
Females (n = 684)	Males (n = 503)	1.15 (0.96, 1.37)	1.54	.124
Wildborn (n = 462)	Zooborn (n = 725)	1.55 (1.24, 1.94)	3.79	<.001
	Birth year	0.983 (0.974, 0.992)	-3.85	<.001
Born 1960–2020 reference:				
Females (n = 684)	Males (n = 503)	1.15 (0.96, 1.37)	1.52	.128
Wildborn (n = 462)	Zooborn (n = 725)	1.46 (1.18, 1.82)	3.45	<.001
Born 1960–1979 (n = 358)	Born 1980–1999 (n = 304)	0.73 (0.57, 0.94)	-2.42	.015
	Born 2000–2020 (n = 525)	0.54 (0.38, 0.77)	-3.42	<.001
Ceratotherium simum ≥5 years of age (n = 995)				
Born 1960–2020 reference:				
Females (n = 587)	Males (n = 408) ^a	1.15 (0.94, 1.39)	1.34	.172
Wildborn (n = 446)	Zooborn (n = 549) ^a	1.22 (0.94, 1.58)	1.50	.133
	Birth year ^a	0.984 (0.973, 0.995)	-2.86	.004
Born 1960–2020 reference:				
Females (n = 587)	Males (n = 408)	1.15 (0.94, 1.39)	1.37	.171
Wildborn (n = 446)	Zooborn (n = 549)	1.15 (0.90, 1.47)	1.12	.265
Born 1960–1979 (n = 330)	Born 1980–1999 (n = 273) ^a	0.74 (0.56, 0.99)	-2.00	.045
	Born 2000–2020 (n = 392) ^a	0.62 (0.38, 0.99)	-2.00	.045
Ceratotherium simum up to 1 year of age, zooborn (n = 934)^b				
Born 1960–2020 reference:				
Females (n = 478)	Males (n = 445)	1.06 (0.78, 1.44)	0.35	.730
	Birth year	0.984 (0.974, 0.994)	-3.28	.001
Born 1960–2020 reference:				
Females (n = 478)	Males (n = 445)	1.07 (0.78, 1.45)	0.40	.687
Born 1960–1979 (n = 100)	Born 1980–1999 (n = 267)	1.00 (0.63, 1.60)	0.00	.998
	Born 2000–2020 (n = 567)	0.63 (0.40, 0.98)	-2.03	.043
Ceratotherium simum up to 1 year of age, zooborn (n = 834)^b				
Born 1980–2021 reference:				
Females (n = 431)	Males (n = 393)	1.20 (0.95, 1.53)	1.54	.124
	Birth year	0.977 (0.967, 0.987)	-3.28	<.001
Born 1960–2021 reference:				
Females (n = 431)	Males (n = 393)	1.20 (0.95, 1.53)	1.54	.124
Born 1980–1999 (n = 267)	Born 2000–2021 (n = 567)	0.61 (0.47, 0.78)	-3.86	<.001

^aExample interpretation: compared to the reference females and wildborn, males and zooborn do not have a significantly ($p > .05$) different mortality, i.e. no difference in survivorship (note that the confidence interval of the coefficient includes 1); because "birth year" has a significant ($p = .004$) factor that is lower than 1 (0.984, and the confidence interval does not include 1), there is a significantly lower mortality (=higher survivorship) for animals of higher birth year (=more recently born); this is also evident when comparing the two cohorts (1980–1999 and 2000–2021) against the reference cohort of 1960–1979.

^bThe difference between the total and the sum of females and males is due to animals of unknown sex

well. For highly charismatic conservation flagship species such as rhinos, that in addition are only present in any one facility at low numbers of individuals, a breed-and-cull strategy, even though likely more rational than a cessation of breeding (Bertelsen, 2018), may be particularly hard to communicate, and not be intuitive for many people. Ideally, more holding space for rhinos, not only in zoos but also in dedicated, separate breeding centers, both in the respective home countries and in ex situ countries, should become available in the near future. In the absence of such options, a debate to which extent differences in population pyramid shape between zoos and the natural habitat (Figures 1 and 2) are desirable or acceptable might have to be held.

Based on survivorship analyses only, we cannot identify the reasons for increased husbandry success in rhinos. Yet, the results clearly suggest that knowledge of rhino biology, and the skill of rhino husbandry, have increased. The relevance of this knowledge and skill for ex situ population management is evidently beyond doubt. However, it is difficult to objectively estimate the exact relevance of this knowledge and skill for the protection of in situ populations. The extent to which the ex situ efforts are considered crucial for the survival of the species, and to which the ex situ derived insights are considered crucial for in situ efforts, will decide how justified individual stakeholders may consider zoo rhino management. Especially for “mammalian megafauna,” ex situ efforts have been described as crucial for species survival (Farhadinia et al., 2020). Under the premise that no animals are taken from protected natural habitats that could also thrive there, we authors consider zoo rhino management an important contribution to global rhino conservation—not only because of the numbers of animals kept alive ex situ and the ambassador and education function of zoo animals, but also due to the expertise gained in managing the species.

ACKNOWLEDGMENTS

This research was made possible by the worldwide information network of zoos and aquariums which are members of Species360 and is authorized by Species360 Research Data Agreement # 2019-Q3-RR3. There is no funding to report. We thank Christine Janis for information regarding the fossil record, and Kees Rookmaker for maintaining the Rhino Resource Center that greatly enhances any literature research on rhinos. Open access funding provided by Universitat Zurich.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest. All authors are either employed by, or have major involvement with, zoological gardens.

DATA AVAILABILITY STATEMENT

Requests for original data should be addressed to Species360 at www.Species360.org. The data used for this study is given in anonymized form in the Supporting Information. The data that supports the findings of this study are available in the Supporting Information material of this article.

ORCID

Marco Roller  <http://orcid.org/0000-0001-5678-0892>

Dennis W. H. Müller  <http://orcid.org/0000-0001-9996-064X>

Mads F. Bertelsen  <http://orcid.org/0000-0001-9201-7499>

Laurie Bingaman Lackey  <http://orcid.org/0000-0002-9612-9807>

Marcus Clauss  <http://orcid.org/0000-0003-3841-6207>

REFERENCES

- Aburto, J. M., Villavicencio, F., Basellini, U., Kjærgaard, S., & Vaupel, J. W. (2020). Dynamics of life expectancy and life span equality. *Proceedings of the National Academy of Sciences*, *117*, 5250–5259.
- Ahmad Zafir, A. W., Payne, J., Mohamed, A., Lau, C. F., Sharma, D. S. K., Alfred, R., Williams, A. C., Nathan, S., Ramono, W. S., & Clements, G. R. (2011). Now or never: What will it take to save the Sumatran rhinoceros *Dicerorhinus sumatrensis* from extinction? *Oryx*, *45*, 225–233.
- Bertelsen, M. F. (2018). Issues surrounding surplus animals in zoos. In R. E. Miller, N. Lamberski, & P. Calle (Eds.), *Fowler's Zoo and Wild Animal Medicine Current Therapy* (Vol. 9, pp. 134–136). WB Saunders.
- Biasetti, P., Hildebrandt, T. B., Göritz, F., Hermes, R., Holtze, S., Galli, C., Lazzari, G., Colleoni, S., Pollastri, I., Spiriti, M. M., Stejskal, J., Seet, S., Zwilling, J., Ngulu, S., Mutisya, S., Kariuki, L., Lokoolool, I., Omondo, P., Ndeereh, D., & de Mori, B. (2022). Ethical analysis of the application of assisted reproduction technologies in biodiversity conservation and the case of white rhinoceros (*Ceratotherium simum*) ovum pick-up procedures. *Frontiers in Veterinary Science*, *9*, 831675.
- Brodie, J. F., Muntifering, J., Hearn, M., Loutit, B., Loutit, R., Brell, B., Uri-Khob, S., Leader-Williams, N., & du Preez, P. (2011). Population recovery of black rhinoceros in north-west Namibia following poaching. *Animal Conservation*, *14*, 354–362.
- Callender, C. (2021). On the horns of a dilemma: Let the Northern white rhino vanish or intervene? *Ethics, Policy & Environment*. <https://doi.org/10.1080/21550085.2021.1961199>
- Clauss, M., & Dierenfeld, E. S. (2008). The nutrition of browsers. In M. E. Fowler & R. E. Miller (Eds.), *Zoo and wild animal medicine Current therapy* (Vol. 6, pp. 444–454). Saunders Elsevier.
- Clauss, M., & Hatt, J.-M. (2006). The feeding of rhinoceros in captivity. *International Zoo Yearbook*, *40*, 197–209.
- Clauss, M., Müller, D. W. H., & Codron, D. (2019). Within-niche pace of life acceleration as a fundamental evolutionary principle: A mammal pilot test case. *Evolutionary Ecology Research*, *20*, 385–401.
- Colchero, F., Rau, R., Jones, O. R., Barthold, J. A., Conde, D. A., Lenart, A., Nemeth, L., Scheuerlein, A., Schoeley, J., Torres, C., Zarulli, V., Altmann, J., Brockman, D. K., Bronikowski, A. M., Fedigan, L. M., Pusey, A. E., Stoinski, T. S., Strier, K. B., Baudisch, A., ... Vaupel, J. W. (2016). The emergence of longevous populations. *Proceedings of the National Academy of Sciences*, *113*, E7681–E7690.
- de Magalhães, J. P., & Costa, J. (2009). A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology*, *22*, 1770–1774.
- Deevey, E. S. (1947). Life tables for natural populations of animals. *The Quarterly Review of Biology*, *22*, 283–314.
- Dennis, P. M., Funk, J. A., Rajala-Schultz, P. J., Blumer, E. S., Miller, R. E., Wittum, T. E., & Saville, W. J. A. (2007). A review of some of the health issues of captive black rhinoceroses (*Diceros bicornis*). *Journal of Zoo and Wildlife Medicine*, *38*, 509–517.
- Edwards, K. L., Walker, S. L., Dunham, A. E., Pilgrim, M., Okita-Ouma, B., & Shultz, S. (2015). Low birth rates and reproductive skew limit the viability of Europe's captive eastern black rhinoceros, *Diceros bicornis michaeli*. *Biodiversity and Conservation*, *24*, 2831–2852.
- Farhadinia, M. S., Johnson, P. J., Zimmermann, A., McGowan, P. J. K., Meijaard, E., Stanley-Price, M., & Macdonald, D. W. (2020). Ex situ

- management as insurance against extinction of mammalian megafauna in an uncertain world. *Conservation Biology*, 34, 988–996.
- Ferreira, S. M., Greaver, C. C., & Knight, M. H. (2011). Assessing the population performance of the black rhinoceros in Kruger National Park. *South African Journal of Wildlife Research*, 41, 192–204.
- Geraads, D. (2011). Rhinocerotidae. In L. Werdelin & W. J. Saunders (Eds.), *Cenozoic mammals of Africa* (pp. 669–683). University of California Press.
- Goddard, J. (1967). Home range, behaviour, and recruitment rates of two black rhinoceros populations. *African Journal of Ecology*, 5, 133–150.
- Havercamp, K., Watanuki, K., Tomonaga, M., Matsuzawa, T., & Hirata, S. (2019). Longevity and mortality of captive chimpanzees in Japan from 1921 to 2018. *Primates*, 60, 525–535.
- Hermes, R., Göritz, F., Saragusty, J., Stoops, M. A., & Hildebrandt, T. B. (2014). Reproductive tract tumours: The scourge of woman reproduction ails Indian rhinoceroses. *PLoS ONE*, 9, e92595.
- Hermes, R., Hildebrandt, T. B., Walzer, C., Göritz, F., Patton, M. L., Silinski, S., Anderson, M. J., Reid, C. E., Wibbelt, G., Tomasova, K., & Schwarzenberger, F. (2006). The effect of long non-reproductive periods on the genital health in captive female white rhinoceroses (*Ceratotherium simum simum*, *Cs cottoni*). *Theriogenology*, 65, 1492–1515.
- Hitchins, P. M., & Anderson, J. L. (1983). Reproduction, population characteristics and management of the black rhinoceros *Diceros bicornis minor* in the Hluhluwe/Corridor/Umfolozi game reserve complex. *South African Journal of Wildlife Research*, 13, 78–85.
- Hubback, T. (1939). The two-horned Asiatic rhinoceros (*Dicerorhinus sumatrensis*). *Journal of the Bombay Natural History Society*, 40, 594–617.
- IUCN. (2021). The IUCN Red List of Threatened Species. Version 2021-3. <https://www.iucnredlist.org>. Accessed on 10.12. 2021.
- Jaakkola, K., & Willis, K. (2019). How long do dolphins live? Survival rates and life expectancies for bottlenose dolphins in zoological facilities vs. wild populations. *Marine Mammal Science*, 35, 1418–1437.
- Jett, J., & Ventre, J. (2015). Captive killer whale (*Orcinus orca*) survival. *Marine Mammal Science*, 31, 1362–1377.
- Kandel, R. C., & Jhala, Y. V. (2008). Demographic structure, activity patterns, habitat use and food habits of *Rhinoceros unicornis* in Chitwan National Park, Nepal. *Journal of Bombay Natural History Society*, 105, 5–13.
- Liu, S., Westbury, M. V., Dussex, N., Mitchell, K. J., Sinding, M. H. S., Heintzman, P. D., Duchêne, D. A., Kapp, J. D., von Seth, J., Heiniger, H., Sánchez-Barreiro, F., Margaryan, A., André-Olsen, R., De Cahsan, B., Meng, G., Yang, C., Chen, L., van der Valk, T., Moodley, Y., ... Gilbert, M. T. P. (2021). Ancient and modern genomes unravel the evolutionary history of the rhinoceros family. *Cell*, 184, 4874–4885.
- Mason, G., Burn, C. C., Dallaire, J. A., Kroshko, J., McDonald Kinkaid, H., & Jeschke, J. M. (2013). Plastic animals in cages: Behavioural flexibility and responses to captivity. *Animal Behaviour*, 85, 1113–1126.
- Miller, M. A., & Buss, P. E. (2003). Rhinocerotidae (Rhinoceroses). In R. E. Miller & M. E. Fowler (Eds.), *Fowler's zoo and wild animal medicine* (Vol. 8, pp. 538–547). Saunders Elsevier.
- Mukinya, J. G. (1973). Density, distribution, population structure and social organization of the black rhinoceros in Masai Mara Game Reserve. *African Journal of Ecology*, 11, 385–400.
- Owen-Smith, N. (1974). The social system of the white rhinoceros. In V. Geist & F. Walther (Eds.), *The behaviour of ungulates and its relation to management* (pp. 341–351). IUCN.
- Owen-Smith, R. N. (1988). *Megaherbivores - the influence of very large body size on ecology*. Cambridge University Press.
- Pearl, R., & Miner, J. R. (1935). Experimental studies on the duration of life. XIV. *The comparative mortality of certain lower organisms. Quarterly Review of Biology*, 10, 60–79.
- Penfold, L. M., Powell, D., Traylor-Holzer, K., & Asa, C. S. (2014). "Use it or lose it": Characterization, implications, and mitigation of female infertility in captive wildlife: Infertility and sustainability. *Zoo Biology*, 33, 20–28.
- Pienaar, D. (1994). Social organization and behaviour of the white rhinoceros. In *Proceedings of a Symposium on "Rhinos as Game Ranch Animals"* (pp. 87–92).
- Pilgrim, M., & Biddle, R. (2020). *EAZA Best practice guidelines black rhinoceros (Diceros bicornis)*. EAZA.
- Pluháček, J., Steck, B. L., Sinha, S. P., & von Houwald, F. (2017). Interbirth intervals are associated with age of the mother, but not with infant mortality in Indian rhinoceroses. *Current Zoology*, 63, 229–235.
- Prothero, D. R. (2005). *The evolution of North American rhinoceroses*. Cambridge UK: Cambridge University Press.
- R Core Team. (2017). R: A language and environment for statistical computing. version 3.4.1. R Foundation for Statistical Computing, Vienna, <http://www.R-project.org/>
- Radeke-Auer, K., Clauss, M., Stagegaard, J., Bruins-Van Sonsbeek, L. G. R., & Lopez, J. (2023). Retrospective pathology review of captive black rhinoceros *Diceros bicornis* in the EAZA ex-situ programme (1995–2022). *Journal of Zoo and Aquarium Research*, 11, 298–310.
- Roller, M., Müller, D. W. H., Bertelsen, M. F., Bingaman Lackey, L., Hatt, J.-M., & Clauss, M. (2021). The historical development of juvenile mortality and adult longevity in zoo-kept carnivores. *Zoo Biology*, 40, 588–595.
- Ryder, O. A., Friese, C., Greely, H. T., Sandler, R., Saragusty, J., Durrant, B. S., & Redford, K. H. (2020). Exploring the limits of saving a subspecies: The ethics and social dynamics of restoring northern white rhinos (*Ceratotherium simum cottoni*). *Conservation Science and Practice*, 2, e241.
- Scherer, L., Bingaman Lackey, L., Clauss, M., Gries, K., Hagan, D., Lawrenz, A., Müller, D. W. H., Roller, M., Schiffmann, C., & Oerke, A.-K. (2022). The historical development of zoo elephant survivorship. *Zoo Biology*, 42, 328–338.
- Schook, M. W., Wildt, D. E., Raghanti, M. A., Wolfe, B. A., & Dennis, P. M. (2015). Increased inflammation and decreased insulin sensitivity indicate metabolic disturbances in zoo-managed compared to free-ranging black rhinoceros (*Diceros bicornis*). *General and Comparative Endocrinology*, 217–218, 10–19.
- Sody, H. J. V. (1959). Das Javanische Nashorn *Rhinoceros sondaicus* historisch und biologisch. *Zeitschrift für Säugetierkunde*, 24, 109–240.
- Subedi, N., Lamichhane, B. R., Amin, R., Jnawali, S. R., & Jhala, Y. V. (2017). Demography and viability of the largest population of greater one-horned rhinoceros in Nepal. *Global Ecology and Conservation*, 12, 241–252.
- Taylor, L. A., Müller, D. W. H., Schwitzer, C., Kaiser, T. M., Codron, D., Schulz, E., & Clauss, M. (2014). Tooth wear in captive rhinoceroses (*Diceros*, *Rhinoceros*, *Ceratotherium*: Perissodactyla) differs from that of free-ranging conspecifics. *Contributions to Zoology*, 83, 107–S1.
- Therneau, T. (2022). A package for survival analysis in R. *R package version*, 33–1. <https://CRANR-project.org/package=survival>
- Tidière, M., Gaillard, J.-M., Berger, V., Müller, D. W. H., Bingaman Lackey, L., Gimenez, O., Clauss, M., & Lemaître, J.-F. (2016). Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. *Scientific Reports*, 6, 36361.
- von Houwald, F. (2015). *EAZA Best Practice Guidelines: Greater one-horned rhinoceros (Rhinoceros unicornis)*. EAZA.
- von Houwald, F. (2016). Causes and prevention of foot problems in Greater one-horned rhinoceros *Rhinoceros unicornis* in zoological institutions. *International Zoo Yearbook*, 50, 215–224.
- Versteeg, L. (2018). *EAZA Best practice guidelines white rhinoceros (Ceratotherium simum)*. EAZA.
- Wang, X., Flynn, L. J., & Fortelius, M. (2013). *Fossil mammals of Asia: Neogene biostratigraphy and chronology*. Columbia University Press.

Wich, S. A., Shumaker, R. W., Perkins, L., & De Vries, H. (2009). Captive and wild orangutan (*Pongo* sp.) survivorship: a comparison and the influence of management. *American Journal of Primatology*, 71, 680–686.

SUPPORTING INFORMATION

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

How to cite this article: Wittwer, A., Roller, M., Müller, D. W. H., Bertelsen, M. F., Lackey, L. B., Steck, B., Biddle, R., Versteegen, L., & Clauss, M. (2023). Historical development of the survivorship of zoo rhinoceroses—A comparative historical analysis. *Zoo Biology*, 1–14.
<https://doi.org/10.1002/zoo.21793>