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Research article

Historical survivorship and demographic structure of zoo-housed hippopotamuses (Hippopotamidae)

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Abstract

Zoos have made efforts to improve the welfare and survival of their animals through ever-evolving husbandry techniques. In principle, this accumulation of expertise and skills should lead to higher survival rates for zoo animals over time, as demonstrated in several zoo animal species in recent years. Hippopotamuses (hippos) are part of the charismatic fauna commonly present in zoos, and their conservation status in natural habitats increases the potential and value that ex situ populations have to offer for their conservation. In this study, historical adult and juvenile survivorship of the two hippo species while kept in zoos was evaluated from 1900 onwards. The survivorship of adult common hippos *Hippopotamus amphibius* has remained unchanged across this timespan while the survivorship of adult pygmy hippos *Choeropsis liberiensis* has seen some progress in the last two decades. For both species, juvenile survival has remarkably improved. The survivorship of common hippos in zoos is superior to that observed in the only documented survivorship data from a free-ranging population. For the common hippo, the absence of improvements in recent decades could either indicate that the species has already reached its optimum lifespan, or that a key husbandry practice has yet to be identified to further enhance survivorship rates. The improvements seen in pygmy hippo may be the result of increased collective efforts in the last two decades to better understand the biology and care of this species, as evidenced by scientific interest and husbandry guidelines. In the population of both species, the proportion of juveniles has decreased and that of adults has increased, with the current barrel-shaped population pyramid in the common hippos creating the risk of jeopardising the long-term maintenance of the population. Especially for common hippos, we suggest that a change in the management approach might be necessary to guarantee population sustainability, with the inclusion of a breed-and-cull strategy.

Introduction

Amid the current biodiversity crisis, the role of ex situ animal populations is a recurrent justification for maintaining animal populations in zoos. However, concerns regarding the care of exotic animals in general are often raised as arguments against this role. This debate becomes more intense when large charismatic fauna are used as examples of the negative effects of zoo housing (Clubb et al. 2008; Hosey et al. 2020). Some alleged effects are higher mortality rates and lower survivorship than those of free-roaming populations, detected in a few populations (Mason 2010), even though in the majority of mammal populations in zoos, survivorship is higher than in the wild (Lynch et al. 2010; Tidière et al. 2016). Nevertheless, in the last half-century, zoos have achieved many positive developments regarding husbandry. These were not just the result of generally increased knowledge of species-specific biology but also a vested interest of zoos in improving husbandry. Moreover, for zoo animals to function as insurance against extinction, understanding the factors influencing the survival of animals in human care is essential to ensure viable populations (Da Rè et al. 2018). Recently, a growing number of publications have assessed if survivorship data from zoo populations are indicative of such developments (Wich et al. 2009; Jett and Ventre 2015; Havercamp et al. 2019; Jaakkola and Willis 2019; Roller et al. 2021; Scherer et al. 2023; Tidière et al. 2023; Wittwer et al. 2023). Their results demonstrate that in the investigated taxa, the efforts made by zoos to improve the welfare and survival of their animals have had positive results.

Hippopotamuses (hereafter termed hippo(s)) are part of the charismatic megafauna commonly found in zoos. There are two extant species, both from Africa - the common hippo *Hippopotamus amphibius*, Linnaeus 1758 and the pygmy hippo *Choeropsis liberiensis*, Morton 1849 (Williams 2017). Although hippos are considered easy to keep in zoos, generally described as being hardy and rarely experiencing disease (Lindau et al. 1982), hippo husbandry at current standards and recommendations can be considered expensive in terms of logistics and infrastructure. In some European legislation (Der Schweizerische Bundesrat 2008; BMEL 2014; Vlamsee Overheid 2022), these animals require a large area in order to accommodate an appropriate social group structure, and enclosures must have an even water/land ratio. Furthermore, in countries with cold winters, indoor facilities must be large enough to encourage activity in the animals and allow social group management throughout the year. The necessity for expansive enclosure sizes is exacerbated by the multiple enclosures needed when social and breeding management requires fusion-fission of the group (Tennant et al. 2018).

Little research has been done on the welfare and behaviour of common hippos in zoos compared to other megafauna species such as elephants (Family Elephantidae) or rhinoceroses (Family Rhinocerotidae) (Tennant et al. 2018; Fernandez et al. 2020). A survey in American zoos found that potential deficits for their behavioural needs are mostly centred around group size and nocturnal foraging, although no indications of reduced welfare were determined (Tennant et al. 2018). In the wild, common hippos can form large groups, called pods, mostly composed of females with their calves. These groups are usually guarded by one territorial male (Karstad and Hudson 1986). Often bachelor males form groups apart in adjacent water bodies. These bachelor males are subordinate to the territorial males and have to engage in violent, sometimes fatal, fighting to defeat the territorial males to gain access to territory and females (Eltringham 1999).

The majority of the surveyed zoos preferred to house two individuals as a breeding pair or to hold female-only groups, as a measure to manage breeding or reduce husbandry costs (Snyder 2015; Tennant et al. 2018). These group sizes are much lower than those observed in the wild, which are around 10 individuals or more (Field 1970; Tennant et al. 2018). On the other hand, the solitary-living pygmy hippo has sometimes been kept in social groups resulting in frequent aggression, injuries and even reported deaths (Flacke et al. 2015).

Common hippos are considered to breed well in zoos (Wheaton et al. 2006). However, their breeding and demographic management bear some challenges. Without providing comparative data, Snyder (2015) claimed that the mortality rate observed in common hippos within the first year of life in zoos (30 to 40%) was higher than in the wild, in spite of the absence of predation in zoos. Breeding management (Tennant et al. 2018) is seen as difficult, not only because of the early puberty observed in zoo hippos, beginning at two years of age (Wheaton et al. 2006), but also due to the complex sociality of hippos, namely in size, dynamics, and group composition. Managing these large and complex groups in limited enclosure spaces or controlling their breeding is a challenge for many holders and may prevent the recruitment of new holders to expand the population (Tennant et al. 2018).

We evaluated birth and death data from zoo-housed common and pygmy hippos to test whether there is a difference in age-related, sex-related, and origin-related (wild versus zoo-born) survivorship between the species. Additionally, we tested whether there was directional development in juvenile mortality (reduction) and adult survivorship (increase) in zoos over time, signalling a positive development in the husbandry provided to these two species. Whenever available, these traits were compared with data from wild populations. In addition, we looked at whether there was a seasonal component in the mortality of juveniles and adults in northern latitudes; in tropical climate species like hippos, winter months might be expected to have a stronger impact on the total number of deaths. Furthermore, we aimed to investigate the demographic structure of the populations over time to identify relevant trends in the age distribution of the zoo populations.

Materials and methods

Dataset

This research on historical survivorship and demographic structure of zoo-housed hippos follows the principles outlined by Scherer et al. (2023), Wittwer et al. (2023), and Scherer et al. (2024) in their research on elephants, rhinoceroses, and giraffes, respectively. The global records of the common hippo populations were obtained from Species360 (ZIMS for Husbandry), an online database platform in current use by more than 1200 institutions worldwide to manage their animal data, such as dates of birth and death from which the subsequent analysis was performed (Species360 Research Data Agreement # 2019-Q3- RR3). The global records of the pygmy hippo were obtained from the international studbook as permitted by the World Association of Zoos and Aquaria (WAZA).

While the input of animal data into ZIMS is mandatory for some zoo associations such as the European Association of Zoos and Aquaria (EAZA), it is not for others such as the American Association of Zoos and Aquaria (AZA). Furthermore, providing historical data is not mandatory for any Species360 member. It must be noted that while it is very unlikely that adult hippos alive at member zoos are not entered into the system due to their visibility, there is no control over whether newborns are consistently entered. The practice of not entering newborn animals until they survived to about one month of age was more common in the early 1900s than it is now, especially when entering historical data into the database (as also suggested in Wittwer et al. 2023). This would result in an underestimation of positive developments in neonate mortality. As another limitation, the datasets allow for analysis of survivorship but do not contain information on the causes of death, so the causes of death leading to any changes in survivorship cannot be analysed objectively.

The dataset was initially curated to exclude repeated registries (e.g. a new registry for the same individual if it was transferred to another zoo instead of keeping a singular registry) or lost to follow-ups. The dataset included information on the sex and whether the animal was wild or zoo-born. We did not know the ages at which wild-born animals were imported; therefore, these animals were excluded from the assessment of juvenile mortality (up to two years of age). Birth dates of wild-born animals in the dataset are typically estimated at the time of import, and their reliability cannot be determined.

For pygmy hippos, the maximum lifespan was defined as 52 years of age while for common hippos it was 62 years of age. These values were decided upon using the oldest animal of each species

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(dead or alive on the endpoint of survival (see text on statistical models)) recorded in each studbook. Only animals born between 1900 and 2023 were included in the analysis. The final data set included 3217 common hippos and 1706 pygmy hippos. For both species, sexual maturity was considered to be at two years of age, based on the earliest observed breeding under human care (Dittrich 1976); this threshold therefore marks the line between juvenile and adult survival. Note that it has been described that wild hippos reach sexual maturity much later than those in zoos (7-17 years) (Sayer and Rakha 1974; Smuts and Whyte 1981), with this range being the result of strong influences of prevailing environmental conditions. Thus, sexual maturity in the wild differs across geographical locations or over time in habitats with highly variable rainfall patterns over years (Peek and O'Connor 2023). However, claims of such great disparity between zoo and wild populations have been disputed on the basis of methodology and comparison with other large mammals, and possibly the age of maturity of wild hippos is much closer to that seen in zoos (Dittrich 1976).

Age pyramids and seasonal patterns of mortality

The dataset was used to depict population pyramids for each species as of 1 January for 1950, 1960, 1970, 1980, 1990, 2000, 2010, and 2020. For each species, using the same counts as for the age pyramids, we calculated and plotted the proportion of calves (< 2 years of age), young adults (≥2 to 10 years of age) and adults (≥10 years of age) across several time points (from 1940 in five-year-intervals to 2020 and then 2022, the last full year of our dataset). We used the same cut-off (10 years of age) that Shannon et al. (2021) used for common hippos to classify fully grown adults when analysing body masses. We applied the same age groups to pygmy hippos.

Seasonal juvenile mortality for each species was plotted (per cohort) as the number of individuals born in a given month and then the proportion of these individuals that were categorised as neonate deaths (dying before one month of age) or surviving calves (living beyond the first month of age). For adult seasonal mortality, we followed a similar plotting approach to Carisch et al. (2017), and also plotted each sex separately. Deaths recorded for 1 January and 31 December were discarded due to their overabundance and were assumed to represent entries in the database aiming for the year of the event without an effort at an accurate record. We expressed the deaths of each month in percentage of the total death count of all months. The mortality of the month with the lowest proportion of deaths was defined as "baseline mortality". To explore the effect that seasonal variations may have on mortality of both juveniles and adults, only individuals in northern temperate regions (Europe, North America (USA and Canada) and East Asia (China, Taiwan, Japan, North Korea, South Korea, Mongolia)) were included. For both cases, all events of birth and death from 1900 to 2023 were considered.

Statistical models

For statistical analyses, the dataset was cropped in subsets to yield different age cut-offs. For adult survivorship, the standard age cut-off used was ≥2 years old matching the age of sexual maturity. The cut-off of ≥4 years old was occasionally used to further analyse the effects of birth type on survival. For juvenile survivorship, the cut-offs of 30 days of age and up to two years of age were analysed. The endpoint of survival was set to 30 August 2023 for the pygmy hippo and 04 September 2023 for the common hippo. Analyses were performed in R (R Core Team 2023) 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. Following Clubb et al. (2008), we assessed the effect of birth year by including it as a continuous variable (either from 1900 or from 1960 onwards) in the model; because individual years in a time series are not independent of each other, this approach must be considered exploratory. To additionally assess the effect of historical time, we also compared birth cohorts (for the periods of 1900–1959, 1960–1979, 1980–1999, 2000–2023) as discrete categories. The two distinct timeframes, 1900–2023 and 1960–2023, are used to account for the lower reliability that animal records had before the 1960s. Additionally, the survival of pygmy versus common hippo was compared using the absolute age, and the relative age in percent of the defined maximum lifespan following Lynch et al. (2010) and Müller et al. (2010), to account for the fact that different species are 'old' at different absolute ages. In all these analyses, interactions between the variables were included; if the interaction was not significant, the model was repeated without it. The significance level was set to 0.05, and p-values between 0.05 and 0.09 were considered trends. The proportional hazards are reported with their 95% confidence interval. For any model for ≥2 years of age animals with the variables sex or birth type (zoo vs wild-born) included, individuals that were marked as unknown for either of the two variables were excluded from the dataset. This resulted in the removal of 130 animals from the dataset (104 common hippos of unknown birth type, 20 common hippos of unknown sex and 6 pygmy hippos of unknown sex).

Due to the visual impression gleaned from the patterns of seasonal mortality for juveniles kept in Northern latitude zoos, the birth season (winter/summer, i.e. October-March/April-September) was additionally assessed in models of juvenile survivorship for a subset comprising animals born in Northern latitude zoos.

It should be noted that the statistical approach we chose does not allow the extrapolation of 'longevity' for different cohorts (such as cohorts with many animals still alive at the defined endpoint). Such extrapolations would require other methods (e.g., Colchero et al. 2016; Aburto et al.2020). Survivorship analyses such as the one performed here can provide summary metrics such as the "median life expectancy" if, in the cohort in question, at least 50% of animals have already died. We consider the choice of the statistical approach to survivorship evaluation partly philosophical; a comparison of methods in Scherer et al. (2024) led us to the conclusion that survivorship data is most intuitively explored and depicted by the traditional Cox proportional hazard analysis and graphs used here. Different analytical approaches by other groups are, of course, welcome.

For visualisation, we display the count data of the respective cohorts in non-transformed plots. These plots do not depict a data model but the actual counts of animals alive and dead; therefore, we do not add any confidence intervals. For a traditional description of the shape of the survivorship curves, we follow Pearl and Miner (1935) and Deevey Jr (1947): Survivorship curves for large precocial mammals with low predation (such as hippos 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 species with high juvenile mortality, which is not expected for hippos. Notably, these shape descriptions apply to a display of the data with a log-transformed y-axis. In order to inspect the shape, we therefore also depict the same data with a log-transformed y-axis in inlets of the untransformed graphs in selected cases. For visual comparison only, survivorship curves from a wild common hippo population from Queen Elizabeth Park, Uganda (data from 1961–1966) for individuals ≥2 years of age were taken from literature (Laws 1968).

Results

Age pyramids and demographic history

Both zoo hippo populations started relatively small and without a clear pyramid-shaped structure (Figure 1), but with the breeding of hippos in zoos, the plots quickly acquired the typical pyramidal shape, with many newborn and juvenile animals. In the common hippo, such a shape was achieved in the 1960s (Figure 1A), while the same can be seen for the pygmy hippo in the 1970s (Figure 1B). However, the most current structure for the common hippo shows a relatively even distribution of animals across age classes while the pygmy hippo retains the pyramidal shape. The common hippo population grew steadily across the second half of the last century, but from the middle 2000s onwards, a decline in the population, an increase in the proportion of adults and a decrease in calves and young adults is observed (Figure 2A). In the pygmy hippo pyramids (Figure 1B), the skewed sex ratio toward females widely described in the literature for this species in zoos is evident

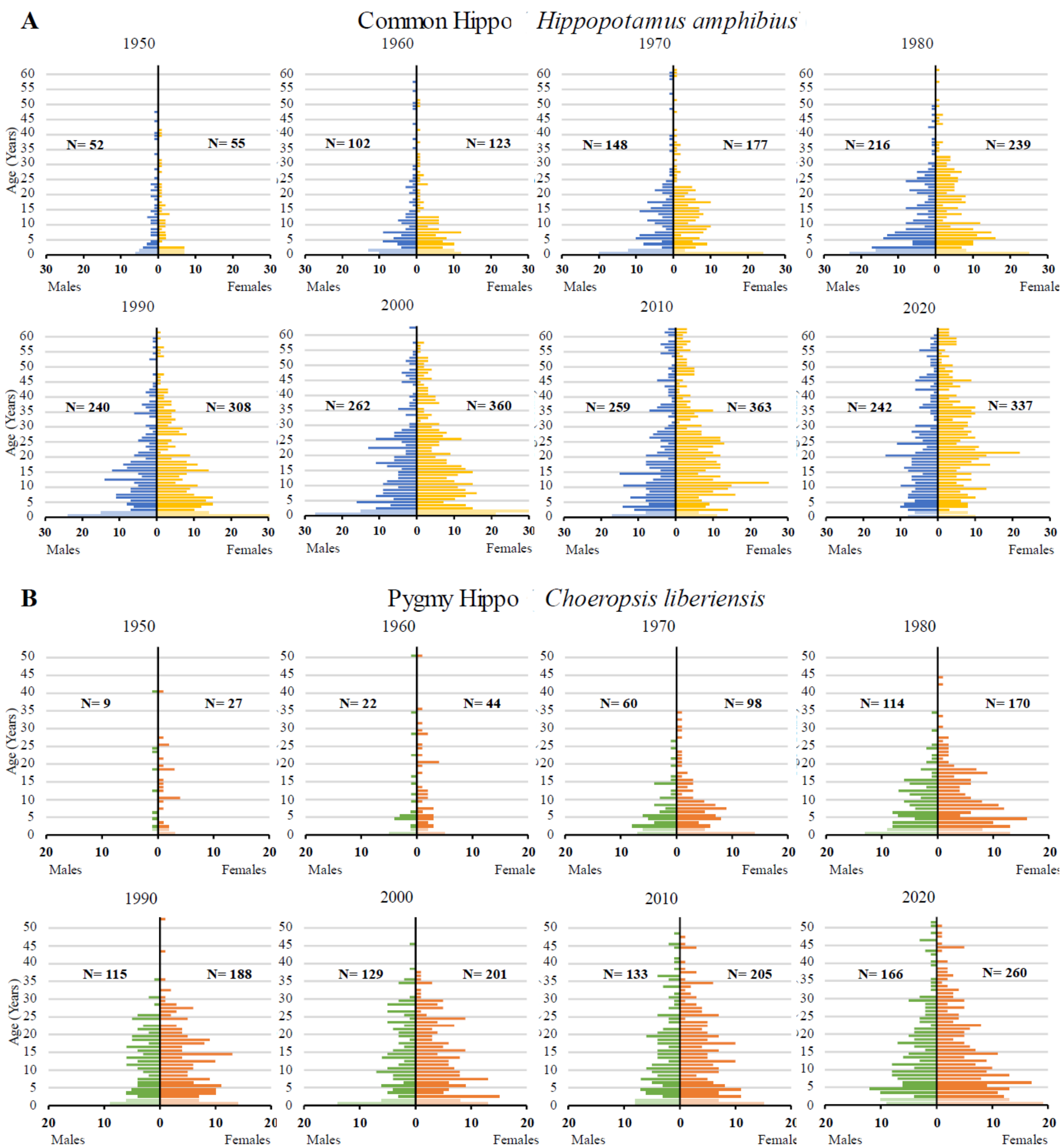

Figure 1. Global zoo-managed population “pyramids” of each hippo species in different decades. The data represent the number of animals alive on 1 January of the respective year. Males on the left side, and females on the right side. The large bold numbers represent the number of animals of each respective sex. Ages classes 0-1 (pre-reproductive) are in lighter shade.

(Zschokke 2002; Saragusty et al. 2012; Flacke et al. 2015; Pluháček and Steck 2015; Da Rè et al. 2018). For the pygmy hippo, a rapid rate of population growth occurred between 1960 and 1980 (Figure 2B) with a relatively high proportion of young animals in the population. In the 1980s, a strong reduction in growth occurred following the importation of the last wild-born individuals. Since the middle 2000s, population growth has regained momentum and is again rapid.

Survivorship analysis: Interspecies comparison

The survivorship lines of the two hippo species follow a clear type I pattern (Figure 3 inlets). For the whole cohort from 1900 until 2023, this translates into a median life expectancy of about 27 years for the common hippo and 23 years for the pygmy hippo for individuals that have surpassed two years of age. It should be noted that this median life expectancy does not apply to most recent cohorts. The survivorship line of the wild common hippo population of Queen Elizabeth Park (Laws 1968) has a steeper decline than the zoo cohorts of common hippos (Figure 3).

The common hippo has a significantly higher survivorship than the pygmy hippo (Table 1). Birth year was a significant factor with z being lower than one, indicating that animals of both species born more recently (=greater year of birth) had higher survivorship. However, there is a significant interaction between species and birth year, indicating that the change over time differed between the two species – being more pronounced in the pygmy hippo (Table 1). Including all animals older than two years of age born since 1900 or only those born after 1960 yielded similar results when comparing the two species (Table 1). When assessing the survivorship of only zoo-born animals up to two years of life, there was also a significant improvement over time for both periods, 1900-2023 and 1960 to 2023. Common hippos had lower juvenile survival in both periods than pygmy hippos (Table 1).

Common hippo

In the assessment of the common hippo alone, there was no improvement in survivorship of adult animals, regardless of whether animals born from 1900 or only born from 1960 onwards

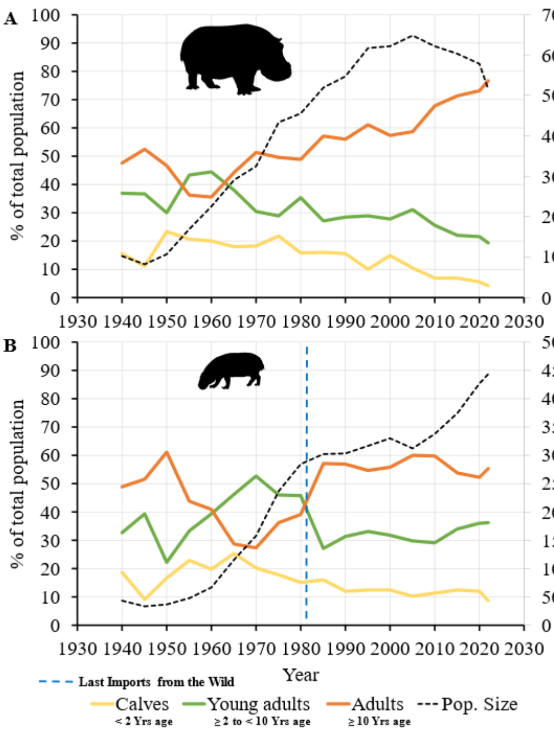

Figure 2. Changes in population size and composition of the global zoo-managed populations of each hippo species. A – Common hippo *Hippopotamus amphibius* B – Pygmy hippo *Choeropsis liberiensis*. The coloured lines represent the proportion of calves, young adults and adults alive in the population at the end of the respective time point; the broken line represents the global population size at the same time point. Pygmy hippo silhouette: ©T. Michael Keesey (after Marek Velechovský)

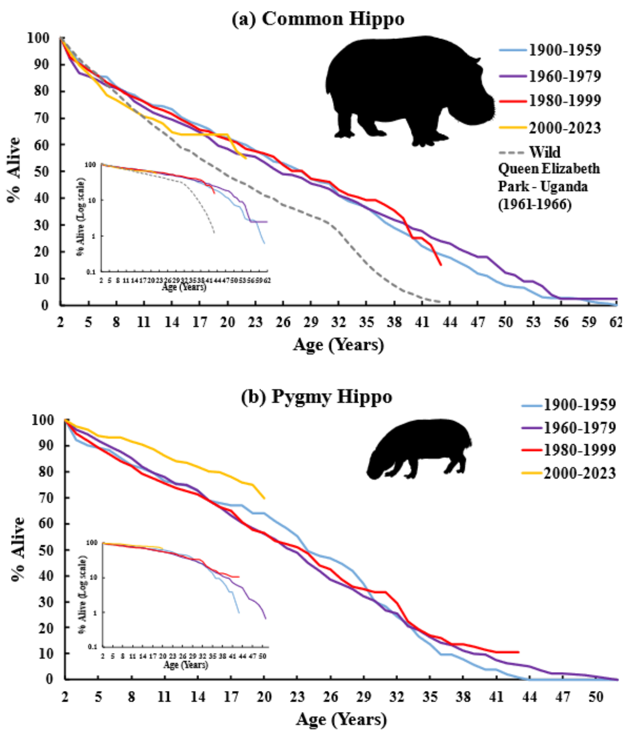

Figure 3. Survivorship of the two hippo species in zoos over time in animals ≥2 years of age since 1900. For statistics, see Tables 2 and 5. Note that statistics were also done using the year of birth as a continuous variable rather than the arbitrary cohorts displayed in the figure. Both zoo-born and wild-born animals are included in the figure. Data from a wild population (Laws 1968) is displayed in the common hippo (a). Maximum lifespans: Pygmy Hippo – 52 years, Common Hippo – 62 Years. Pygmy hippo silhouette: ©T. Michael Keesey (after Marek Velechovský)

Table 1. Comparative survivorship analyses (Cox proportional hazards) for the two hippo species in zoos worldwide.

Model		Coefficient (95% CI)	z	P
All animals ≥2 Years of age[a] From 1900 to 2023				
Reference: *C. liberiensis* (n=1039)	*H. amphibius* (n=1646)	$7.33e^{-10}$ ($1.74e^{-13}$, $3.08e^{-06}$)	-4.94	<.001***
	Birth Year	0.978 (0.972, 0.984)	-6.14	<.001***
	Species x Birth Year[b]	1.03 (1.02, 1.04)	5.52	<.001***
From 1960 to 2023				
Reference: *C. liberiensis* (n=936)	*H. amphibius* (n=1318)	$1.44e^{-25}$ ($2.13e^{-32}$, $9.77e^{-19}$)	-7.13	<.001***
	Birth Year	0.978 (0.972, 0.984)	-6.87	<.001***
	Species x Birth Year[b]	1.03 (1.02, 1.04)	7.14	<.001***
Survival till 30 days of age (zoo-born animals only) From 1900 to 2023				
Reference: *C. liberiensis* (n=1039)	*H. amphibius* (n=1646)	0.96 (0.855, 1.079)	-0.69	0.493
	Birth Year	0.995 (0.993, 0.997)	-4.23	<.001***
From 1960 to 2023				
Reference: *C. liberiensis* (n=936)	*H. amphibius* (n=1318)	0.967 (0.855, 1.093)	-0.54	0.587
	Birth Year	0.994 (0.99, 0.997)	-3.44	<.001***
Survival till 2 years of age (zoo-born animals only) From 1900 to 2023				
Reference: *C. liberiensis* (n=1039)	*H. amphibius* (n=1646)	1.26 (1.15, 1.39)	4.77	<.001***
	Birth Year	0.993 (0.991, 0.994)	-7.8	<.001***
From 1960 to 2023				
Reference: *C. liberiensis* (n=936)	*H. amphibius* (n=1318)	$5.36e^{+05}$ ($1.86e^{-06}$, $7.78e^{+10}$)	2.18	0.029*
	Birth Year	0.992 (0.987, 0.997)	-3.31	<.001***
	Species x Birth Year[b]	0.994 (0.988, 0.9995)	-2.14	0.033*

Abbreviation: CI (Confidence Interval). [a]Relative age was used in the model; [b]Model has a significant interaction.

were included in the model (Table 2, Figure 3a). The survival curve maintained the type I pattern across all cohorts (Figure 3a). Survivorship was significantly lower in males than in females (Table 2, Figure 4a). Wild-born animals had significantly higher survival than zoo-born animals in the period 1900–2023 but lower survival in the period 1960–2023 (Table 2; Figure 5a). However, when analysing animals older than four years of age, no difference is seen between wild-born and zoo-born animals during the period 1900–2023 (Table 2). Significant interactions between birth year and either sex or birth type indicate that the effect of birth year did not follow the same pattern for sexes or birth types.

Survivorship of juvenile animals up to 30 days of age improved in both periods with a particularly remarkable improvement in the 2000–23 cohort compared to 1900–59 and 1960–79 (Table 3, Figure 6a). No difference in survivorship was found regarding sex in zoo-born animals during their first 30 days of life (Table 3). During their first two years of life, survivorship improved generally over time. During their first two years of life, males had lower survivorship than females (Table 4). The day 0, day 30, first-year and second-year mortality was 15.2%, 33.2%, 43.2% and 54.8% in the 1900–59 cohort; 16.2%, 30.7%, 49.9%, and 62.3% in the 1960–79 cohort and 10.9%, 22.2%, 23.4%, 30.6%, and 38.6% in the 2000–23 cohort.

Pygmy hippo

When assessing the pygmy hippo, there was a significant improvement in adult survivorship, irrespective of whether animals born from 1900 or only born from 1960 onwards were included in the model (Table 5, Figure 3b). The survival curves also maintained the type I pattern (Figure 3b). Males had lower survivorship than females and wild-born animals had higher survival than zoo-born animals in the period 1900–2023; however, the same patterns cannot be observed in the 1960–2023 period (Table 5, Figure 4b).

Significant improvement in juvenile survivorship up to 30 days of age is observed in the 1900–2023 as well as in the 1960–2023 period (Table 6). The most recent cohort, 2000–23 has the most significant improvement in juvenile survivorship when compared with either the 1900–59 or 1960–79 cohorts (Table 6, Figure 6b). Zoo-born males had lower survivorship during their first 30 days of life than females (Table 6). Overall, survivorship during the first two years of life improved over time. Survivorship of zoo-born

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Table 2. Adult (≥2 years old) survivorship analyses (Cox proportional hazards) for common hippo *Hippopotamus amphibius* in zoos worldwide for different age groups and cohorts.

Model		Coefficient (95% CI)	z	P
H. amphibius ≥2 Years of age From 1900 to 2023 (n=1523)				
Reference: Females (n=797)	Males (n=726)	1.425 (1.258, 1.614)	5.57	<.001***
Zoo-Born (n=1383)	Wild-born (n=140)	0.811 (0.661, 0.994)	-2.02	0.043*
	Birth Year	0.998 (0.995, 1.001)	-1.39	0.165
From 1960 to 2023 (n=1235)				
Reference: Females (n=654)	Males (n=581)	1.486 (1.28, 1.72)	5.272	<.001***
Zoo-Born (n=1208)	Wild-born (n=27)	$2.17e^{+63}$ ($3.79e^{+04}$, $1.24e^{+122}$)	2.113	0.035*
	Birth Year	1 (0.997, 1.01)	0.822	0.411
	Birth Type x Birth Year[b]	0.929 (0.867, 0.995)	-2.111	0.035*
Cohorts from 1900 to 2023 (n=1523)				
Reference: Females (n=797)	Males (n=726)	1.5 (1.01, 2.24)	1.986	0.047*
Zoo-Born (n=1383)	Wild-born (n=140)	0.905 (0.724, 1.132)	-1.993	0.046*
Born 1900-59 (n=288)	Born 1960-79 (n=329)	1.042 (0.772, 1.406)	-0.895	0.371
	Born 1980-99 (n=476)	0.946 (0.686, 1.306)	-2.81	0.005*
	Born 2000-23 (n=430)	0.365 (0.218, 0.613)	-0.069	0.945
	Male x Born 1980-99[b]	0.595 (0.361, 0.979)	2.437	0.015*
Cohorts from 1960 to 2023 (n=1235)				
Reference: Females (n=654)	Males (n=581)	1.239 (0.986, 1.56)	1.839	0.065
Zoo-Born (n=1208)	Wild-born (n=27)	0.961 (0.607,1.52)	-0.17	0.865
Born 1960-79 (n=329)	Born 1980-99 (n=476)	0.741 (0.579, 0.95)	-2.384	0.017*
	Born 2000-23 (n=430)	1.027 (0.754, 1.4)	0.169	0.866
	Male x Born 1980-99[b]	1.536 (1.105, 2.14)	2.553	0.011*
H. amphibius ≥4 Years of age From 1900 to 2023 (n=1341)				
Reference: Females (n=654)	Males (n=624)	1.387 (1.211, 1.588)	4.73	<.001***
Zoo-Born (n=1206)	Wild-born (n=135)	0.898 (0.727, 1.109)	-1	0.316
	Birth Year	0.998 (0.995, 1)	-1.08	0.278

Abbreviation: CI (Confidence Interval); [b]Model has a significant interaction.

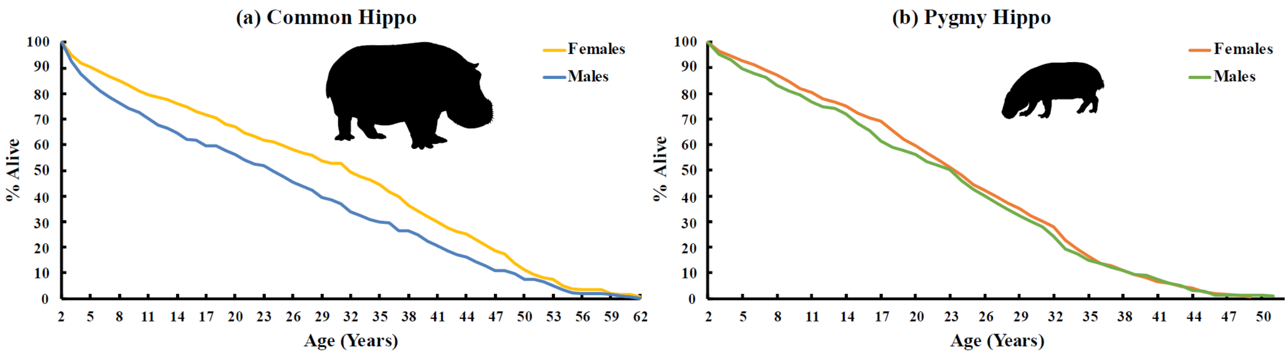

Figure 4. Survivorship of the two hippo species in zoos compared between sexes in animals ≥2 years of age since 1900. For statistics, see Tables 2 and 5. Pygmy hippo silhouette: ©T. Michael Keesey (after Marek Velechovský)

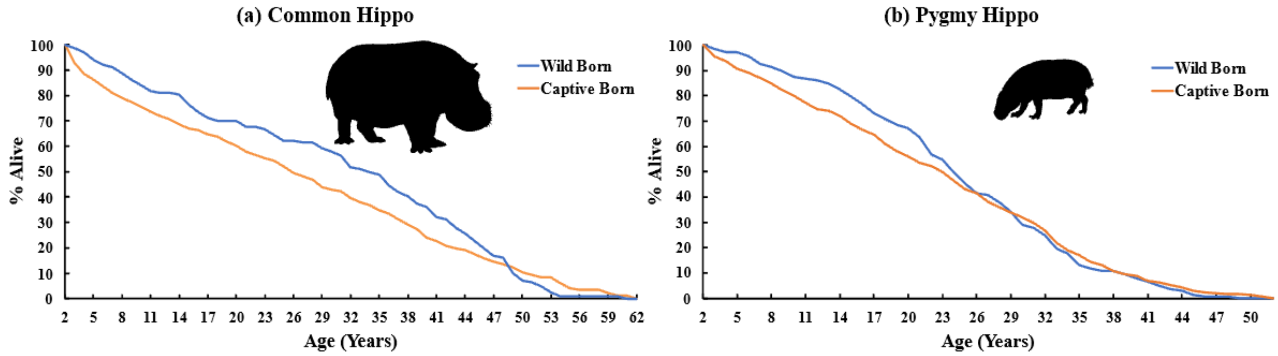

Figure 5. Survivorship of the two hippo species in zoos compared between zoo-born and wild-born in animals ≥2 years of age since 1900. For statistics, see Tables 2 and 5. Pygmy hippo silhouette: ©T. Michael Keesey (after Marek Velechovský)

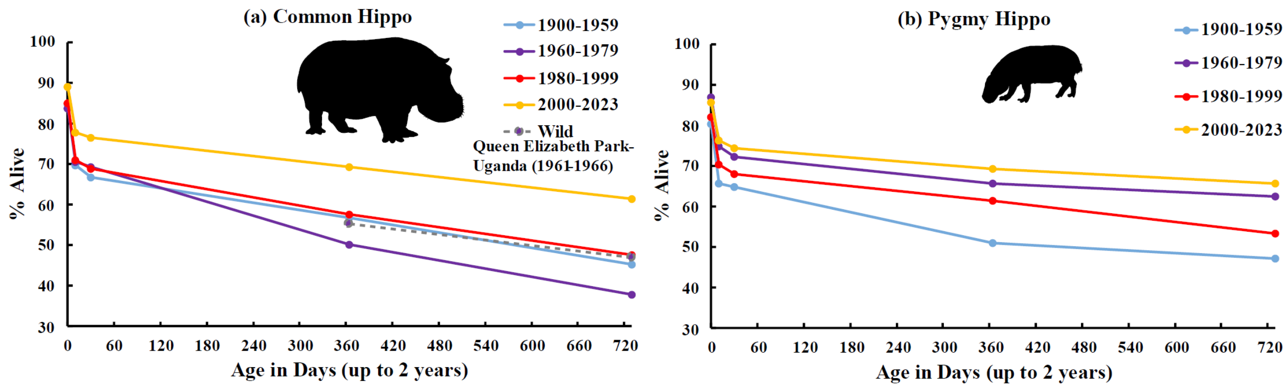

Figure 6. Neonate survival of the two hippo species in zoos. For statistics see Tables 3, 4, 6 and 7. Data from a wild population is displayed in the common hippo (a). Pygmy hippo silhouette: ©T. Michael Keesey (after Marek Velechovský)

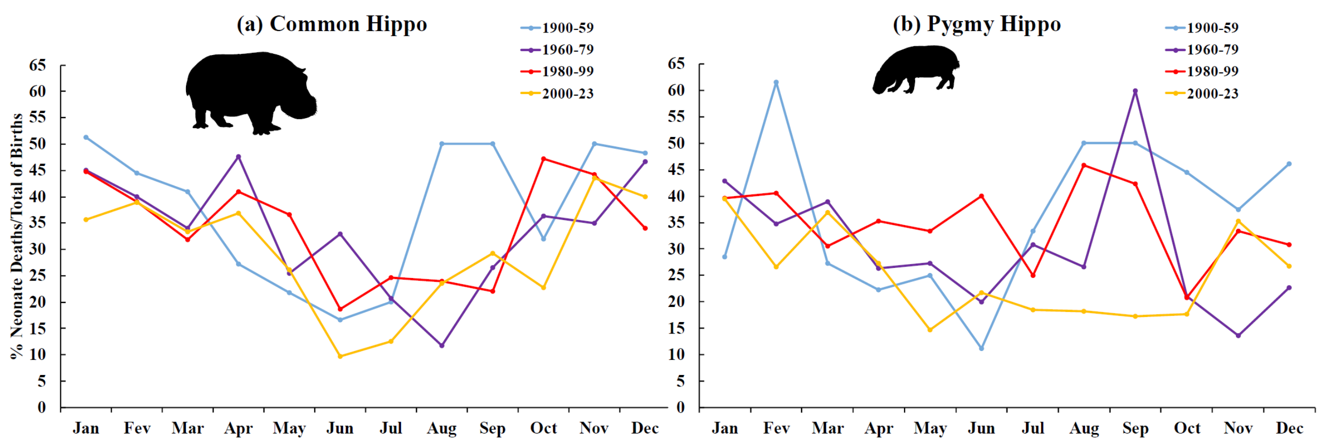

Figure 7. Seasonal juvenile mortality of the two hippo species in zoos by cohorts. These percentages are based on the total number of births observed in a given month in N. America, Europe and East Asia. Pygmy hippo silhouette: ©T. Michael Keesey (after Marek Velechovský)

http://doi/org/10.19227/jzar.v13i2.953

Table 3. Juvenile survivorship till 30 days of age analyses (Cox proportional hazards) for common hippo *Hippopotamus amphibius* in zoos worldwide for different age groups and cohorts.

Model		Coefficient (95% CI)	z	P
H. amphibius survival till 30 days of age (zoo-born animals only) From 1900 to 2023 (n=2941)				
Reference: Females (n=1314)	Males (n=1402)	1.076 (0.927, 1.249)	0.96	0.336
	Unknown (n=225)	4.514 (3.739, 5.45)	15.68	<.001***
	Birth Year	0.995 (0.992, 0.998)	-3.52	<.001***
From 1960 to 2023 (n=2552)				
Reference: Females (n=1148)	Males (n=1214)	1.046 (0.89, 1.229)	0.55	0.585
	Unknown (n=190)	4.403 (3.584, 5.409)	14.12	<.001***
	Birth Year	0.992 (0.988, 0.997)	-3.39	<.001***
Cohorts from 1900 to 2023 (n=2941)				
	Males (n=1402)	1.088 (0.937, 1.263)	1.11	0.269
	Unknown (n=225)	4.706 (3.893, 5.687)	16.02	<.001***
Born 1900-59 (n=389)	Born 1960-79 (n=825)	0.957 (0.774, 1.183)	-0.41	0.685
	Born 1980-99 (n=998)	0.985 (0.802, 1.210)	-0.15	0.885
	Born 2000-23 (n=729)	0.64 (0.509, 0.804)	-3.82	<.001***
Cohorts from 1960 to 2023 (n=2552)				
	Males (n=1214)	1.057 (0.899, 1.242)	0.67	0.501
	Unknown (n=190)	4.552 (3.702, 5.598)	14.37	<.001***
Born 1960-79 (n=825)	Born 1980-99 (n=998)	1.027 (0.869, 1.214)	0.32	0.753
	Born 2000-23 (n=729)	0.67 (0.551, 0.814)	-4.03	<.001***

Abbreviation: CI (Confidence Interval).

Table 4. Juvenile survivorship till two years of age analyses (Cox proportional hazards) for common hippo *Hippopotamus amphibius* in zoos worldwide for different age groups and cohorts.

Model		Coefficient (95% CI)	z	P
H. amphibius survival till 2 years of age (zoo-born animals only) From 1900 to 2023 (n=2941)				
Reference: Females (n=1314)	Males (n=1402)	1.222 (1.096, 1.362)	3.62	<.001***
	Unknown (n=225)	4.577 (3.888, 5.389)	18.26	<.001***
	Birth Year	0.993 (0.99, 0.995)	-7.31	<.001***
From 1960 to 2023 (n=2552)				
	Males (n=1214)	1.234 (1.098, 1.387)	3.54	<.001***
	Unknown (n=190)	4.645 (3.885, 5.553)	16.85	<.001***
	Birth Year	0.983 (0.98, 0.987)	-9.68	<.001***
Cohorts from 1900 to 2023 (n=2941)				
Reference: Females (n=1314)	Males (n=1402)	1.234 (1.107, 1.375)	3.79	<.001***
	Unknown (n=225)	4.902 (4.158, 5.78)	18.92	<.001***
Born 1900-59 (n=389)	Born 1960-79 (n=825)	1.208 (1.03, 1.418)	2.32	0.020*
	Born 1980-99 (n=998)	0.981 (0.836, 1.15)	-0.24	0.811
	Born 2000-23 (n=729)	0.573 (0.479, 0.686)	-6.09	<.001***
Cohorts from 1960 to 2023 (n=2552)				
Reference: Females (n=1148)	Males (n=1214)	1.245 (1.108, 1.399)	3.68	<.001***
	Unknown (n=190)	4.765 (3.981, 5.702)	17.04	<.001***
Born 1960-79 (n=825)	Born 1980-99 (n=998)	0.811 (0.718, 0.917)	-3.36	<.001***
	Born 2000-23 (n=729)	0.476 (0.411, 0.552)	-9.88	<.001***

Abbreviation: CI (Confidence Interval).

Table 5. Adult (≥2 years old) survivorship analyses (Cox proportional hazards) for pygmy hippo *Choeropsis liberiensis* in zoos worldwide for different age groups and cohorts.

Model		Coefficient (95% CI)	z	P
C. liberiensis ≥2 Years of age From 1900 to 2023 (n=1033)				
Reference: Females (n=630)	Males (n=403)	$1.32e^{+09}$ (149.7, $1.17e^{+16}$)	2.57	0.010*
	Wild-born (n=137)	$1.35e^{-16}$ ($1.44e^{-25}$, $1.3e^{-07}$)	-3.47	<.001***
Zoo-Born (n=902)	Birth Year	0.989 (0.984, 0.994)	-4.06	<.001***
	Sex x Birth Year[b]	0.989 (0.982, 0.998)	-2.57	0.010*
	BirthType x Birth Year[b]	1.02 (1.01, 1.03)	3.45	<.001***
From 1960 to 2023 (n=930)				
Reference: Females (n=569)	Males (n=361)	0.963 (0.805, 1.15)	-0.4	0.677
Zoo-Born (n=854)	Wild-born (n=82)	0.87 (0.67, 1.13)	-1.05	0.295
	Birth Year	0.978 (0.97, 0.99)	-5.4	<.001***
Cohorts from 1900 to 2023 (n=1033)				
Reference: Females (n=630)	Males (n=403)	1.502 (1, 2.24)	2	0.046*
Zoo-Born (n=902)	Wild-born (n=137)	0.905 (0.724, 1.132)	-0.87	0.382
Born 1900-59 (n=103)	Born 1960-79 (n=280)	1.042 (0.772, 1.406)	0.27	0.790
	Born 1980-99 (n=275)	0.946 (0.686, 1.305)	-0.34	0.736
	Born 2000-23 (n=375)	0.365 (0.218, 0.613)	-3.82	<.001***
	Male x Born(1980-99)b	0.595 (0.361, 0.979)	-2.04	0.041*
Cohorts from 1960 to 2023 (n=930)				
Reference: Females (n=569)	Males (n=361)	0.969 (0.81, 1.16)	-0.34	0.732
Zoo-Born (n=854)	Wild-born (n=82)	1.02 (0.787, 1.317)	0.14	0.890
Born 1960-79 (n=280)	Born 1980-99 (n=275)	0.884 (0.7, 1.08)	-1.2	0.229
	Born 2000-23 (n=375)	0.367 (0.255, 0.528)	-5.4	<.001***
C. liberiensis ≥4 Years of age From 1900 to 2023 (n=927)				
Reference: Females (n=565)	Males (n=362)	$2.99e^{+08}$ (8.53, $1.04e^{+16}$)	2.2	0.028*
Zoo-Born (n=794)	Wild-born (n=133)	$1.46e^{-16}$ ($5.73e^{-26}$, $3.74e^{-07}$)	-3.3	<.001***
	Birth Year	0.99 (0.984, 0.996)	-3.41	<.001***
	Sex x Birth Year	0.99 (0.982, 0.999)	-2.2	0.028*
	BirthType x Birth Year[b]	1.02 (1.01, 1.03)	3.29	<.001***

Abbreviation: CI (Confidence Interval); [b]Model has a significant interaction.

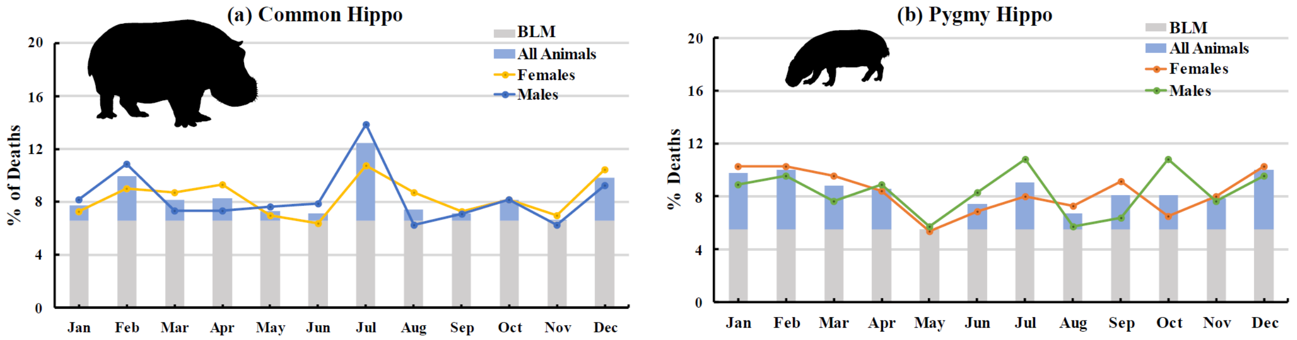

Figure 8. Seasonal adult (>2 years of age) mortality of the two hippo species in zoos. These proportions are based only on animals from North America, Europe and East Asia. BLM: Baseline mortality in grey. Pygmy hippo silhouette: ©T. Michael Keesey (after Marek Velechovský)

Table 6. Juvenile survivorship till 30 days of age analyses (Cox proportional hazards) for pygmy hippo *Choeropsis liberiensis* in zoos worldwide for different age groups and cohorts. Unknown refers to individuals of unknown sex.

Model		Coefficient (95% CI)	z	P
C. liberiensis survival till 30 days of age (zoo-born animals only) From 1900 to 2023 (n=1544)				
Reference: Females (n=864)	Males (n=608)	1.372 (1.127, 1.671)	-3.25	0.002*
	Unknown (n=72)	4.869 (3.567, 6.645)	9.973	<.001***
	Birth Year	0.993 (0.989, 0.997)	3.14	0.001*
From 1960 to 2023 (n=1442)				
Reference: Females (n=807)	Males (n=570)	$9.23e^{-09}$ ($1.93e^{-19}$, 0.044)	-1.47	0.140
	Unknown (n=65)	$8.03e^{+14}$ (7.25, $8.92e^{+28}$)	2.08	0.037*
	Birth Year	0.989 (0.981, 0.998)	-2.55	0.011*
	Unknown x Birth Year[b]	0.9838 (0.968, 1)	-1.97	0.049*
Cohorts from 1900 to 2023 (n=1544)				
Reference: Females (n=864)	Males (n=608)	3.049 (1.49, 6.238)	3.05	0.002*
	Unknown (n=72)	3.602 (1.162, 11.169)	2.22	0.026*
Born 1900-59 (n=102)	Born 1960-79 (n=320)	1.416 (0.757, 2.646)	1.09	0.276
	Born 1980-99 (n=513)	1.204 (0.654, 2.217)	0.6	0.551
	Born 2000-23 (n=609)	0.95 (0.514, 1.755)	-0.16	0.869
	Male x Born 1960-79[b]	0.231 (0.098, 0.54)	-3.38	<.001***
Cohorts from 1960 to 2023 (n=1442)				
Reference: Females (n=807)	Males (n=570)	0.703 (0.443, 1.115)	-1.5	0.134
	Unknown (n=65)	6.821 (3.239, 14.36)	5.05	<.001***
Born 1960-79 (n=320)	Born 1980-99 (n=513)	0.85 (0.598, 1.209)	-0.9	0.366
	Born 2000-23 (n=609)	0.671 (0.469, 0.959)	-2.19	0.029*
	Male x Born 1980-99[b]	2.288 (1.303, 4.016)	2.88	0.004*
	Male x Born 2000-23[b]	2.054 (1.159, 3.64)	2.46	0.014*

Abbreviation: CI (Confidence Interval); [b]Model has a significant interaction.

males was only significantly lower than females when animals from 1900 to 2023 were included in the model (Table 7). The day 0, day 30, first-year and second-year mortality was 19.6, 35.3%, 49% and 52.9% in the 1900–59 cohort; 13.1%, 27.8%, 34.4% and 37.5% in the 1960–79 cohort and 14.4%, 25.7%, 30.7% and 34.3% in the 2000–23 cohort.

Seasonal patterns of mortality

Seasonal juvenile mortality in common hippos kept at Northern latitude zoos seemed to follow a U-shaped pattern with remarkably higher mortality during the winter months (Figure 7). The Cox proportional hazard analysis for the effects of the season (Table 8) confirms that the individuals born in winter (October-March) had lower survival than those born in summer (April-September). There was no significant interaction between the season or the year of birth or the birth cohorts, indicating no change of the seasonal pattern over time. For pygmy hippos, neither the effect of season nor its interaction with year of birth or birth cohorts were significant (Table 8). Adult mortality for both common hippo and pygmy hippo was relatively evenly distributed across the year (Figure 8).

Discussion

Previous studies have revealed positive development in zoo adult survivorship in large terrestrial mammals such as elephants (Scherer et al. 2023), rhinoceroses (Wittwer et al. 2023), and giraffes (Scherer et al. 2024), as well as in other groups such as marine mammals (Tidière et al. 2023) or carnivores (Roller et al. 2021). This suggests continuous general improvements in animal husbandry over the last decades. The results of our study demonstrate that although both hippo species have a similar survivorship overall, with a very similar median life expectancy, they have different historical patterns of adult survivorship in Species360 member zoos over the last 120 years (Figure 3). Adult survivorship of common hippo older than two years of age appears

Table 7. Juvenile survivorship till two years of age analyses (Cox proportional hazards) for common hippo *Choeropsis liberiensis* in zoos worldwide for different age groups and cohorts. Unknown refers to individuals of unknown sex.

Model		Coefficient (95% CI)	z	P
C. liberiensis survival till 30 days of age (zoo-born animals only) From 1900 to 2023 (n=1544)				
Reference: Females (n=864)	Males (n=608)	1.343 (1.137, 1.586)	3.47	<.001***
	Unknown (n=72)	4.997 (3.763, 6.635)	11.12	<.001***
	Birth Year	0.991 (0.988, 0.995)	-4.91	<.001***
From 1960 to 2023 (n=1442)				
Reference: Females (n=807)	Males (n=570)	2.34e^{-05}(2.35e^{-14}, 2.3e^{+04})	-1.01	0.313
	Unknown (n=65)	3.35e^{+18}(7.4e^{+05}, 1.5e^{+31})	2.87	0.004*
	Birth Year	0.989 (0.982, 0.996)	-3	0.003*
	Male x Birth Year[b]	1.01 (0.995, 1.02)	1.03	0.301
	Unknown x Birth Year[b]	0.98 (0.966, 0.994)	-2.8	0.006*
Cohorts from 1900 to 2023 (n=1544)				
Reference: Females (n=807)	Males (n=570)	2.34e^{-05}(2.35e^{-14}, 2.3e^{+04})	-1.01	0.313
	Unknown (n=65)	3.35e^{+18}(7.4e^{+05}, 1.5e^{+31})	2.87	0.004*
	Birth Year	0.989 (0.982, 0.996)	-3	0.003*
	Male x Birth Year[b]	1.01 (0.995, 1.02)	1.03	0.301
	Unknown x Birth Year[b]	0.98 (0.966, 0.994)	-2.8	0.006*
Cohorts from 1900 to 2023 (n=1544)				
Reference: Females (n=864)	Males (n=608)	2.091 (1.18, 3.706)	2.53	0.011*
	Unknown (n=72)	4.377 (1.876, 10.212)	3.42	<.001***
Born 1900-59 (n=102)	Born 1960-79 (n=320)	0.956 (0.596, 1.533)	-0.19	0.852
	Born 1980-99 (n=513)	0.974 (0.622, 1.525)	-0.12	0.907
	Born 2000-23 (n=609)	0.657 (0.416, 1.038)	-1.8	0.072
	Male x Born 1960-79[b]	0.402 (0.202, 0.801)	-2.59	<.001*
Cohorts from 1960 to 2023 (n=1442)				
Reference: Females (n=807)	Males (n=570)	0.841 (0.573, 1.235)	-0.883	0.377
	Unknown (n=65)	8.197 (4.076, 16.483)	5.903	<.001***
Born 1960-79 (n=320)	Born 1980-99 (n=513)	1.019 (0.756, 1.375)	0.125	0.901
	Born 2000-23 (n=609)	0.687 (0.503, 0.94)	-2.349	0.019*
	Male x Born 1980-99[b]	1.846 (1.16, 2.939)	2.585	0.010*
	Male x Born 2000-23[b]	1.644 (1.013, 2.67)	2.01	0.044*

Abbreviation: CI (Confidence Interval); [b]Model has a significant interaction.

to be essentially unchanging (at a high level) across the cohorts, whereas an improvement is observed in the pygmy hippo. Whilst Flacke et al. (2016) did not find any statistical difference in mortality rates for pygmy hippos between 1919–1940 and 1976–2014 for any age class, the present study emphasises improvement in the last two decades (2000–23). However, remarkable improvements in juvenile survivorship are observed in both species.

The difference in survivorship improvements may be attributed to the fact that in common hippos, which are relatively hardy (not too sensitive to cold, disease or stress, and easy to feed), adult survivorship reached peak values relatively early compared to the more delicate pygmy hippo. Another factor potentially explaining the recent improvement in pygmy hippo survivorship may not only be the existence of husbandry guidelines, which were recently updated (von Houwald et al. 2020) but also the fact that the pygmy hippo studbook has always contained information on husbandry practices. Even though direct effects are difficult to prove, previous studies suggested an association between husbandry guidelines and historical husbandry success (Müller et al. 2011; Tidière et al. 2023; Scherer et al. 2024). Such efforts also manifest themselves in recent research on pygmy hippo care in zoos focusing on topics such as diet, disease, and causes of mortality, among others (Fisher et al. 2007; Nees et al. 2009; Taylor et al. 2013; Flacke et al. 2015; Flacke et al. 2016; Da Rè et al. 2018; deMaar et al. 2021). Whereas the pygmy hippo population is managed by a WAZA international studbook, the common hippo population is managed by separate regional studbooks, and fewer guidelines are available (Jones 2008; Snyder 2015).

Table 8. Survivorship analyses (Cox proportional hazards) for seasonal mortality for juvenile (till 30 days of age) hippos in zoos of the northern hemisphere (Europe, North America and East Asia).

Model		Coefficient (95% CI)	z	P
H. amphibius juvenile season mortality till 30 days of age (zoo-born and temperate northern hemisphere animals only) From 1900 to 2023 (n=2056)				
Reference: Summer (n=1178)	Winter (n=878)	1.695 (1.453, 1.976)	6.73	<.001***[a]
	Birth Year	0.996 (0.993, 0.999)	-2.35	0.019*[a]
	Winter x Birth Year	1 (0.994, 1)	0.14	0.886
Cohorts from 1900 to 2023 (n=2056)				
Reference: Summer (n=1178)	Winter (n=878)	1.684 (1.444, 1.964)	6.64	<.001***[a]
Born 1900-59 (n=324)	Born 1960-79 (n=669)	0.901 (0.719, 1.131)	-0.9	0.37[a]
	Born 1980-99 (n=673)	0.919 (0.734, 1.151)	-0.74	0.46[a]
	Born 2000-23 (n=390)	0.731 (0.56, 0.953)	-2.32	0.02*[a]
	Season x Cohort	-	-	n.s.
C. liberiensis juvenile season mortality till 30 days of age (zoo-born and temperate northern hemisphere animals only) From 1900 to 2023 (n=1149)				
Reference: Summer (n=479)	Winter (n=670)	1.171 (0.945, 1.449)	1.45	0.149[a]
	Birth Year	0.994 (0.989, 0.998)	-2.75	0.006*[a]
	Season x Birth Year	1 (9.96e-01, 1.015)	1.12	0.265
Cohorts from 1900 to 2023 (n=1149)				
Reference: Summer (n=479)	Winter (n=670)	1.177 (0.951, 1.458)	1.497	0.134[a]
Born 1900-59 (n=94)	Born 1960-79 (n=247)	0.78 (0.522, 1.165)	-1.21	0.225[a]
	Born 1980-99 (n=369)	0.941 (0.648, 1.367)	-0.32	0.75[a]
	Born 2000-23 (n=439)	0.664 (0.455, 0.968)	-2.13	0.034*[a]
	Season x Cohort	-	-	n.s.

Abbreviation: CI (Confidence Interval); n.s. not significant; [a]Statistics for the model but without interactions when no significant interactions are found (statistics for the interaction are also displayed).

Common hippos are generally described as very sturdy and disease-resistant (Lindau et al. 1982; Snyder 2015) and perhaps 'naturally well-adapted' to husbandry under human care, suggesting that very little remains to improve their adult survivorship further. In any case, whether the stagnation seen in common hippo is the result of an intrinsic biological limitation of the species to live longer, irrespective of the husbandry, or due to requirements not addressed by the current husbandry system, is difficult to tell. In the case of an intrinsic limitation, one might usually expect a type I survivorship as detected in the present study. As highlighted by Tennant et al. (2018), research on common hippo care in zoos remains rather neglected. Nevertheless, many zoos have been making great efforts to build new and improved hippo enclosures in the last 20 years. Such examples are the innovative Zoo Berlin's Hippo House built in 1997 (Schlaich and Schober 1997), followed by Disney's Animal Kingdom's Hippo River (1998), Bioparc Valencia's Kitum Cave (2008), Cologne Zoo's Hippodom (2010), Prague Zoo's Hippo Pavilion (2012), Wroclaw Zoo's Africarium (2014), Cincinnati Zoo's Hippo Cove (2016), Dallas Zoo's Zambezi River (2016), ZooParc Beauval's Hippo Reserve (2016), among others (information gleaned from the respective zoos's websites). While definitely making impressive exhibits, the welfare and husbandry aspects of these enclosures have, to our knowledge, not been evaluated so far. Whether these modern enclosures will result in increases in common hippo survivorship is impossible to predict. As a long-lived species, the effects of current developments in husbandry will only be detectable in terms of adult survivorship patterns many years from now (Tidière et al. 2016; Scherer et al. 2023). Given that common hippos also achieved high longevities in 'old style' enclosures (J. Pluháček pers. obs.), adult survivorship may not be the most suited indicator of the quality of husbandry in this species. However, the observation that juvenile survivorship of common hippos increased distinctively in recent years (in the 2000–2023 cohort) could also be considered an indication that the modern, more spacious enclosures have a positive effect.

The survivorship of common hippos in the wild, as described by Laws (1968) for Queen Elizabeth Park, appears to be lower than the one observed in the common hippo population from zoos. Similar results have been previously reported when comparing zoo data of common hippos to that of Laws' (1968) wild population (Lynch et al. 2010; Tidière et al. 2016). Wild hippo populations are known to suffer strong fluctuations in their mortality rates (which shape the pattern of a survival curve) due to rapid variations in rain patterns, food availability, poaching pressure and disease outbreaks (Laws 1968; Lewison 2007; Chomba 2013). All these factors impacting hippo mortality in the wild have no impact on zoo populations. Whether the data collected by Laws (1968) was during a high or low mortality rate period influenced by any of these environmental factors is unknown. Although this may suggest that common hippos achieve longer lives under human care, it is important to stress that no safe conclusions can be taken when only a single wild population is used as a comparison.

Adult male common hippos in zoos show lower survivorship than females (Figure 4, Table 2), which might highlight the present difficulties in managing the social and territorial behaviour of hippos in zoos, in particular for males. For both sexes, introducing a new individual to an established group is always a risky procedure due to potential incompatibility that may lead to aggression and fatalities (Jones 2008). Young males must be separated from the group when an adult dominant male is present to prevent fighting (Jones 2008), recreating the dynamic seen in the wild (Eltringham 1999). We expect that efforts are made to keep individuals separate in eventual antagonistic behaviour and prevent fights; however, facilities that allow separation may not always have been available to zoos and fights might have sometimes occurred, with some leading to fatalities (Jones 2008). The data did not allow determining if these social grouping management challenges have affected males more often than females. Furthermore, the absence of a significant difference in adult mortality between the two sexes in pygmy hippo, which is mostly managed as a solitary animal, suggests that social biology may have contributed to the observed pattern. For instance, Tidière et al. (2015) described that males of polygamous zoo ruminants have a shorter lifespan than males of monogamous species, and Carisch et al. (2017) described that in zoo ruminants, males of polygamous species have more pronounced seasonal mortality than those from monogamous species.

The high mortality of juvenile male pygmy hippos (up to 30 days of age) but the absence of such a difference in adults (≥2 years of age) found in our analysis corroborates previous findings related to the biased sex ratio described for the zoo population. The increased mortality of young males is one of the contributors to the skew in sex ratio (Zschokke 2002; Saragusty et al. 2012; Pluháček and Steck 2015; Da Rè et al. 2018). Our results show that overall, there is higher mortality in juvenile males than in females, but when analysing just the most recent period (1960–2023), this difference is no longer significant (Tables 6 and 7), suggesting that juvenile male mortality was reduced. In the study of Flacke et al. (2016), the main causes of juvenile death were weakness, trauma and maternal neglect. Our analysis shows that improvement in juvenile survivorship is evident, at least in the most recent cohort (2000–23). Such improvement could be the result of important historical husbandry alterations, for example, improved hygiene standards, recognition that this species does not give birth in water like the common hippo, and separation of the male during the calf's birth and rearing (Flacke et al. 2016). The inbreeding level has been pointed out as being related to mortality in juvenile pygmy hippos, suggesting that population management may also play a role in the mortality rates (Da Rè et al. 2018).

For common hippos, distinct improvements were made in juvenile survivorship in the last two decades (2000–23). While the historical survival of juvenile common hippos (between one and two years of age) in zoos seems to have been similar to the wild, 53% in Queen Elizabeth Park (Laws 1968), the recent improvement is remarkable. However, the 39% of juvenile mortality (until 2 years of age) observed in the 2000–23 cohort is still comparable to the 42% described by Peek and O'Connor (2023) for a wild hippo population in Zimbabwe. Juvenile mortality in common hippos is more prevalent during winter months in zoos in the temperate northern hemisphere (Figure 7a, Table 8). This may be linked to the extensive time that the animals must stay indoors, and hence in closer contact with conspecifics. Indoor enclosures for common hippos are often considered small (Tennant et al. 2018), which may potentiate the risk of adults involuntarily drowning or trampling, or deliberately attacking young calves, and which might also lead to suboptimal hygienic conditions, for example in terms of water quality. However, to our knowledge, evidence to support this reasoning does not exist. The absence of the same pattern in pygmy hippo might support this claim due to this species' smaller space requirements, because it gives birth on land, and is generally kept solitarily.

Regarding the survivorship between zoo-born and wild-born hippos, we observed different results when using different age cut-offs for common hippos (Table 2). Wild-born common hippos from two years of age onwards had higher survivorship than zoo-born specimens, but this was no longer visible when analysing animals from four years of age onwards. Moreover, Kohler et al. (2006) could not find any significant differences between wild-born and zoo-born animal survivorship after five years of age in several zoo populations. The difference seen between these different age cut-offs suggests that many wild-born hippos were imported older than two years of age, leading to a spurious underestimation of mortality in this subpopulation (as no mortality at lower ages could be reported for this group). Similar results were seen in the rhinoceros zoo population (Wittwer et al. 2023). Thus, the act of importation, per se, filters out the mortality, overestimating the survivorship in the wild-born sub-population if the animals are imported above the age cut-off chosen for the analysis. However, because the age at the time of import was not available to us, we could not control for this effect in another way. Additionally, the practice that wild-born animals were often placed in empty enclosures without conspecifics (J. Pluháček pers. obs.) possibly reduced fatalities due to intra-specific aggression.

The historical population pyramids of common hippos in zoos show a progression from a narrow-base pyramid (probably due to the import of animals from the wild) towards, first, a wide-base pyramid shape typical of a fully breeding population, but then towards the columnar pattern typical of an ageing population with little reproduction (Figure 1A). In common hippos, breeding is limited by both segregation of sexes and contraception (M. Roller and J. Pluháček pers. obs.). A similar development of the population pyramid that bespeaks a limitation of offspring production has been noted in giraffes (Scherer et al. 2024). While reproductive senescence or infertility is of great general concern in breeding programmes (Penfold et al. 2014), common in mammals (Lemaître et al. 2020), and an evident danger for population sustainability when the proportion of old individuals increases, hippos seem to be able to breed across almost their whole lifespan (Laws and Clough 1966; Lemaître et al. 2020; Pluháček and Garguláková 2021). Therefore, breeding could theoretically be instigated even in an older population if sufficient male-female pairs exist, and if considerations of placing offspring would not predominate.

The population pyramid development in the common hippo zoo population indicates a dilemma that might occur in many zoo populations: At some point, an expansion of the population is no longer possible due to a saturation of holding space and increasing husbandry success reducing uncontrolled trauma- or disease-related mortality. The limited space will by necessity be filled with individuals of advanced age, and reproduction needs to be reduced or even halted. In other words, historical progress in husbandry leads to a development that may make populations less sustainable – unless a management strategy of controlled mortality ('management euthanasia' or 'culling') is instigated (Bertelsen 2019). Management euthanasia is part of the currently endorsed population management strategies of both AZA (2016) and EAZA (2024), has been repeatedly promoted in the zoo community (Bertelsen 2019; Clauss et al. 2025), and has been specifically recommended in the common hippo EAZA Ex Situ Programme (EEP) (Pluháček and Garguláková 2021). We advocate that by allowing young animals to be born and replacing older individuals (breed-and-cull), this strategy could reverse the demographic trend evident in the population pyramids and make the population more sustainable in the long term. By contrast, pygmy hippos do not seem to suffer from a reduction in population size or reduction in breeding, possibly also because their smaller size makes the recruitment of new holding institutions easier.

We emphasize that increased and continuous attention to hippo husbandry and behaviour is needed, and an ethical obligation of zoos – as is sustainable and responsible population management. Thus, a shift towards approaches that safeguard the long-term sustainability and health of ex situ populations, such as management euthanasia, will be important for the conservation of these iconic animals. Furthermore, the expertise obtained with these species in zoos can yield important knowledge and skills that can be utilized for the management of wild populations. For instance, for the pygmy hippo, due to its evasiveness in the wild, most of what is known about the species' biology was obtained from zoo-kept animals. Well-managed zoo hippo populations not only represent potential insurance against extinction but function as ambassadors and as education and research assets that strengthen the one-plan approach for global hippo conservation (Conde et al. 2013; Farhadinia et al. 2020).

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