







# The historical development of zoo elephant survivorship

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## Abstract

In the discussion about zoo elephant husbandry, the report of Clubb et al. (2008, *Science* 322: 1649) that zoo elephants had a “compromised survivorship” compared to certain non-zoo populations is a grave argument, and was possibly one of the triggers of a large variety of investigations into zoo elephant welfare, and changes in zoo elephant management. A side observation of that report was that whereas survivorship in African elephants (*Loxodonta africana*) improved since 1960, this was not the case in Asian elephants (*Elephas maximus*). We used historical data (based on the Species360 database) to revisit this aspect, including recent developments since 2008. Assessing the North American and European populations from 1910 until today, there were significant improvements of adult ( $\geq 10$  years) survivorship in both species. For the period from 1960 until today, survivorship improvement was significant for African elephants and close to a significant improvement in Asian elephants; Asian elephants generally had a higher survivorship than Africans. Juvenile ( $< 10$  years) survivorship did not change significantly since 1960 and was higher in African elephants, most likely due to the effect of elephant herpes virus on Asian elephants. Current zoo elephant survivorship is higher than some, and lower than some other non-zoo populations. We discuss that in our view, the shape of the survivorship curve, and its change over time, are more relevant than comparisons with specific populations. Zoo elephant survivorship should be monitored continuously, and the expectation of a continuous trend towards improvement should be met.

## KEYWORDS

husbandry, mortality, Proboscidea, progress, survival

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## 1 | INTRODUCTION

When discussing the relevance and justification of zoological gardens, charismatic flagship species play a peculiar role as outstanding examples used to discuss the effect of captivity on animals. In maybe the most memorable publication of the recent past that assessed the effect of captivity on a nondomestic species, Clubb et al. (2008) concluded that zoo elephants (*Loxodonta africana*, *Elephas maximus*) had a “compromised survivorship.” The judgment of “compromised” was made when comparing zoo elephant survival against “two well-documented in situ populations judged to yield demographic benchmarks that zoos should reasonably meet or exceed” (Clubb et al., 2009). To generate these benchmarks, survival data in the in situ populations was corrected for human-induced mortality in wild African elephants, and for the consequence of “breaking in” Asian timber elephants (Clubb et al., 2008; Mason & Veasey, 2010b).

Possibly also in reaction to this publication, research on zoo elephant welfare intensified (Mason & Veasey, 2010a), leading to one of the most comprehensive, concerted investigations of welfare for nondomestic species (Carlstead et al., 2013) with results documented in a special issue of a scientific journal (Meehan et al., 2016), and many more studies than can be cited here. Zoo elephant husbandry has undergone distinct changes during the past 25 years. In particular, a shift from “direct contact” to “protected contact” systems began with a concomitant abandoning of physical coercion and chaining (Proctor & Brown, 2015; Wilson et al., 2015). The awareness of the relevance of social structures of elephant herds led to a different approach to group composition and kin separation (Finch et al., 2021; Schmid et al., 2001; Schmidt & Kappelhof, 2019). Intensive building activity led to new elephant enclosures around the world that not only provide more absolute space per animal but also more structure and animal-environment interaction potential (Finch et al., 2021; Glaeser et al., 2021). Obesity has been considered a problem in elephant husbandry and reproduction (Clubb et al., 2009; Hatt & Clauss, 2006), yet there is indication that body condition scores—at least in the European populations—have tended to decrease since 2000 (Schiffmann et al., 2019). Major standard textbooks on elephant medicine have been published since 1990 (Csuti et al., 2001; Fowler & Mikota, 2006; Mikota et al., 1994), providing information for improved medical care. Due to the long lifespan of elephants, the putative effects these changes might have on their survivorship may only take effect in the future.

The publication by Clubb et al. (2008) derived from a report on zoo elephant welfare (Clubb & Mason, 2002), in which numerical data in the form of “medium life span” had been compared between zoo elephants and elephants from in situ reference populations. These data had been criticized for two reasons: (i) deriving a mean life expectancy while including animals subject to historical husbandry conditions might not reflect current husbandry practices; (ii) calculating an average age at death for all animals that have died does not account for the potential lifespans of those animals still alive (Wiese & Willis, 2004).

In the reverberations of the original publication, one of its findings and resulting recommendations seems to have gone largely unnoticed. Clubb et al. (2008) noted that “zoo African adult survivorship has improved in recent years” (without a similar development in the Asian elephants), and Clubb et al. (2009) recommended that the reasons for the difference between the species in this respect should be investigated. For different nondomestic species, a historical improvement of zoo survivorship has been documented, including orangutans (*Pongo* sp.) (Wich et al., 2009), orcas (*Orcinus orca*) (Jett & Ventre, 2015), bottlenose dolphins (*Tursiops truncatus*) (Jaakkola & Willis, 2019) or chimpanzees (*Pan troglodytes*) (Havercamp et al., 2019), and many members of the Carnivora (Roller et al., 2021). Irrespective of the question how far off zoos may (or may not) be from a specific benchmark, the question whether zoos are making progress in the husbandry of a species, in terms of improving in the measure under investigation, is also a crucial one.

Our aim in this contribution was to reassess potential historical changes in zoo elephant juvenile mortality and adult survival, including the new data available since 2008. Because such analyses may hinge on the data set used for the evaluation, we used a double approach. First, we used all data on elephants born between 1910 and 2019 available in the Species360 database, excluding only individuals with implausible data. Second, we used a carefully curated data set using various supplemental information and criteria. We performed analyses on the whole data set to reflect changes since the beginning of zoo husbandry, as well as only on animals born since 1960 for a direct comparison with Clubb et al. (2008) and an assessment of more recent developments.

## 2 | MATERIALS AND METHODS

We obtained records for both elephant species from Species360 (ZIMS for Husbandry), an online database platform that is used by more than 1200 zoos worldwide to manage their animal data, with dates of birth and death, from which the subsequent data were calculated (Species360 Research Data Agreement # 2019-Q3-RR3). The assumed maximum longevity was based on the AnAge database (de Magalhães & Costa, 2009). Thus, the maximum lifespan was set to 65 years in African and 79 years in Asian elephants. For the first data set (“uncurated data set”), the only correction applied to the data was the exclusion of those individuals with implausible ages (e.g., animals with a death date before their birth date, or elephants reportedly more than 100 years old), leading to the elimination of nine individuals from the data set (total  $n = 765$  African and 1380 Asian elephants born between 1910 and 2019 alive at  $\geq 10$  years of age), and any animals lost to follow-up. This data set was only used to assess the historical development of survival of individuals  $\geq 10$  years of age.

Subsequently, this data set was curated (“curated data set”). All elephants were excluded that were not kept in Europe and North America, reflecting the assumption that historical developments should be most evident in these regions with a long history of elephant husbandry by a large number of zoos in the data set. Note

that this does not imply a lesser standard of husbandry in other countries, only that historical developments may be less easily traced. Any multiple entries (e.g., if an animal was entered as a new individual in the database rather than continuing its record after transfer to another zoo) were excluded, updating the history of the respective animal. For African elephants, any known forest elephants *Loxodonta cyclotis* ( $n = 34$  animals) were excluded, assuming that this species may react differently to captivity than *L. africana*. Lost-to-follow-up animals were excluded. Animals known to have lived in zoos, but not present in the Species360 data set, were added, utilizing information available online at The Elephant Database (Koehl, 2022).

Due to these additions, the final data set included 1082 African and 1949 Asian elephants (born between 1910 and 2019). This data set was also used to assess the historical development of survival of individuals  $\geq 10$  years of age. From this data set, we pruned only zoo-born animals to additionally assess survival up to 10 years of age. In the experience of one of the coauthors (L. B. L.), 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. This would result in an underestimation of positive developments in neonate mortality (Roller et al., 2021). The same might apply for stillbirths.

The endpoint of survival was set to the end of March 2022. We followed Clubb et al. (2008) in analyzing juvenile (animals  $< 10$  years of age) and adult (animals  $\geq 10$  years of age) separately, because these represent different life stages also in terms of zoo management. 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 [CI] 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 1910–1939, 1940–1959, 1960–1989, 1990–2009, 2010–2019) as discrete categories or the year of birth as a continuous variable, both for the whole data set and only for individuals born from 1960 onwards. 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. Additionally, the survival of African vs Asian elephants was compared for all animals born since 1960, using either the absolute age or the relative age (in % of the defined maximum lifespan, see above). In these analyses, the species  $\times$  year of birth interaction was also 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 .05 and .09 were considered "close to significant." The proportional hazards are reported with their 95% CI. For visual comparison only, survival curves for individuals  $\geq 10$  years of age were taken from the literature (Clubb et al., 2008; Foley & Faust, 2010; Gough & Kerley, 2006; Mar, 2007; Moss, 2001; Sukumar, 1992; Wittemyer et al., 2013).

### 3 | RESULTS

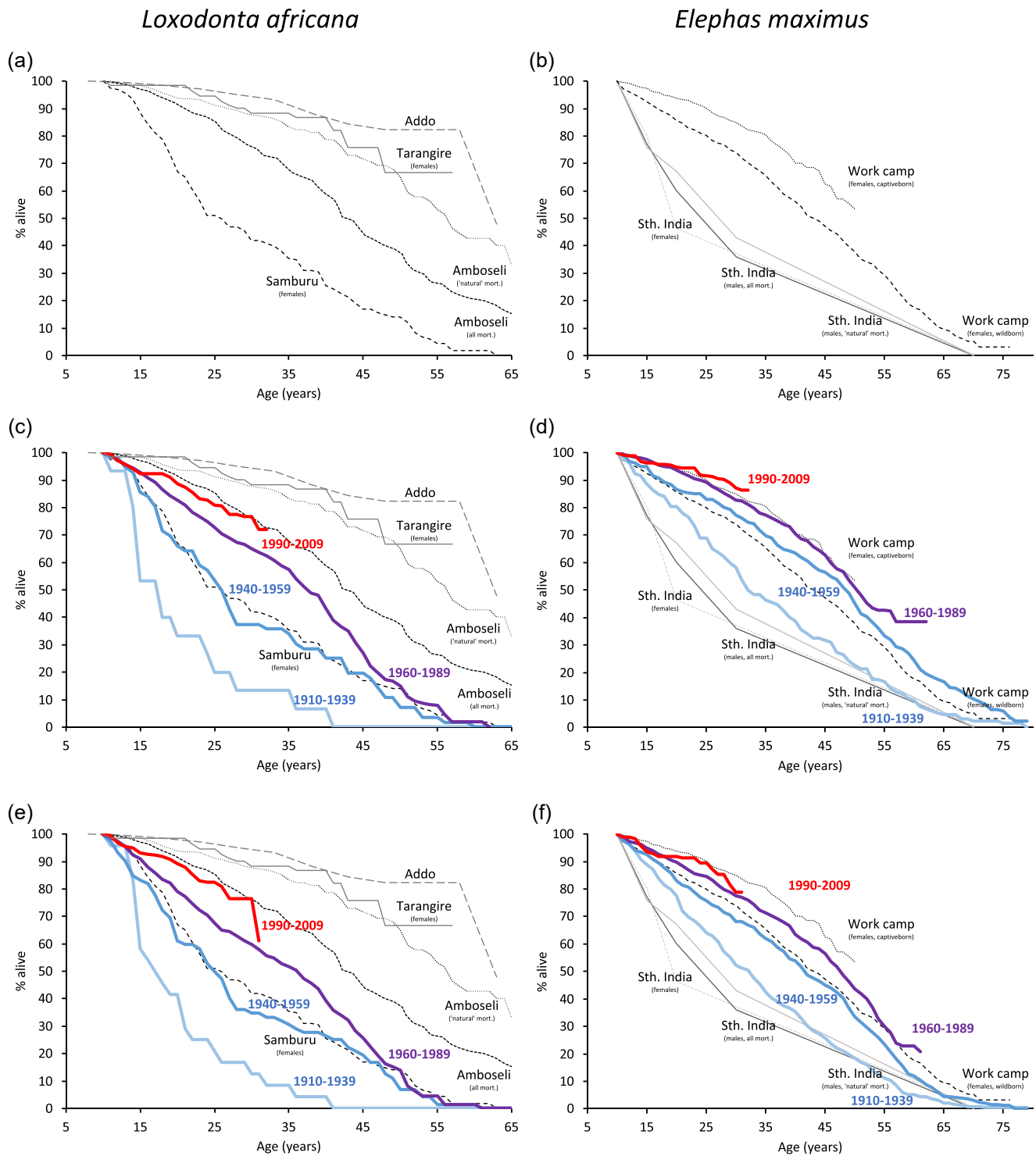
There is distinct variation in data from "free-ranging" and "in situ" (aka "non-zoo") populations from the literature (Figure 1a,b). For African elephants, survivorship has been published that is both lower and higher than the Amboseli population used as the reference by Clubb et al. (2008). For Asian elephants, the—to our knowledge—only data for a free-ranging population is one with intense conflict with humans, and its survivorship is distinctively lower than that for Myanmar timber elephants used as the reference by Clubb et al. (2008).

For the total global zoo population ("uncurated data set"), an improvement of survival of animals  $\geq 10$  years of age over time appeared evident for both species (Figure 1c,d), which was confirmed by statistical analyses (Table 1). The improvement was more distinct in African than in Asian elephants, due to the poor survival of the earliest cohort of imported African elephants. The historical improvement was significant, irrespective of whether it was assessed by distinct cohorts or by birth year as a continuous variable. For the cohort approach, the proportional survival hazard decreased over time, again indicating continuous improvement. For African elephants, the improvement over time using birth year as a continuous variable was significant, irrespective of whether all animals born since 1910 or only those born since 1960 were considered; note that the proportional hazard coefficients for the birth year were very similar for the two cohorts. In Asian elephants, improvement over time was only significant for the data set of animals born since 1910, but not for animals born only since 1960 (Table 1). For the most recent time period of the discrete categories (2010–2019), the analysis did not yield a reliable result, due to the small sample size (yet results were identical when running the analysis without this cohort).

Very similar results were obtained for the combined North American and European population ("curated data set," Figure 1e,f, Table 2). However, in this case, also for Asian elephants born only since 1960, there was a close to significant improvement with time when using year of birth as a continuous variable ( $p = .070$ , Table 2).

When comparing the two species for all animals born since 1960  $\geq 10$  years of age with absolute ages, there was significant survivorship improvement with time, and Asian elephants had a significantly higher survivorship; however, there was a significant species  $\times$  birth year interaction, making these findings unreliable (Table 3). This interaction was not significant when comparing the species with relative ages. In this case, overall survivorship again increased over time, and survivorship was significantly higher in the Asian compared to the African species (Table 3).

For the survival of zoo-born animals from birth to 10 years of age, there was no significant difference between birth cohorts, and no significant effect of birth year, in African elephants (Table 4, Figure 2a), indicating that juvenile survival has not changed from 1960 to 2019. For Asian elephants, earlier cohorts were available, and juvenile survival was significantly higher in two more recent cohorts compared to the oldest cohort (Figure 2b). However, the proportional survival hazard did not indicate a change between 1960 and 2019, and birth year as a continuous variable had no significant



**FIGURE 1** Survivorship graphs for African (*Loxodonta africana*; a, c, e) and Asian (*Elephas maximus*; b, d, f) elephants. “Natural” populations (a, b) of African elephants for Addo Elephant National Park (Gough & Kerley, 2006), Tarangire National Park (Foley & Faust, 2010), Karibu Amboseli National Park (excluding human-caused mortality from Moss, 2001; total mortality from Clubb et al., 2008), Samburu and National Springs National Reserves (Witemyer et al., 2013) and of Asian elephants for Myanmar Timber elephants (Mar, 2007) and a free-ranging population in southern India (Sukumar, 1992); zoo populations by individual birth cohorts (c–f), for the global zoo populations (c, d) (“uncurated data sets”; for statistics, see Table 1), and the combined North American and European zoo populations (e, f) (“curated data sets”; for statistics, see Table 2).

**TABLE 1** Survivorship analyses (Cox proportional hazards) for African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants kept globally in zoos ("uncurated data set"), including animals  $\geq 10$  years of age; models included either distinct periods (birth cohorts 1910–1939, 1940–1959, 1960–1989, 1990–2009, 2010–2019) as factors or the year of birth as a continuous variable

Species	Model		Coefficient (95% CI)	z	p
<i>L. africana</i>	Distinct periods (reference: 1910–1939, n = 15)	1940–1959 (n = 56)	0.40 (0.22–0.71)	-3.14	.002
		1960–1989 (n = 500)	0.22 (0.12–0.37)	-5.66	<.001
		1990–2009 (n = 174)	0.14 (0.07–0.27)	-6.03	<.001
		2010–2019 (n = 18)	0.00 (0.00, NA)	-0.01	.988
	Birth year (since 1910)	(n = 765)	0.97 (0.97–0.98)	-8.37	<.001
	Birth year (since 1960)	(n = 694)	0.97 (0.96–0.98)	-8.37	<.001
<i>E. maximus</i>	Distinct periods (reference: 1910–1939, n = 132)	1940–1959 (n = 241)	0.55 (0.44–0.68)	-5.42	<.001
		1960–1989 (n = 610)	0.42 (0.34–0.52)	-7.96	<.001
		1990–2009 (n = 351)	0.24 (0.15–0.39)	-5.97	<.001
		2010–2019 (n = 44)	0.00 (0.00, NA)	-0.01	.990
	Birth year (since 1910)	(n = 1380)	0.98 (0.98–0.99)	-8.24	<.001
	Birth year (since 1960)	(n = 1007)	0.99 (0.98–1.00)	-1.38	.167

Abbreviation: CI, confidence interval.

**TABLE 2** Survivorship analyses (Cox proportional hazards) for African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants kept at European and North American zoos ("curated data set"), including animals  $\geq 10$  years of age; models included either distinct periods (birth cohorts 1910–1939, 1940–1959, 1960–1989, 1990–2009, 2010–2019) as factors or the year of birth as a continuous variable

Species	Model		Coefficient (95% CI)	z	p
<i>L. africana</i>	Distinct periods (reference: 1910–1939, n = 24)	1940–1959 (n = 72)	0.39 (0.25–0.63)	-3.88	<.001
		1960–1989 (n = 610)	0.24 (0.16–0.37)	-6.68	<.001
		1990–2009 (n = 158)	0.14 (0.08–0.25)	-6.82	<.001
		2010–2019 (n = 19)	0.00 (0.00, NA)	-0.02	.988
	Birth year (since 1910)	(n = 883)	0.97 (0.97–0.98)	-9.01	<.001
	Birth year (since 1960)	(n = 787)	0.97 (0.96–0.98)	-5.10	<.001
<i>E. maximus</i>	Distinct periods (reference: 1910–1939, n = 248)	1940–1959 (n = 328)	0.65 (0.55–0.77)	-4.98	<.001
		1960–1989 (n = 630)	0.45 (0.39–0.53)	-9.43	<.001
		1990–2009 (n = 187)	0.33 (0.20–0.53)	-4.61	<.001
		2010–2019 (n = 23)	0.00 (0.00, NA)	-0.02	.983
	Birth year (since 1910)	(n = 1416)	0.98 (0.98–0.99)	-9.66	<.001
	Birth year (since 1960)	(n = 840)	0.99 (0.98–1.00)	-1.81	.070

Abbreviation: CI, confidence interval.

effect, regardless of whether all animals or only animals born since 1960 were considered (Table 4).

When comparing the species for juvenile survivorship for animals born from 1960 onwards, there was no change with time, but Asian elephants were close to having a significantly lower survivorship ( $p = .080$ , Table 5). The current Day 0 and first-year-mortality were 19% and 26% for African and 15% and 22% for Asian elephants, respectively (Figure 3).

## 4 | DISCUSSION

This study indicates that comparatively continuous progress has been made in zoo elephant husbandry in terms of adult survivorship. In particular, contrary to earlier statements (Clubb et al., 2008, 2009), this progress is not limited to African but is evident in Asian elephants as well. By contrast, no continuous change in juvenile survivorship was detected.

**TABLE 3** Survivorship analyses (Cox proportional hazards) for African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants kept at European and North American zoos ("curated data set"), including animals  $\geq 10$  years of age born since 1960; models compared the species either using absolute age or the relative age (in % of maximum longevity, set at 65 years for *L. africana* and 79 years for *E. maximus* and included the year of birth as a continuous variable

Model		Coefficient (95% CI)	z	p
Absolute age (reference: <i>L. africana</i> , n = 787)	<i>E. maximus</i> (n = 840)	0.00 (0.00–0.17)	-2.07	.038
	Birth year	0.97 (0.96–0.98)	-5.23	<.001
	Year x species interaction	1.02 (1.01–1.03)	2.02	.043
Relative age (reference: <i>L. africana</i> , n = 787) <sup>a</sup>	<i>E. maximus</i> (n = 840)	0.74 (0.63–0.85)	-4.05	<.001
	Birth year	0.98 (0.97–0.99)	-5.02	<.001
	Year x species interaction	1.01 (0.99–1.03)	1.50	.134

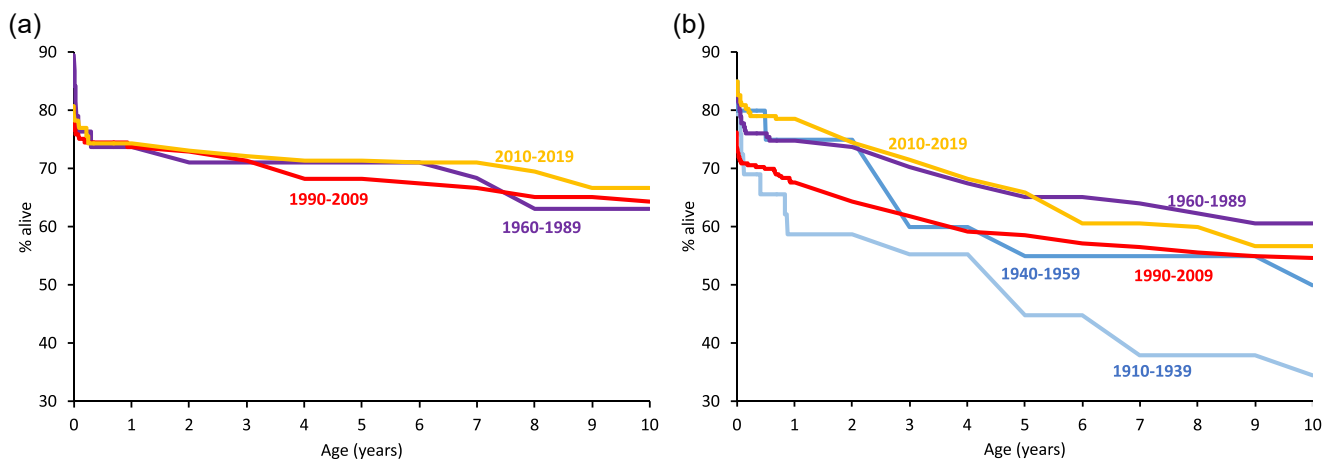
Abbreviation: CI, confidence interval.

<sup>a</sup>As the year x species interaction was not significant, model parameters for Species and birth year are from the model without the interaction.

**TABLE 4** Survivorship analyses (Cox proportional hazards) for zoo-born African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants kept at European and North American zoos ("curated data set"), including deaths up to 10 years of age; models included either distinct periods (birth cohorts 1910–1939, 1940–1959, 1960–1989, 1990–2009, 2010–2019) as factors or the year of birth as a continuous variable

Species	Model		Coefficient (95% CI)	z	p
<i>L. africana</i>	Distinct periods (reference: 1960–1989, n = 38)	1990–2009 (n = 129)	1.01 (0.55–1.84)	0.03	.976
		2010–2019 (n = 78)	0.94 (0.48–1.82)	-0.19	.848
	Birth year (since 1960)	(n = 245)	1.00 (0.98–1.01)	-0.54	.590
<i>E. maximus</i>	Distinct periods (reference: 1910–1939, n = 29)	1940–1959 (n = 20)	0.69 (0.32–1.49)	-0.95	.345
		1960–1989 (n = 175)	0.53 (0.32–0.88)	-2.46	.014
		1990–2009 (n = 306)	0.66 (0.41–1.07)	-1.68	.094
		2010–2019 (n = 172)	0.53 (0.32–0.88)	-2.45	.014
	Birth year (since 1910)	(n = 702)	1.00 (0.99–1.00)	-1.54	.125
	Birth year (since 1960)	(n = 653)	1.00 (0.99–1.01)	0.25	.797

Abbreviation: CI, confidence interval.



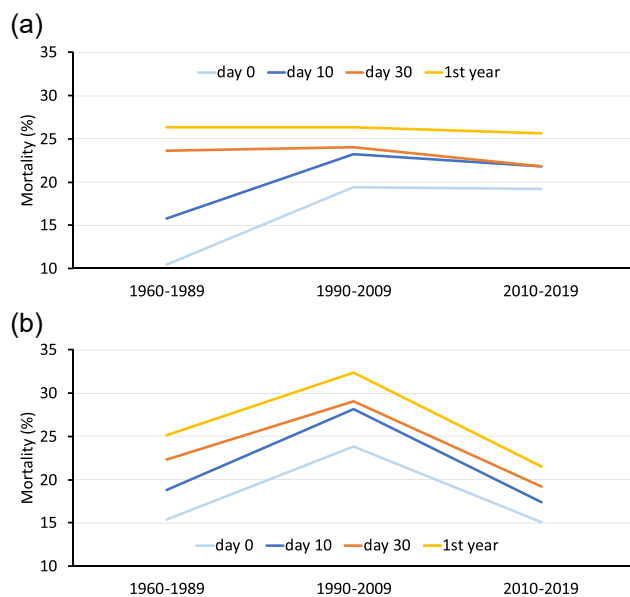
**FIGURE 2** Survivorship graphs for African (*Loxodonta africana*; a) and Asian (*Elephas maximus*; b) zoo-born elephants of the combined North American and European zoo populations ("curated data set") up to the age of 10 years by individual birth cohorts (for statistics, see Table 4).

**TABLE 5** Survivorship analyses (Cox proportional hazards) for African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants kept at European and North American zoos (“curated data set”), including deaths up to 10 years of age of animals born since 1960; model included the year of birth as a continuous variable

Model		Coefficient (95% CI)	z	p
Absolute age	<i>E. maximus</i>	1.25 (0.97–1.60)	1.75	.080
(reference: <i>L. africana</i> , n = 245) <sup>a</sup>	Birth year	1.00 (0.99–1.01)	0.02	.985
	Year x species interaction	0.01 (0.99–1.03)	0.64	.524

Abbreviation: CI, confidence interval.

<sup>a</sup>As the year x species interaction was not significant, model parameters for species and birth year are from the model without the interaction.



**FIGURE 3** Juvenile Mortality for African (*Loxodonta africana*; a) and Asian (*Elephas maximus*; b) zoo-born elephants of the combined North American and European zoo populations (“curated data set”).

When assessing progress, the initial conditions against which subsequent developments are compared clearly influence the outcome of the assessment. In zoo elephants, this is obvious in two different aspects: (i) the time frame of the evaluation—how far back in time data are included, and (ii) the difference between the two elephant species. For both species, there was a distinct improvement in survivorship over time when early elephant husbandry from 1910 onwards was included in the analysis, irrespective of the data set used (Tables 1 and 2). This was also visible in the survivorship displays (Figure 1c–f). Even though we can safely assume poor husbandry standards for many zoo elephants in the first half of the previous century, zoos were nevertheless learning lessons at the time, improving elephant survivorship. When assessing only animals born since 1960, the

comparison with the poor survivorship periods of 1910–1959 no longer provides a negative background against which more recent results can stand out. Yet, there is still clear evidence for progress in African elephants (as also observed by Clubb et al., 2008), irrespective of the data set used. In Asian elephants, however, the results are not as clear-cut. For the “uncurated data set” that was based only on the Species360 database, our analysis yielded the same result as that of Clubb et al. (2008), that is, no progress in survivorship (Table 1). Using the “curated data set,” by contrast, our analysis indicated a close to significant result (at  $p = .070$ , Table 2) for an improvement of survivorship over time also in the Asian species since 1960 in the combined North American and European zoo population.

An unexpected and interesting side observation was that the survivorship curves of Asian zoo elephants from 1960 onwards appear better for the global population (the “uncurated data set” including all Species360 entries) (Figure 1d) compared to the North American and European zoo population (“curated data set,” Figure 1f). We hypothesize that this might indicate a particularly good survival in parts of the world where Asian zoo elephants face climatic conditions closer to those of their natural habitat. This question deserves further scrutiny in the future.

A visual inspection of Figure 1 indicates that the less evident improvement in Asian elephants is unlikely to be due to a peculiar susceptibility to low survivorship in the Asian species—on the contrary. For the respective decades, Asian elephant adult survivorship always appears higher than that of the African elephants, and in direct comparison, adult Asian elephants have a significantly higher survivorship than the African species (Table 3). In other words, a less distinct recent progress in Asian elephant survivorship most likely stems from the fact that progress is less easily made and detected when starting from better baseline conditions. The statistical difference between the species matches a subjective impression that African elephants are somewhat more difficult to keep in managed care (reviewed historically in Clubb & Mason, 2002). Apart from a potentially more excitable nature, and the evident fact that African elephant females may be more prone to incidents related to their protruding tusks than Asian elephant females with non-protruding tusks, the species might differ in their susceptibility to climatic conditions. Additionally, Asian elephants imported from range countries may have been more likely to originate from work camps, and might have been more used to managed care than their African counterparts. However, to our knowledge, evidence for these hypotheses does not exist. For female African elephants, a higher sensitivity for ovarian cycle problems than in Asian elephants was detected (Brown et al., 2016; Oerke et al., 2002), pointing toward a generally more sensitive nature of this species. As stated before, obesity is considered a problem in zoo elephants. The fact that for the European population, African elephants had significantly higher body condition scores than Asian elephants (Schiffmann et al., 2018), and the observation that the numerical decrease in the populations’ average body condition score over recent years was statistically significant in Asian but not African elephants (Schiffmann

et al., 2019), might indicate a higher propensity for obesity, or a higher feeding intensity, in the African species.

It is not surprising that the results of analyses depend on the data sets used for the evaluation. Given the stark contrast between the different historical periods since 1910, and the generally lower survivorship in African elephants, a historical change in survivorships was evident irrespective of whether the Species360 data set was curated or not. By contrast, in Asian elephants with their generally higher survivorship, an indication for improvement since 1960 was only evident using the curated data set. This data set excluded zoos not located in North America and Europe, and was used for two reasons. First, to assure comparability to the approach of Clubb et al. (2008), and second because of the untested assumption that these facilities have a long history of elephant husbandry and therefore might have accrued expertise over the decades. In this curated data set, animals missing from the Species360 data were added, and mistakes in the Species360 data due to faulty entries were corrected. However, all this curation itself unlikely explains a difference to the result found by Clubb et al. (2008), who also constrained their analysis to North American and European Zoos, and also used similar sources for data set curation. When constraining our “curated data set” to animals born between 1960 and 1998 (mimicking the adult population  $\geq 10$  years of age available to Clubb et al. [2008]), and using the age of the animals in 2008 and their alive/death status at the time ( $n = 717$ ), we also do not find a significant change in the proportional cox hazard with birth year (coefficient 0.98, 95% CI: 0.96–1.01,  $z = -1.36$ ,  $p = .175$ ). Therefore, in our view the most parsimonious explanation for the difference in the results are the additional years of data available for our analysis, which we tentatively interpret as an indication of improved adult survivorship mainly due to more recent developments in zoo elephant management.

Given the large variety of changes in elephant husbandry in recent decades, it is unlikely that improvements can be narrowed down to a single factor. Rather, a variety of specific improvements might act in concert. For example, Wendler et al. (2020) showed that foot health in European Asian zoo elephants was not related to a single factor but to a series of factors corresponding to modern husbandry. These included larger indoor and outdoor enclosures, a higher proportion of the enclosure covered by sand, larger group sizes, more free choice for elephants whether they want to be outdoors or indoors, as well as larger keeper teams. It is important that current elephant facilities embrace all adequate modern husbandry concepts, both in terms of architectural and management approaches (Bolechova et al., 2020). Given the comparatively low number of zoo elephants when compared to other populations submitted to demographic analyses, the generally high longevity and slow generation turnover of elephants when compared to many other mammals, and the fact that individuals exposed to historically unfavorable husbandry will continue to be part of the current zoo populations for many years, future progress in terms of adult survivorship may still take decades before becoming more evident.

Juvenile survivorship was evaluated based on individuals born in zoos. In Asian elephants, historical data with a particularly poor juvenile survivorship were available. Therefore, some differences between time periods were significant; nevertheless, there was no evident improvement in juvenile survivorship since 1960 in either species (Table 4). As stated in the method section, it should be kept in mind that neonate mortality reporting was likely less stringent in earlier days of zoo husbandry than it is today, which might mask positive developments. Juvenile survivorship in Asian elephants was significantly lower than in African elephants (Table 5), an observation made before (Stevenson, 2004). In recent years, this most likely also reflects the impact of elephant herpes virus, an endemic infectious disease that represents the most common cause of death in juvenile Asian elephants in Western zoos (Fuery et al., 2020; Hoornweg et al., 2021; Perrin et al., 2021). A seeming increase in newborn mortality in 1990–2009 may also be related to a higher proportion of primiparous births at this time (Stevenson, 2004), an effect also reported in the Myanmar timber elephant population (Mar et al., 2012). Mason & Veasey, (2010b), reviewing the work of Saragusty et al. (2009), suggested some numerical improvement in first-year mortality for both elephant species in Europe. The average first-year mortality of 21% for African elephants reported by Saragusty et al., (2009) (1962–2006) is of a similar magnitude as the 26% of our data set. For Asian elephants, first-year mortalities reported in the literature (1960–2006) are of a magnitude of 40% (Faust et al., 2006; Saragusty et al., 2009), which is higher than our recent finding of 22%. If viewed on its own, and compared to other zoo animals where sometimes distinct changes across decades can be observed (Roller et al., 2021), juvenile mortality might be considered stable in zoo elephants. With the transition to protected contact and an increase in more natural births in female groups rather than by isolated individuals, the establishment of matrilineal skilled in giving birth support may still take some time (Prahl, 2009). Additionally, paying more attention to keeping adult animals, and especially breeding females, in an adequate body condition (Schiffmann et al., 2019; Sullivan et al., 2016) should also address the high birth weights and associated risk of stillbirths observed in zoo elephants (Dale, 2010; Kurt & Mar, 1996).

In any assessment of health or welfare, it is important to set the stage for possible outcomes of the evaluation, and how these outcomes will be interpreted. This applies to methodological issues, as demonstrated by Ertl et al. (2020) using the example of zoo elephant foot health. These authors demonstrated that the summative outcome of a survey—in one sentence, whether the zoo population would be considered “generally healthy” or “generally affected with foot problems”—hinges critically on the scoring system used. A rough summative score displayed the zoo population as diseased, whereas a detailed score resulted in a distribution expected for a generally healthy population. Yet, apart from methodological issues, philosophical issues apply as well. Regarding survivorship data, particularly in the discussion on elephants, one important question is which benchmark it should be compared to for interpretation



(Clubb et al., 2009; Mason & Veasey, 2010b), and what potential consequences one will derive from such a comparison.

On the one hand, there are ecological situations where members of any animal population die from various factors that derive from their own (genetically and epigenetically predetermined) propensity for survivorship, as well as from biotic and abiotic factors. Biotic factors include intraspecific as well as interspecific conflict, the latter including not only animal–animal and human–animal but also plant–animal interactions and parasitic, microbial, fungal, and viral diseases. Abiotic factors mainly relate to climatic conditions and the resulting availability of food resources (and in rare cases tectonic events). Given that management under human care aims at protecting from biotic and abiotic causes of mortality, survivorship would be expected to be generally higher, or its inverse—the rate of ageing—would be expected to be lower in zoos compared to natural habitats (Lemaître et al., 2013; Ricklefs, 2010; Tidière et al., 2016). On the other hand, it is unlikely that any real-life situation will achieve a survivorship that corresponds to only the species-specific intrinsic propensity for ageing and survival. The use of demographic data of specific (free-ranging or managed) populations for political decision-making must be evaluated against this background.

Does it make sense to use the comparatively high juvenile survivorship of the Samburu elephant population (Wittemyer et al., 2005) as a benchmark for juvenile zoo elephants rather than the lower juvenile survivorship of the Amboseli elephant population (Clubb et al., 2008), as suggested by Mason & Veasey, (2010b), yet then use the higher adult survivorship of the Amboseli population as the benchmark for adult zoo elephants rather than the comparatively low adult survivorship of the Samburu population (cf. Figure 1)? This suggestion might be questioned, because it is based on the assumption that juvenile and adult survivorship are so unrelated as to justify using these data from different populations, yet we know that density-dependent effects occur in free-ranging elephant populations (Hanks & McIntosh, 1973; Laws et al., 1975). To what extent is it reasonable to exclude certain types of mortality from benchmark populations, such as human-caused mortality from Amboseli (Moss, 2001) or from South Indian elephants (Sukumar, 1992), yet accepting other causes of death that could, in theory, stem from the fact that the respective populations could not expand beyond their present habitats—because of human activities? These questions are rhetorical, yet we place them here because in our—admittedly subjective—view, the major impact of the comparison with thus-derived benchmarks has been a rhetorical one: zoo elephant survival is “compromised” (Clubb et al., 2008). Yet, what are the consequences of such a statement? If such a statement is used to derive political decisions, how is this applied to the similarly “compromised” historical survivorship of certain free-ranging populations as compared to the historical survivorship of other free-ranging populations? Additionally, one could also question whether can we use historical survivorship data for certain free-ranging populations without knowing how the survivorship of these populations is changing over time.

With respect to Asian elephant populations, given that adult survivorship in zoos is better than in a historic free-ranging population, yet worse than in a historic population of timber elephants (Figure 1d,f), can this specific observation serve as an argument for banning Asian elephant zoo husbandry yet promoting the existence of free-ranging populations? Can it serve as an incentive to promote the management of Asian elephants under husbandry conditions that mimic those of the timber elephant population, including the domination by humans and spending major parts of the day hobbled or chained (Mar, 2007)? Or would one advocate phasing out the free-ranging population because of its (historical) low survivorship?

With respect to African elephant populations, adult survivorship in zoos is better than in one historic free-ranging population, tends to approach the actual survivorship of another historic free-ranging population, yet is far lower than that of a two other historic free-ranging populations. Can these specific observations serve as an argument for banning African elephant zoo husbandry yet promoting those free-ranging populations that did historically not achieve the survivorship of the best populations? Or would one advocate—applying the same set of standards—the phasing out of those free-ranging populations that are far off the ideal situation of the populations with the highest survivorship?

In our view, the answer to these rhetorical questions is that survivorship data should not be used in this way—as a seemingly scientific addition to a political discussion. Hutchins (2006) already explained that the question of whether a certain population should be maintained or not is an ethical (and hence, a political) but not a scientific one, and that the variation of conditions observed in nature precludes unambiguous comparisons with other conditions. Therefore, we propose that the shape of the survivorship patterns, and their development over time (which is mostly not available for free-ranging populations), should be major criteria in the discussion about the appropriateness of elephant husbandry, alongside many other physical and psychological health criteria, rather than comparisons to selectively corrected one-point measurements of free-ranging populations.

Survivorship curves for large precocial mammals with reduced exposure to predation should have a convex or “Type I” shape (Pearl, 1927), irrespective of whether historical populations achieve this shape or not. For zoo elephants, the historical development was from a concave (“Type III”) survivorship curve between 1910 and 1959 to a straight-line (“Type II”) shape around 1960–1989 towards possibly convex shapes in the more recent past. This development is positive, yet something to be expected, not celebrated. To which extent this development should have been faster, and which rate of improvement should be expected in the future, is debatable. In our view, it is important that this development continues, and that no regression will occur. In this respect, survivorship analyses are important as one of several monitoring systems. High husbandry standards in terms of space offered and used, social group composition and management, enclosure structure, nutrition, activity, appropriate cognitive challenges, sleep, a scarcity of accidents, and general physical health, need to be further pursued.

Finally, population-wide survivorship analyses reflect a total of measures taken by individual zoos, such as specific changes in husbandry and management, yet cannot themselves recommend specific measures. To understand changes in survivorship, detailed historical analyses of husbandry practices are required, just as detailed analyses of land use, climate and density-dependent effects would be necessary to understand historical changes in survivorship in free-ranging populations. Even though often considered academically uninspiring, regular, standardized surveillance of husbandry practices is an important tool for the global zoo community, and should be instigated and promoted for any species in which husbandry improvement is considered critical.

## ACKNOWLEDGMENTS

This study 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. We thank Dan Koehl of The Elephant Database for his ongoing contribution to global knowledge of elephants, and Anouk Petitpierre for generous statistical advice. There is no funding to report. Open access funding provided by Universitat Zurich.

## CONFLICTS OF INTEREST

All authors are either employed by, or have major involvement with, zoological gardens.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article. Data used in the present study are available in anonymized for as online supplementary information. Requests for original data on a species level should be addressed to Species360 at [www.Species360.org](http://www.Species360.org).

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**How to cite this article:** Scherer, L., Bingaman Lackey, L., Clauss, M., Gries, K., Hagan, D., Lawrenz, A., Müller, D. W. H., Roller, M., Schiffmann, C., & Oerke, A.-K. (2023). The historical development of zoo elephant survivorship. *Zoo Biology*, 42, 328–338. <https://doi.org/10.1002/zoo.21733>