JZAR JOURNAL OF ZOO AND AQUARIUM RESEARCH
www.jzar.org

Research article

Assessing zoo giraffe survivorship: Methodological aspects, historical improvement and a rapid demographic shift

Lara Scherer[1], Laurie Bingaman Lackey[2], Max Hahn-Klimroth[3], Dennis W. H. Müller[4], Marco Roller[5], Mads F. Bertelsen[6], Jörg Jebram[7], Paul W. Dierkes[3] and Marcus Clauss[1]

[1]Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland.
[2]1230 Oakland Street, Hendersonville, North Carolina, USA.
[3]Faculty Biological Sciences, Bioscience Education and Zoo Biology, Goethe-University Frankfurt, Max-von-Laue-Str. 13, 60438 Frankfurt am Main, Germany.
[4]Zoological Garden Halle (Saale), Fasanenstr. 5a, 06114 Halle (Saale), Germany.
[5]Zoological Garden Karlsruhe, Ettlinger Str. 6, 76137 Karlsruhe, Germany.
[6]Copenhagen Zoo, Roskildevej 38, 2000 Frederiksberg, Denmark.
[7]von Opel Hessische Zoostiftung, Georg von Opel - Freigehege für Tierforschung, Am Opel-Zoo 3, 61476 Kronberg im Taunus, Germany.

Correspondence, Marcus Clauss, email; mclauss@vetclinics.uzh.ch

Keywords: husbandry, *Giraffa camelopardalis*, mortality, progress, survival

Article history:
Received: 02 Oct 2023
Accepted: 01 Mar 2024
Published online: 30 Apr 2024

Abstract

Giraffe have been kept in zoos for a long time. They have traditionally been considered difficult to maintain due to various husbandry requirements, including their nature as intrinsic browsers. However, zoo animals are expected to achieve higher survivorship than free-ranging conspecifics due to protection against dangers that would be experienced in their natural habitat. Global zoo giraffe data was analysed for historical developments of juvenile and adult survivorship, assessing the data with various demographic measures and comparing it to that of populations from natural habitats. Additionally, zoo population structure was analysed, in particular with respect to two events that occurred in parallel in 2014—a recommendation to restrict the number of new offspring given by the European Endangered Species Programme (EEP) studbook coordinator and the culling of a designated 'surplus' giraffe at Copenhagen Zoo that attracted global media attention. Both juvenile and adult giraffe survivorship has increased over time, suggesting advances in giraffe husbandry. For juveniles, this process has been continuous, whereas for adults the major progress has been in the most recent cohort (from 2000 onwards), in parallel with the publication of various husbandry guidelines. Zoo giraffe survivorship is now generally above that observed in natural habitats. Simple survivorship analyses appear suitable to describe these developments. Since 2014, the global giraffe population has undergone a rapid demographic shift from a growing to an ageing population, indicating a drastic limitation of reproduction rather than a system where reproduction is allowed and selected animals are killed (and possibly fed to carnivores). Thus, giraffe are both a showcase example for the historical progress made in zoo animal husbandry due to efforts of the zoo community and serve as an example to discuss implications of different methods of zoo population management.

Introduction

Worldwide, zoos have a mission to promote nature and species conservation (e.g. Barongi et al. 2015) and sustainability (e.g. WAZA 2020) and to educate about these aims (e.g. Thomas 2020). Many zoos pursue this conservation work while displaying animals kept under high welfare standards (e.g. Mellor et al. 2015; Rose and Riley 2022). Maintaining viable, self-sustainable small populations of selected species is an integral part of this mission (e.g. Barongi et al. 2015; Pizzutto et al. 2021; Powell et al. 2019).

Amongst other factors, zoos use fascination with nondomestic animals to attract, inspire and educate visitors. Giraffe hold a great fascination for humans. This is recorded in literature describing the very first individuals to come to Asia, Europe and America as early as the 15th century (Clayton 2023; Lagueux 2003; Lebleu 2020; Ringmar 2006), in the prominent role of the giraffe in evolutionary theory (Lamarck 1809) and

in a dramatised account of the fate of zoo giraffe (Ledgard 2006). Additionally, giraffe have been used in the zoo community itself as showcase examples for animal welfare considerations (Rose 2023; Veasey et al. 1996).

Despite their global popularity, giraffe populations in natural habitats have greatly decreased in recent decades (Muller et al. 2018). Several species of giraffe have been proposed (Coimbra et al. 2021; Petzold et al. 2020) but the IUCN SSC Giraffe and Okapi Specialist Group currently recognises a single species which is listed as vulnerable on the IUCN Red List (Muller et al. 2018). Habitat loss (mostly due to increasing agricultural activities), biological resource use (hunting and snaring animals) and human intrusions and disturbance due to war and civil unrest are key drivers of population declines (Brown et al. 2023; Muller et al. 2018). Among ruminants, giraffe have particularly slow life histories with exceptionally high longevity and a long gestation period (Müller et al. 2011a), which makes population regrowth after a decline more difficult (Carmona et al. 2021). Thus, while in the past giraffe may have mainly been kept in zoos for their fascinating appearance and to educate the public, maintaining a rescue population ex situ has become an important issue, as for mammalian 'megafauna' in general (Farhadinia et al. 2020). Three sub-species in the European zoo population were designated as 'insurance populations' in the most recent regional collection plan of the Antelope and Giraffid Taxon Advisory Group (Hofman et al. 2022).

Historical evidence suggests that the first attempts at individual giraffe husbandry commenced in the 15th century in Europe and China (Berland 2017; Ringmar 2006). Historically, medical problems in zoo giraffes included hoof overgrowth (Bertelsen 2015); premature dental wear (Clauss et al. 2007); general feeding- and digestive tract-related problems due to the logistical challenge of providing sufficient amounts of browse (Hummel and Clauss 2006); widespread occurrence of sudden death without clinical symptoms termed 'peracute mortality' (Junge and Bradley 1993)—or 'serous fat atrophy' syndrome (Clauss et al. 2006; Potter and Clauss 2005) because a lack of body fat stores was the only remarkable necropsy finding; jaw fractures (Remport et al. 2022); uroliths (Sullivan et al. 2010); and oral stereotypies (Bashaw et al. 2001; Veasey et al. 1996). Additionally, chemical immobilisation has been a major challenge in giraffes (Bertelsen 2015).

However, vast progress has been made in giraffe husbandry. This is reflected in dedicated husbandry guidelines (Burgess 2004; EAZA 2006; Jolly 2003); improved chemical immobilisation regimes (Bertelsen 2015); the use of training for medical procedures (Dadone et al. 2016); increased space made available to giraffe in new zoo enclosures, in particular in indoor facilities (Kauffels 2008) and increased attention to enclosure substrate for hoof health (Weitkamp 2016); expansion of animal surveillance into the night-time (Burger et al. 2021; Duggan et al. 2016); recognition of a complex social system in giraffe (Bashaw et al. 2007; Muller and Harris 2022); documented improvements in feeding regimes with an increased use of lucerne hay and reduction in grains and fruit, as well as increased efforts to provide browse (Gussek et al. 2017; Monson et al. 2018; Schüßler et al. 2017); improvements in feed presentation methods that, together with diet changes, reduce stereotypies (Depauw et al. 2023; Walldén 2023); and a seeming trend of observing fewer cases of serous fat atrophy (Bertelsen 2015) corresponding to the finding of higher body condition scores in zoo-housed compared to free-ranging giraffe (Clavadetscher et al. 2021).

Given these various areas of improvement, giraffe survivorship in zoos would be expected to have increased, similar to observations in various other animal groups (Havercamp et al. 2019; Jett and Ventre 2015; Roller et al. 2021; Scherer et al. 2023; Tidière et al. 2023 Wich et al. 2009; Wittwer et al. 2023). For free-ranging animals, in addition to anthropogenic threats of poaching and habitat loss, natural predation on calves, food scarcity and climate extremes are risk factors for morbidity and mortality (Bond et al. 2023; Lee et al. 2016a; Strauss et al. 2015; Walker et al. 1987). Zoo animals should be protected against these risks and would be expected to achieve higher survival rates than many free-ranging populations. Rather than using the term 'survivorship', a more intuitive measure like 'average lifespan' or 'average longevity' is often preferred. Average lifespan can only be reliably calculated in cohorts of which all individuals have died (Wiese and Willis 2004). Therefore, if the average lifespan or longevity of the current population is to be described, this means that population demography must be modelled, extrapolating for those cohorts in which individuals are still alive.

As in many other ungulates, the size and composition of giraffe groups in wild populations fluctuate dynamically throughout the day, but non-random associations between adult females, and linking of female groups by roaming adult males, result in a socially structured, multilevel society (Lavista Ferres et al. 2021; VanderWaal et al. 2014). Younger males often form unstable bachelor groups and older males may become more solitary as they age (Pratt and Anderson 1985; VanderWaal et al. 2014). Mating success of adult males in the wild is unknown but it is speculated that mating is dominated by a minor fraction of males, resulting in a high variance in lifetime reproductive success (Bercovitch and Berry 2010). In human care, breeding groups are generally kept as harems with one adult male and two to more than ten adult females. The resulting surplus of males and the facts that giraffe can live relatively long lives but space for population growth in zoos is limited, make the giraffe a candidate for various management options including contraception (Schwarzenberger et al. 2022), sexual segregation including bachelor groups as occurring in the natural habitat, or a breed and cull system that allows more animals to be born than can be placed, with subsequent killing of selected individuals (EAZA 2023). Young giraffe are often predated upon by lions, which also take down, albeit less frequently, adult giraffe (Strauss and Packer 2013). Thus, giraffe might be considered ideal candidates for a breed and feed system where culled animals can be fed to a zoo's own carnivores. In parallel to the recommendation to reduce the number of new giraffe offspring given by the European Endangered Species Programme (EEP) studbook coordinator (J. Jebram, personal communication), the culling of a designated 'surplus' giraffe at Copenhagen Zoo in 2014 attained global media attention and triggered discussions regarding ethics (Bertelsen 2014, 2018; Cohen and Fennell, 2016; Powell and Ardaiolo 2016; Powell et al. 2018; Zimmerman et al. 2014). This made giraffe a showcase species in the discussion of how zoos should manage populations.

The present study had the following aims: (i) to assess the historical development of global zoo giraffe survivorship, assessing adult and neonate/juvenile survivorship separately and comparing different methodological approaches, with the expectation that survivorship in zoos has improved over time; (ii) to compare zoo survivorship to data from populations in African wildlife reserves, with the expectation that at least for more recent decades, survivorship in zoo populations is higher than that reported for natural habitats and (iii) to assess the demographic development of the global zoo giraffe population, in particular with respect to the parallel EEP recommendation to reduce breeding and the globally perceived 2014 culling of a surplus animal, with the expectation that the demographic structure of the global zoo population changed around that time. Due to the parallelism of events, it is not possible to weigh the effects of either event on demographic development but only to assess a temporal association with both or none.

Materials and methods

The evaluation followed the approach outlined by Roller et al. (2021) and Scherer et al. (2023). Records were obtained for *Giraffa camelopardalis* from Species360 (ZIMS for Husbandry), an online database platform used by more than 1,200 zoos worldwide to manage animal data. It contains dates of birth and death (as well as dates when some animals were lost to follow-up), from which the subsequent data were calculated (Species360 Research Data Agreement # 2019-Q3-RR3). Reporting of animal data into this repository is mandatory for zoos accredited by the European Association of Zoos and Aquaria (EAZA) but not for others such as members of the American Association of Zoos and Aquariums (AZA) and not for historical data of any region (Scherer et al. 2023). The data were curated manually for duplicate 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). The final zoo dataset included data from 1900 onwards for a total of 11,674 individuals.

It is very unlikely that adult animals alive at zoos using Species 360 are not recorded in the system, but there is no independent control of whether newborns are consistently entered. In the experience of one co-author (L. Bingaman Lackey), not entering newborn animals until they had survived to about one month of age was more common in earlier decades of the last century than it is now, especially when entering historical data into the database. This would result in an underestimation of positive developments in neonate mortality. The dataset used here did not indicate cause of death; thus it was not possible to differentiate between individuals that died or were euthanised due to disease and individuals that were culled for management reasons. The data included information on the sex and whether the animal was born in the wild or at a zoo. The ages at which wild-born animals were imported were not available; these animals were excluded from the assessment of juvenile mortality (up to 4 years of age—giraffe are sexually mature at around 4 years; Bertelsen 2015). For statistical analyses, the dataset was pruned in different ways to yield defined subsets that are explained with their respective result. The endpoint of survival was set to 1 November 2022.

Finally, survivorship data based on mark-resight methods were collated from published literature (Foster and Dagg 1972; Leuthold and Leuthold 1978; Pellew 1983; Strauss et al. 2015).

The data were used for three different analyses.

Survivorship analyses

To assess survivorship, the Cox proportional hazard analysis in R (R Core Team 2023) with the survival package (Therneau 2022) was applied (for example R code, see Supplementary Information) using the age of an individual and 'event' (death/lost to follow-up 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. Sex and origin (wild-born or zoo-born) were analysed as covariables in some models. Proportionality of hazards was tested either by comparing birth cohorts (for the periods of 1900–1929, 1930–1959, 1960–1979, 1980–1999 and 2000–2019) as discrete categories or the year of birth as a continuous variable. Use of discrete categories is considered less informative and was chosen to facilitate visualisation. In order to assess whether very old historical data had an influence on the outcome, models were run for all data and for data since 1960. 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 juvenile survivorship, zoo-born animals only up to the age of four years were analysed. For adult survivorship, all animals that reached the age of 4 years were included in the analyses, testing for effects of sex and origin (wild-born or zoo-born). To assess whether the inclusion or exclusion of 390 animals lost to follow-up made a difference to the outcome, the analyses were repeated with and without these animals. Survivorship analyses do not yield information on mean life expectancy but can yield information on median life expectancy (the age that 50% of the investigated cohort reached)—if at least 50% of the investigated cohort has already died.

Graphical depictions of survivorship curves include curves from the literature for several free-ranging giraffe populations. Notably, no data on individual life histories from decade-long observations are available for giraffe. Rather, these data for free-ranging populations derive from shorter observation periods and indicate survival for specific age classes of calves, subadults and adults but do not yield information on how adult mortality changes as the end of the maximum lifespan is approached. Assuming that adult giraffes are subject to 'senescence', i.e. an increase in the likelihood of dying towards older ages, then the data used here for natural habitats represent an underestimate of old-age mortality, i.e. an overestimation of old-age survivorship.

Demographic modelling

Other demographic measures, in particular age-specific life expectancy (how many more years an animal of a specific age would, on average, still live) and age-specific lifespan equality were analysed. Equality is a dimensionless measure that indicates whether the age-specific average life expectancy is evenly distributed across all individuals—i.e. if they all reach that average—or if that life expectancy has a wide distribution around its mean—i.e. if some animals live distinctively shorter and some distinctively longer (Aburto et al. 2020; Colchero et al. 2016). These measures cannot be derived directly from survivorship counts but require mathematical modelling (described in the Supplementary Information). The model is based on the 'Siler mortality' (Siler 1979) that models age-specific mortality risk as first descending with age (a high neonate mortality that decreases as neonates survive), a basal mortality (that affects all ages) and then a mortality that increases again with age (senescence, an increasing likelihood of dying as maximum longevity is approached). The model parameters allow an estimate of age-specific mortality (what is the average mortality at a specific age?), age-specific life expectancy (what is the average additional years an individual of a specific age will live?), age-specific survivorship (what percentage of the cohort is still alive at a specific age?) and age-specific lifespan equality (how closely distributed around their mean are the additional years that an individual of a specific age class will live?). In contrast to the Cox proportional hazard analysis, this model cannot use birth year as a continuous variable to assess developments over time but requires a priori distinction of different cohorts. The same cohorts were used as for the graphical depiction of survivorship analyses (1900–1929, 1930–1959, 1960–1979, 1980–1999, 2000–2019). Because the model requires data from birth to death, i.e. must include neonates, only zoo-born animals were used, excluding the 1900–1929 cohort that mostly included wild-born animals.

Population development

The annual number of births from 1950 to 2022, population pyramids and the respective percentages of calves (0–1 year), subadults (1–5 years) and adults (>5 years) of the global zoo population were compared to corresponding data from free-ranging populations (which was not available at the chosen cutoff for subadults of 4 years). Data for population pyramids were as per 31 December of the respective year. Due to the absence of

a differentiation in adult age classes in studies on free-ranging animals, no reliable pyramids can be constructed for these populations. The resulting data displays were assessed visually for changes around 2014 when both the EEP recommendation for a reduction in breeding and the prominent case of a zoo giraffe cull occurred.

Results

Survivorship analyses

Regardless of whether animals lost to follow-up were included in or excluded from the analysis, there was a significant reduction in mortality (i.e. an increase in survivorship) over time (Table 1, Figure S1). From here on, all results are reported for the dataset including animals lost to follow-up.

Juvenile survivorship was significantly higher for females than for males and increased significantly with later birth year, irrespective of whether all data or only data since 1960 were used (Table 2). Significant increases in survivorship in specific birth cohorts, as compared to the earliest cohort, were only detected when birth cohorts since 1960 were used; this was possibly due to the low sample size of earlier cohorts (Table 2). When compared to data from free-ranging populations, juvenile survivorship was generally higher in the zoo population for animals born after 1980 (Figure 1).

For animals ≥4 years of age, there was a significant increase in survivorship over time and a significantly lower survivorship for males, irrespective of the time period or whether distinct periods or birth year were used as a covariable (Table 2). Generally, zoo-born animals had a significantly better survivorship than wild-born animals. Giraffe born in the most recent cohort (2000–2019) had particularly high survivorship (Figure 2). The median total life expectancy for giraffe ≥4 years of age increased from 11 years in animals born in 1900–1929 to 13 years in animals born in 1960–1979 to 17 years in animals born in 2000–2019. Median life expectancy of all zoo-born animals at time of birth (i.e. including juvenile mortality) increased from 4.5 years in animals born in 1960–1979 to 9 years in animals born in 2000–2019.

When compared to data for free-ranging populations (derived from age class-specific mortality estimates without data for old

Table 1. Survivorship analyses (Cox proportional hazards) for giraffe *Giraffa camelopardalis* kept globally in zoos, including animals ≥4 years of age; models include either distinct periods (birth cohorts 1900–1929, 1930–1959, 1960–1979, 1980–1999, 2000–2019) as factors or the year of birth as a continuous variable

Model		Coef (95%CI)	z	P
Born 1990–2019				
Excluding animals lost to follow-up (n=5658)				
reference: 1900-1929 (n=53)	1930-1959 (n=342)	0.665 (0.498, 0.889)	-2.755	0.006
	1960-1979 (n=1020)	0.840 (0.635, 1.111)	-1.223	0.221
	1980-1999 (n=1754)	0.797 (0.601, 1.057)	-1.577	0.115
	2000-2019 (n=2489)	0.506 (0.379, 0.675)	-4.638	<0.001
	Birth year	0.993 (0.991, 0.994)	-7.403	<0.001
Including animals lost to follow-up (n=6048)				
reference: 1900-1929 (n=57)	1930-1959 (n=370)	0.657 (0.491, 0.878)	-2.840	0.005
	1960-1979 (n=1104)	0.816 (0.617, 1.079)	-1.425	0.154
	1980-1999 (n=1957)	0.758 (0.572, 1.004)	-1.932	0.053
	2000-2019 (n=2560)	0.512 (0.384, 0.683)	-4.556	<0.001
	Birth year	0.993 (0.991, 0.995)	-7.114	<0.001
Born 1960-2019				
Excluding animals lost to follow-up (n=5263)				
reference: 1960-1979 (n=1020)	1980-1999 (n=1754)	0.958 (0.881-1.042)	-1.0001	0.317
	2000-2019 (n=2489)	0.610 (0.551-0.676)	-9.450	<0.001
	Birth year	0.988 (0.986-0.991)	-8.862	<0.001
Including animals lost to follow-up (n=5621)				
reference: 1960-1979 (n=1104)	1980-1999 (n=1957)	0.937 (0.862-1.018)	-1.546	0.122
	2000-2019 (n=2560)	0.635 (0.574-0.704)	-8.713	<0.001
	Birth year	0.989 (0.986-0.992)	-8.326	<0.001

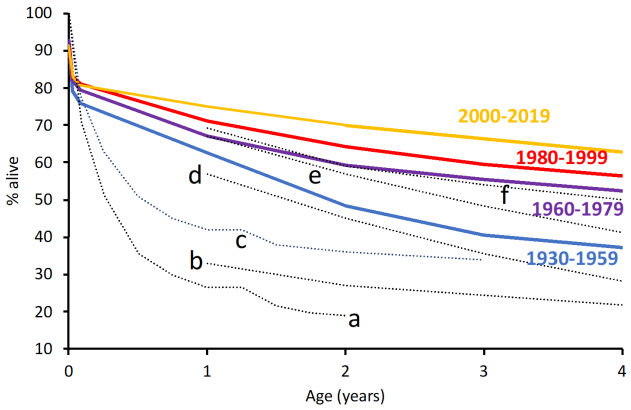

Figure 1. Juvenile survivorship (from neonates to animals of 4 years of age) in the global zoo giraffe *Giraffa camelopardalis* population displayed as separate birth cohorts for zoo-born animals. Data from free-ranging populations is plotted for comparison: a) Foster and Dagg (1972), read from graph; b) Leuthold and Leuthold (1978); c) Pellew (1983), read from graph; d,e) Strauss et al. (2015); f) Lee and Bond (2022). Note that many studies on free-ranging populations do not provide resolution of mortality within the first year of life.

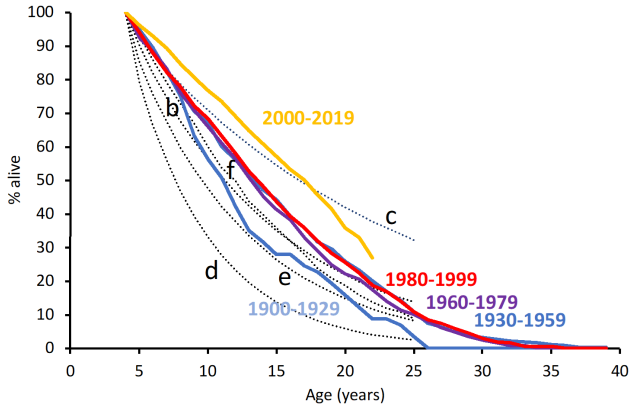

Figure 2. Adult survivorship (≥4 years of age) in the global zoo giraffe *Giraffa camelopardalis* population displayed as separate birth cohorts (wild- and zoo-born animals). Data based on 'adult mortality' (without specific information on the mortality of old adults) from free-ranging populations is plotted for comparison: b) Leuthold and Leuthold (1978); c) Pellew (1983); d,e) Strauss et al. (2015); f) Lee and Bond (2022).

mature specimens), adult zoo giraffe achieved a survivorship similar to or better than free-ranging populations (Figure 2). The only free-ranging population that appeared to have a better adult survivorship for all but the most recent cohort was that of Tsavo observed by Leuthold and Leuthold (1978); the median life expectancy for animals ≥4 years of age was, however, similar to that of the 2000-2019 cohort (Figure 2). When considering Tsavo's population from birth onwards, its median life expectancy would be lower than that of the recent zoo cohort due to higher juvenile mortality in the natural habitat.

Demographic modelling

Demographic modelling revealed a decrease in giraffe mortality and an increase in survivorship and life expectancy across the chosen time intervals (Figure 3A–C). Notably, due to improved neonate mortality equality at birth improved across these time periods. As animals no longer died uniformly at a comparatively young age—instead some reached much older ages—equality decreased in more recent periods for animals that had reached the age of 4 years (Figure 3D). Life expectancy increased from 13.5±0.8 years in animals born in 1960–1979 to 15.1±0.2 years in animals born in 2000–2019. Thus, when plotting equality versus life expectancy, there was a linear increase in the relationship for these measures at birth and a decrease at 4 years of age (Figure 4). The actual data and the model outcome are depicted in Figure 3B.

Life expectancy of all zoo-born animals at the moment of birth (i.e. including juvenile mortality) increased from 6.0±0.2 years in animals born in 1960–1979 to 9.1±0.2 years in animals born in 2000–2019.

Population development

After a long period of increasing giraffe births, there was a dramatic decline in births after 2014 (Figure 5A). Correspondingly, the shape of the population pyramids changed from a clear pyramidal pattern in 2010 to a columnar pattern in 2022 (Figure 5B). Development of the global population showed an increase in the proportion of mature adults and a decrease in the proportion of subadults to values observed in free-ranging populations between 1970 and 1990 (Figure 5C). Since 2014, there has been a rapid decline in the proportion of calves and subadults and a concomitant steep increase in the proportion of mature adults beyond those observed in natural habitats (Figure 5C).

The male to female ratio at birth was close to 1:1, with extremes in 1950 (0.83:1) and 2017 (1.24:1). Adult male to female ratios were generally lower, e.g. at 0.44:1 in 1980 or 0.47:1 in 2000 and increased steadily from 0.60:1 in 2014 to 0.68:1 in 2022.

Discussion

This study indicates that over time, there have been improvements in juvenile and adult giraffe survivorship in zoos. While these improvements were continuous for juveniles, adult survivorship between 1930 and 1999 stagnated on a level above that observed in most free-ranging populations and increased particularly in the last two decades. Analysing the data using a common demographic model yields similar results without adding information. The population development shows a drastic shift after 2014.

Methodological aspects: Dataset curation

In a previous publication on zoo elephant survivorship, animals lost to follow-up were excluded from the dataset with no relevant effect of data curation (i.e. only including animals from Europe and North America) (Scherer et al. 2023). In the current study, there was a significant reduction in mortality (i.e. an increase in survivorship) over time regardless of whether animals lost to follow-up were included in or excluded from the analysis. This suggests that smaller scale corrections do not influence the overall recent trend of increased survivorship.

Nevertheless, it is important that data are correct. It is important to understand that data ownership in the Species360

Table 2. Survivorship analyses (Cox proportional hazards) for giraffe *Giraffa camelopardalis* kept globally in zoos including animals lost to follow up; models include either distinct periods (birth cohorts 1900–1929, 1930–1959, 1960–1979, 1980–1999, 2000–2019) as factors or the year of birth as a continuous variable

Model		Coef (95%CI)	z	P
Giraffa camelopardalis up to 4 years of age, zoo-born born 1900-2019 (n=9634) reference:				
females (n=4665) 1900-1929 (n=13)	males (n=4969)	1.604 (1.514-1.699)	16.016	<0.001
	1930-1959 (n=205)	1.355 (0.665-2.759)	0.836	0.403
	1960-1979 (n=1606)	1.055 (0.526-2.116)	0.151	0.880
	1980-1999 (n=3582)	0.880 (0.440-1.763)	-0.359	0.719
	2000-2019 (n=4228)	0.595 (0.297-1.192)	-1.464	0.143
females (n=4665)	males (n=4969)	1.602 (1.512-1.697)	15.980	<0.001
born 1960-2019 (n=9416) reference: females (n=4564) 1960-1979 (n=1606)	Birth year	0.987 (0.985-0.988)	-16.260	<0.001
	males (n=4852)	1.604 (1.512-1.701)	15.755	<0.001
	1980-1999 (n=3582)	0.835 (0.773-0.901)	-4.639	<0.001
	2000-2019 (n=4228)	0.565 (0.522-0.611)	-14.233	<0.001
	males (n=4852)	1.603 (1.511-1.700)	15.730	<0.001
	Birth year	0.986 (0.984-0.987)	-14.970	<0.001
Giraffa camelopardalis ≥ 4 years of age born 1900-2019 (n=6048) reference:				
females (n=3478) wild-born (n=1057) 1900-1929 (n=57)	males (n=2570)	1.541 (1.443-1.646)	12.855	<0.001
	zoo-born (n=4991)	0.823 (0.751-0.902)	-4.162	<0.001
	1930-1959 (n=370)	0.657 (0.491, 0.878)	-2.840	0.005
	1960-1979 (n=1104)	0.816 (0.617, 1.079)	-1.425	0.154
	1980-1999 (n=1957)	0.758 (0.572, 1.004)	-1.932	0.053
	2000-2019 (n=2560)	0.512 (0.384, 0.683)	-4.556	<0.001
females (n=3478) wild-born (n=1057)	males (n=2570)	1.509 (1.413-1.612)	12.267	<0.001
	zoo-born (n=4991)	0.928 (0.846-1.018)	-1.583	0.113
	Birth year	0.993 (0.991-0.995)	-7.114	<0.001
born 1960-2019 (n=5621) reference:				
females (n=3228) wild-born (n=699) 1960-1979 (n=1104)	males (n=2393)	1.548 (1.444-1.660)	12.288	<0.001
	zoo-born (n=4922)	0.803 (0.730-0.884)	-4.474	<0.001
	1980-1999 (n=1957)	0.937 (0.862-1.018)	-1.546	0.122
	2000-2019 (n=2560)	0.635 (0.574-0.704)	-8.713	<0.001
females (n=3228) wild-born (n=699)	males (n=2393)	1.537 (1.434-1.648)	12.090	<0.001
	zoo-born (n=4922)	0.855 (0.775-0.943)	-3.131	0.002
	Birth year	0.989 (0.986-0.992)	-8.326	<0.001

system lies with the zoo that kept the animal. While evident duplicates were excluded from analysis, they cannot be corrected in the Species360 database—this can only be done by Species360 staff after consultation with the respective zoos. In the process of data curation for this project, about 300 messages were sent in Species360 to ask for a data update for specific entries. This is a normal process in a dataset of several hundred thousand individuals to which so many different people make contributions.

Methodology: Choice of demographic approach

The main difference between the two approaches chosen in this study is that survivorship analysis, including the Cox proportional hazard analysis, is based on simple counts in the original data—how many animals survived to a certain age. It is easy to assess survivorship development of certain age groups individually, such

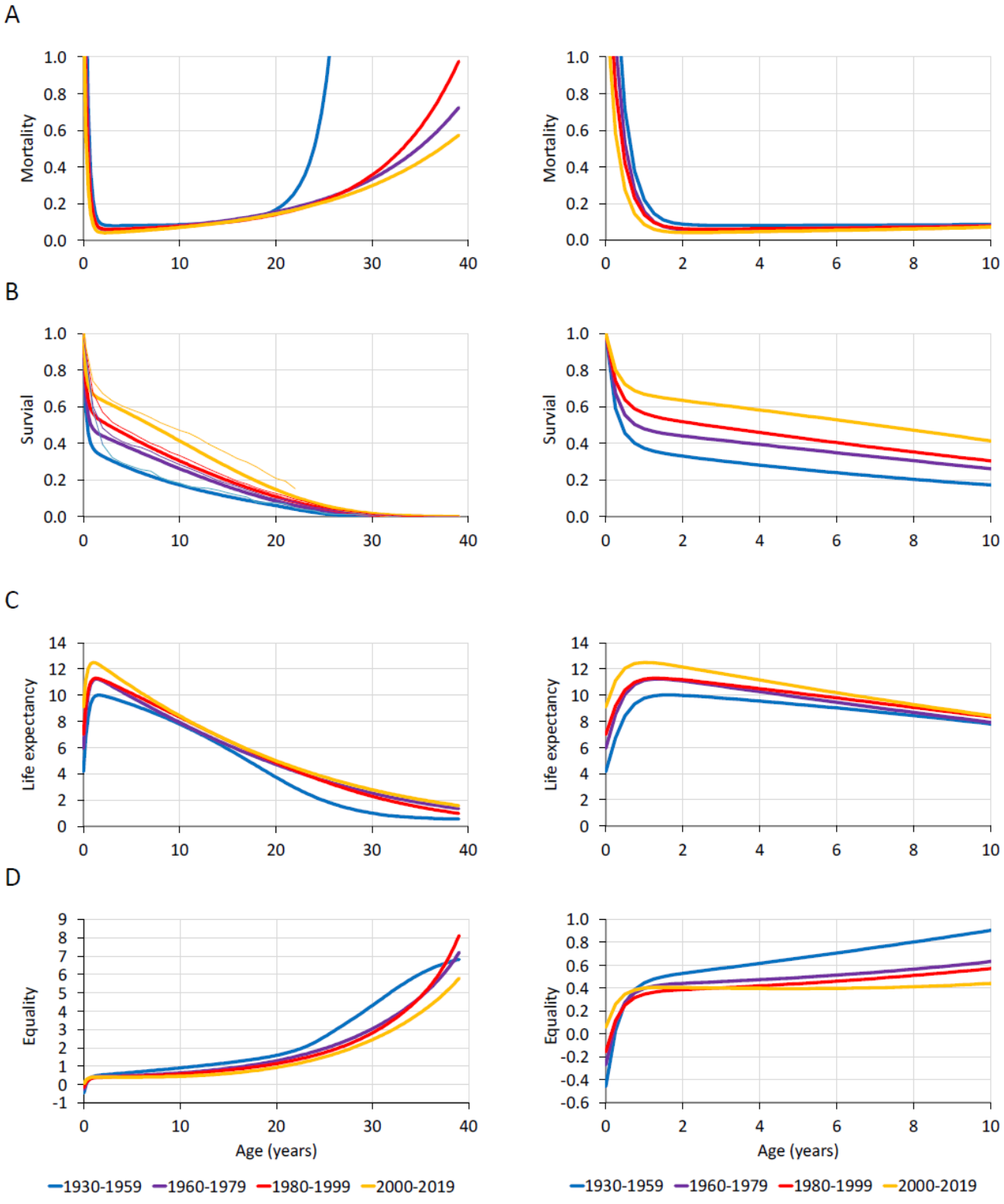

Figure 3. Modelled demographic measures in the global zoo-born giraffe *Giraffa camelopardalis* population for different time periods. In the left column, the whole lifetime of the species is reflected; in the right column, for a better evaluation of the initial years, the same displays are given for the first ten years of life. (A) age-specific mortality (the mortality at any given age; note that the model yields very high neonate mortality); (B) age-specific survival (the proportion of the population alive at a given age; note the original data on which the model was based in thin lines); (C) age-specific additional life expectancy (how many additional years an animal is expected to live at a given age); (D) age-specific equality (how equally the additionally expected years are spread across the population at a specific age). Note that the ranking of the birth cohorts is uniform across A–C, with lower mortality, higher survival and higher life expectancy for the most recent cohort. By contrast, ranking of cohorts changes with age, with the cohort with the lowest neonate mortality having the highest equality at birth and the cohort where animals die sooner after reaching maturity having the highest equality from about one year of age.

as neonates versus adults.

By contrast, demographic modelling based on Siler mortality assumes a certain (very realistic) data pattern and fits a corresponding mathematical equation to data covering all life stages together. In the case of 'open cohorts' where a certain proportion of the animals is still alive (i.e. cohorts born rather recently), this also implies some imputation or extrapolation of population development beyond the present. This is visualised in Figure 3B. It is unlikely that this extrapolation will lead to results that do not correctly reflect reality; yet it nevertheless represents a step that might be considered unnecessary.

An important reason for the use of demographic modelling may be the desire to express population development with estimates of how the average life expectancy has changed over time. Rather than simply stating that 'survivorship improved', one might want to express this in a relevant measure. In the case of the giraffe, demographic modelling shows that the average total life expectancy of a zoo giraffe that reaches the age of 4

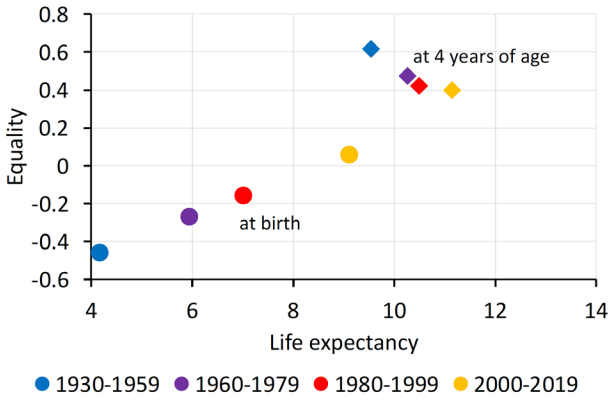

Figure 4. The relationship between age-specific life expectancy (at birth or at 4 years of age) with age-specific equality. Note the consistent increase in both values at birth over historical time, but the opposite trend at 4 years of age.

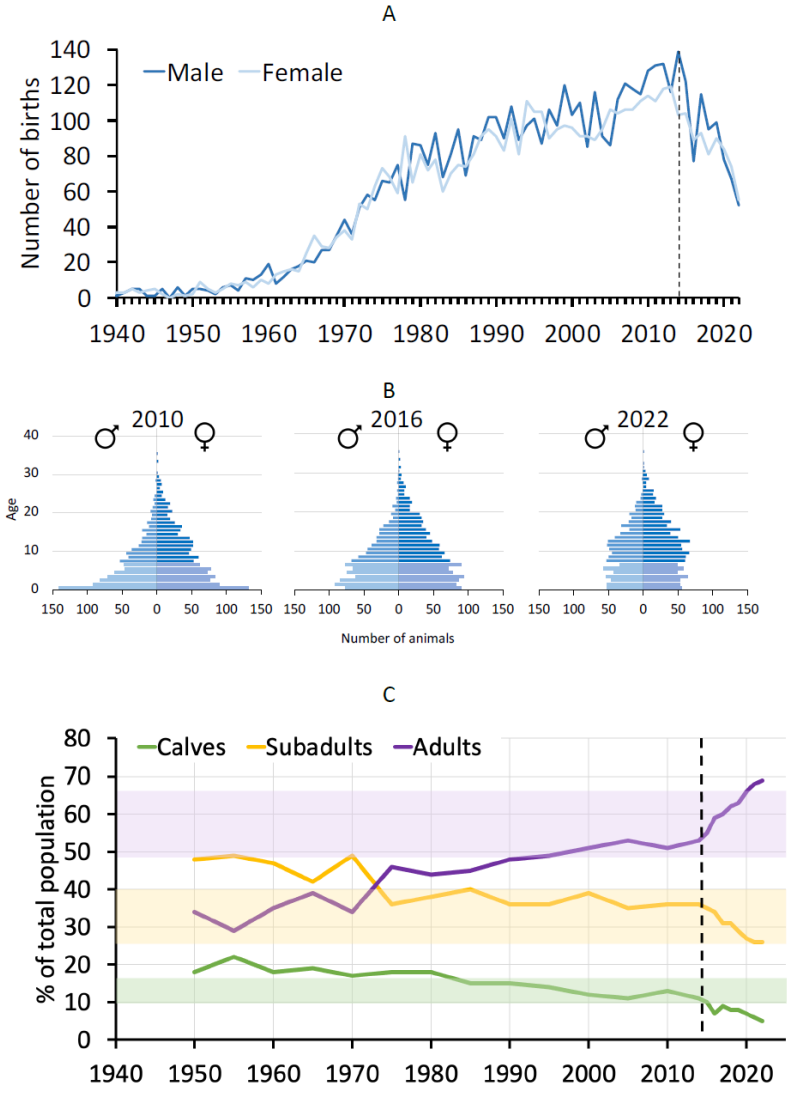

Figure 5. Indications for a rapid demographic transition in the global zoo giraffe *Giraffa camelopardalis* population: (A) number of births per year, with a distinct decrease after 2014 (dashed line); (B) changing population pyramid from a growing population in 2010 to an ageing population in 2022; (C) a slow shift in the proportions of calves, subadults and adults over time with a distinct acceleration of the respective trends after 2014 (dashed line). The shaded areas represent the percentages observed in natural habitats (sources in Figures 1 and 2).

Journal of Zoo and Aquarium Research 12(2) 2024
http://doi/org/10.19227/jzar.v12i2.798

years increased from 13.5 years in animals born in 1960–1979 to 15.1 years in animals born in 2000–2019. This statement is not necessarily superior to that derived from the counting approach that indicates a median total life expectancy of 13 years in animals born in 1960–1979 to 17 years in animals born in 2000–2019 in the same group—except that the concept of a 'mean' may be more intuitive for most people than a median. The magnitude of the described effect can be grasped with both statements.

Recently, the pattern that life expectancy and equality (at birth) increase monotonously within and across populations, as shown in the global zoo giraffe population (Figure 4), has been described for human and primate populations (Colchero et al. 2016, 2021) and in four marine mammal species kept in zoos (Tidière et al. 2023) as a near-universal pattern. As explained by Aburto et al. (2020), this pattern derives from the fact that the major contributor to the increase in lifespan is a reduction in neonate/juvenile mortality. Thus, when assessing all animals from birth onwards, equality does not appear to provide more information than the assessment of neonate/juvenile survivorship itself. Importantly, setting aims for equality is less straightforward than aiming to reduce mortality and increase lifespan and survivorship. This is exemplified in the development of equality for animals ≥4 years of age in Figure 4: here, the improvement of lifespan—a clearly positive development—is linked to a decrease in equality. This is because not all animals in all zoos have longer lifespans; some individuals still die as early as in previous decades, whereas other individuals now live longer lives. This is how demographic progress is expected to occur in general in a population spread out across many different facilities that do not make synchronised husbandry changes. Calculation of equality might be of interest in the future, to determine a 'turning point' where equality increases again with increasing lifespan for adult animals, indicating that the proportion of adults that achieve the ('new') long lifespan increases to the point that a majority of them reach 'old age'. Whether the pattern of the four data points for adult animals in Figure 4, where the decrease in equality from the last-but-one to the most recent decade is less steep than the preceding steps, already indicates such a development can only be judged in the future. Given the more detailed consideration necessary to interpret the direction of equality development, this measure might be considered less suitable for an intuitive communication of demographic developments to a larger public.

Comparisons with free-ranging populations

In natural habitats, adult giraffe mortality has repeatedly been described as comparatively low, with major effects on population development caused by juvenile and subadult survival (reviewed in Lee et al. 2022). Adult survival is typically higher in protected areas even though densities of natural predators are highest there, and lower in areas with less wildlife protection where poaching by humans is more prevalent (Lee et al. 2016b). Conversely, juvenile survival is often relatively higher outside of protected areas due to lower densities of natural predators (Lee et al. 2016b; Muller 2018). Estimating neonate survival is difficult (Foster 1966; Lee and Bond 2022; Leuthold and Leuthold 1978). After birth, female giraffe hide their young and only attend to them for brief spells of nursing for the first one to three weeks of life (Langman 1977). It is only after this period that the mother brings her calf to join a nursery herd. Therefore, detecting a neonate giraffe in a natural habitat is difficult. Neonate survival is apparently related to a coat pattern more beneficial for camouflage (Lee et al. 2018). Newborns are often only counted for the first time when seen with the nursery herd. For example, Mitchell et al. (2010) stated that, although neonates are frequently predated upon, skeletons of neonates are hardly ever detected. To account for this difficulty, birth estimates for free-ranging populations are sometimes based on the ratio of the number of calves to the number of adult females present in an area (Strauss et al. 2015), with some studies (e.g. Bond et al. 2021; Lee et al. 2016b) correcting the calf count for both imperfect detectability and neonatal calf survival. To what extent data from natural habitats therefore represent underestimates of birth and hence neonate mortality remains uncertain. For the same reasons, detailed causes of neonate mortality cannot be elucidated in natural habitats. While predation is most likely the immediate reason, it is difficult to speculate to what extent predispositions—'weak' neonates—contribute to a neonate becoming prey. In theory, this question is fundamental to the interpretation of zoo neonate mortality: would a certain proportion of neonates of a species be predisposed to not survive, irrespective of the presence of predators? In order to answer this question, studies comparing natural habitats with and without predator presence would be welcome (sensu Muller et al. 2018).

In natural habitats, a generally lower survivorship for males than for females has been described repeatedly (Lee et al. 2022; Strauss et al. 2015). In the zoo population, male survivorship is also lower, as described in general for males of polygamous species kept in zoos (Müller et al. 2011b; Tidière et al. 2015). To what degree this is caused by selective culling of male animals cannot be deduced based on the data available, which do not include cause of death.

Historic developments

Considerations of neonate survival in natural habitats have important implications for evaluation of zoo conditions. Whereas the results of this study suggest that a certain proportion of neonate mortality can be avoided by husbandry improvements, it is not clear whether the potential for such an improvement is already fully realised in the 2000–2019 cohort. Does the residual neonate mortality in this cohort represent a natural, intrinsic characteristic of the species or could neonate mortality be even further reduced? If future evaluations indicate a stagnation at this level, it would not be clear whether the level was species-specific or whether important husbandry solutions for a further reduction in neonate mortality had not been found or applied. Only if future evaluations indicate further improvement would there be a reliable answer, which nevertheless does not solve the question of 'species-specific, intrinsic neonate mortality'. This also applies to adult mortality; there is no way of knowing when the full survival potential of a species has been attained.

Single case reports of successful hand-rearing of giraffe calves that were rejected by their mothers had already been published in the 1960s (Savoy 1966; Zellmer 1961). However, recently, more detailed protocols are available including detailed growth curves and descriptions of optimal hand-rearing formula (Casares et al. 2012; Meuffels et al. 2019). Neonatal intensive care of giraffe calves has become more common in cases of inadequate transfer of passive immunity, diarrhoea or pneumonia, with excellent survival rates reported in the literature (Dixon et al. 2021). Additionally, knowledge about nursing of neonates by giraffe mothers has increased (Gloneková et al. 2016). To what degree this contributes to overall improvement of neonate survival cannot be evaluated. Hand-rearing is discussed controversially in management of zoo animals due to implications for the social behaviour of the respective individuals (e.g. Porton and Niebruegge 2006 for primates).

Whereas neonate survivorship increased continuously across the observation period (Figure 1), this was not the case for adult survivorship (Figure 2). Adult survivorship in this study shows a distinct increase between early giraffe husbandry in the 1900–1929 cohort and the subsequent cohorts between 1930–1999. Within the latter period, even though neonate survivorship kept increasing, adult survivorship showed neither progress nor deterioration. Historically, this was a period when the medical

and husbandry problems mentioned in the introduction were described. The fact that major survivorship progress occurred in the 2000–2019 cohort might be related to the fact that important documents that attempted to improve giraffe husbandry recommendations appeared at the beginning of this period (Burgess 2004; EAZA 2006; Jolly 2003) and were summarised later on (Gage 2019). While this explanation cannot be scientifically tested, the parallelism is suggestive. It would match the general observation across zoo ruminants that those species for which dedicated WAZA studbooks (with husbandry recommendations) exist generally achieve higher relative longevity (Müller et al. 2011b).

It may be difficult to single out individual measures that particularly contributed to improved survivorship in the last 20 years. Across ruminants, browsing species are generally more difficult to maintain to high relative longevities than grazing species (Müller et al. 2011b). As strict natural browsers, giraffe may be particularly susceptible to feeding-related problems and distinct advances in the understanding of giraffe and browser nutrition were made in the respective time period (Clauss et al. 2001; Duggan et al. 2016; Gussek et al. 2018; Hatt et al. 2005; Kearney 2005; Monson et al. 2018; Okabe et al. 2023; Sullivan et al. 2010). Advances were summarised for the zoo community (Anon. 2005; Clauss and Dierenfeld 2008; Hummel and Clauss 2006; Valdes and Schlegel 2012) and sometimes proactively distributed to zoos keeping giraffe. One potential effect was the documented historical improvement of giraffe diets at least in Europe, evident when comparing results of diet surveys from 2005 (Hummel et al. 2006) and 2015 (Gussek et al. 2017). Efforts to further improve giraffe husbandry are ongoing (e.g. Depauw et al. 2023; Razal et al. 2024; Rose 2023).

As stated by Roller et al. (2021) and Scherer et al. (2023), such historical improvements should be considered normal outcomes of an engaged field of professionals, and never be considered finished. However, they do emphasise that efforts made are worthwhile. This may mean that survivorship targets need to be re-adjusted; there is growing concern about population sustainability, which could dictate the need for culling of older post-reproductive individuals to provide space for breeding. While essential for the population, this would decrease average longevity.

A rapid demographic shift

A distinct reduction in breeding recommendations by the European studbook coordinator (J. Jebram, personal communication) occurred around the same time that the culling of a single genetically and demographically surplus giraffe gained massive public attention. The temporal association among these two events, the distinct decline in births and the rapid shift in population structure are evident (Figure 5). The sudden drop in recommended giraffe reproduction led to a distinct increase in the proportion of adult animals and a decrease in the proportion of juveniles in the population, with a rapid shift in population pyramid from that of a growing to an ageing population. In human populations, such a shift does not occur as rapidly as in the global zoo giraffe population; it typically takes several decades (Saroha 2018). For human populations, such a change in the population pyramid is a desired effect of improved living conditions and healthcare but comes with cultural and economic challenges. In the zoo community, management of geriatric animals is now receiving more attention (Brando and Chapman 2023), suggesting that the trend observed in giraffe in the present study is not limited to this species.

In the case of giraffe, it is tempting to interpret the immediate adherence to the recommendation to reduce breeding partly as a reaction to the 2014 Copenhagen culling—possibly, zoos wanted to avoid the necessity of culling and the potential associated public reactions. It is impossible to gauge the amount of population management culling that was performed before or after 2014 based on the data available for the present study. The slight but continuous increase in the proportion of adult males might be an indication of generally better living conditions in zoos in general (so that males survive longer despite their propensity for higher mortality), an indication that selective culling of males was reduced after the 2014 incident, or both. To the knowledge of the European studbook coordinator (J. Jebram, personal communication) and following a statement by AZA in 2014 (AZA 2014), selective male culling was not used by many zoos. However, about 10 cases have been reported in Scandinavia (Sauer et al. 2016).

Among the different issues surrounding such a demographic shift, three in particular are notable: the ethical implications of rejecting a 'breed and cull' or 'breed and feed' system, the risk it implies for population management and the consequences for the educational mission of nature and species conservation. A decision against a 'breed and feed' system and therefore reducing offspring production implies denying zoo animals reproductive activity and their corresponding social systems, including, for example, allonursing behaviour in giraffe (Gloneková et al. 2016). In two cases of female giraffe that gave birth and raised young, oral stereotypies decreased, illustrating the positive effect of nurturing offspring (Schüßler et al. 2015; Walldén 2023). Ethical implications must be balanced with the necessity that zoo carnivores are fed. A decision against a zoo-based 'breed and feed' system simultaneously fosters, by market demand, the use of carnivore food derived from production animal systems that traditionally keep animals under conditions that typically would be considered inferior to those of zoo animals. This relates to the reproductive management of production animals including natural or assisted breeding, the timing of separation of parent and offspring and the species-specific social systems, space, housing, diet provision, enrichment and conditions linked to the killing of the animal such as transport and stress due to the setting of a typical commercial slaughterhouse.

In terms of population management, it appears self-evident that a population in a growth stage (as in the left population pyramid of Figure 5B) is resilient and can be managed at low risk, because the harvest (killing) of animals is a process that can occur instantaneously or with a very short preparation period. By contrast, managing an ageing population (as in the right population pyramid of Figure 5B) is more complex and hence considerably more risky. This is because the recruitment of necessary juveniles is a process that implies decisions based on analysed necessity, and the communication of these decisions to the corresponding zoos, which have to act on these recommendations (e.g. by allowing animals access to each other or terminating contraception). The sum of all these steps causes a long reaction period. To this, the gestation period and time to sexual maturity must be added, as well as the uncertainties of mate acceptance, conception, juvenile survivorship, unpredictability of contraception reversibility (Penfold et al. 2014), reduced competence of mother animals (which is important in giraffe: Gloneková et al. 2020) as well as keepers due to the rareness of births and random hazards that cannot be predicted (e.g. an epizootic with resulting transport restrictions). These factors make this approach more prone to failure, which may be risky given the small sizes of many zoo populations. Additionally, whether certain contraceptive methods may make various animals, including giraffe, susceptible to reproductive tract tumours cannot be excluded to date (Doden et al. 2021) with potential consequences for an individual's welfare.

In terms of the educational aspect, the outsourcing of killing animals required as carnivore food, potentially combined with deliberate avoidance of the topic of death altogether, is in conflict

with the aim of educating zoo visitors about nature and ecosystem function, and also about the human food chain, its mode of operation and its impact on the environment. Thus it generally conflicts with educational aims like sustainability and transparent accountability for one's actions and their consequences, including the realistic constraints under which ex-situ conservation has to operate. With respect to these aims, an important insight and important consequences of the 2014 Copenhagen Zoo culling are often forgotten. Whereas in the estimated total of 300,000 online media comments there were more negative (16.6%) than positive (4.4%) comments, the large majority were classified as neutral (79.1%) (Zimmerman et al. 2014), suggesting that the (often overlooked) majority of the public is open to debate. The scientific director of Copenhagen Zoo—the person publicly perceived as responsible and accountable—was elected 'citizen of the year' in the aftermath (Vesterberg 2014). Rather than only being evidence for the dangers of public reactions, the case of the 2014 Copenhagen Zoo culling thus also demonstrates that a large segment of the public values responsible, transparently communicated, holistic approaches.

In the case of zoo giraffe, the large population size, together with a considerable number of new giraffe enclosures currently planned at various zoos across Europe, makes a timely change in demographic development feasible. In the EEP, giraffe are currently managed by subspecies, with breeding recommendations for *Giraffa camelopardalis rothschildi, G. c. reticulata, G. c. antiquorum* and currently also *G. c. angolensis* (J. Jebram, personal communication).

Conclusion

Evaluation of the zoo giraffe population demonstrates an improvement in neonate/juvenile and adult survival over time, with zoo giraffe having higher survivorship than free-ranging giraffe. Although no direct proof can be provided, this is most likely an effect of the common effort of the global zoo community to enhance giraffe husbandry.

Given limitations on the number of giraffe that can be maintained in zoos, this husbandry success leads to a situation where either breeding has to cease or animals need to be selectively removed by culling. The perception of the public's reaction to a specific case of culling of a zoo giraffe (and feeding it to the zoo's lions) may have encouraged many zoos to choose to cease breeding, with a concomitant demographic shift towards a zoo population with a large number of old animals. Such a choice has ethical implications not only with respect to the decision of culling of a specific animal, but also with respect to living conditions of groups with limited offspring, the culling of alternative individuals required as food for zoo's carnivores, sustainability and education, as well as making population management more risky.

Acknowledgments

This research was made possible by the worldwide information network of zoos and aquariums which are members of Species360 and is authorised by Species360 Research Data Agreement # 2019-Q3-RR3. MHK and PWD were supported by Opel-Zoo Foundation Professorship in Zoo Biology from the "von Opel Hessische Zoostiftung".

References

Aburto J.M., Villavicencio F., Basellini U., Kjærgaard S., Vaupel J.W. (2020) Dynamics of life expectancy and life span equality. *Proceedings of the National Academy of Sciences* 117(10): 5250–5259. doi:10.1073/pnas.1915884117

Anonymous (2005) *The Giraffe Nutrition Workshop Proceedings.* Chicago, Illinois: Lincoln Park Zoo.

AZA (2014) *Statement by Association of Zoos and Aquariums Regarding the Euthanasia of Giraffe at the Copenhagen Zoo.* Available at https://www.aza.org/aza-news-releases/posts/statement-by-association-of-zoos-and-aquariums-regarding-the-euthanasia-of-giraffe-- (accessed 22 September 2023).

Barongi R., Fisken F.A., Parker M., Gusset M. (2015) *Committing to Conservation: The World Zoo and Aquarium Conservation Strategy.* Gland, Switzerland: WAZA Executive Office.

Bashaw M.J., Tarou L.R., Maki T.S., Maple T.L. (2001) A survey assessment of variables related to stereotypy in captive giraffe and okapi. *Applied Animal Behaviour Science* 73(3): 235–247. doi:10.1016/S0168-1591(01)00137-X

Bashaw M.J., Bloomsmith M.A., Maple T.L., Bercovitch F.B. (2007) The structure of social relationships among captive female giraffe (*Giraffa camelopardalis*). *Journal of Comparative Psychology* 121(1): 46–53. doi:10.1037/0735-7036.121.1.46

Bercovitch F.B., Berry P.S.M. (2010) Reproductive life history of Thornicroft's giraffe in Zambia. *African Journal of Ecology* 48(2): 535–538. doi:10.1111/j.1365-2028.2009.01145.x

Berland J. (2017) Attending the giraffe. *Humanimalia* 9(1): 22–45. doi:10.52537/humanimalia.9612

Bertelsen M.F. (2014) On the euthanasia of surplus animals and the role of zoos in alleviating biological illiteracy – lessons learned. *Proceedings of the International Conference on Diseases of Zoo and Wild Animals*, 65–67.

Bertelsen M.F. (2015) Giraffidae. In: Miller R.E., Fowler M.E. (eds.). *Fowler's Zoo and Wild Animal Medicine Vol. 8*. St. Louis, Missouri: Elsevier Saunders, 602–610.

Bertelsen M.F. (2018) Issues surrounding surplus animals in zoos. In: Miller R.E., Lamberski N., Calle P. (eds.). *Fowler's Zoo and Wild Animal Medicine Current Therapy, Volume 9.* St. Louis, Missouri: WB Saunders, 134–136.

Bond M.L., König B., Ozgul A., Farine D.R., Lee D.E. (2021) Socially defined subpopulations reveal demographic variation in a giraffe metapopulation. *Journal of Wildlife Management* 85(5): 920–931. doi:10.1002/jwmg.22044

Bond M.L., Ozgul A., Lee D.E. (2023) Effect of local climate anomalies on giraffe survival. *Biodiversity and Conservation* 32: 3179–3197. doi:10.1007/s10531-023-02645-4

Brando S., Chapman S. (eds.). (2023) *Optimal Wellbeing of Ageing Wild Animals in Human Care.* Cham, Switzerland: Springer International.

Brown M.B., Fennessy J.T., Crego R.D., Fleming C.H., Alves J., Brandlová K., Fennessy S., Ferguson S., Hauptfleisch M., Hejcmanova P., Hoffman R., Leimgruber P., Masiaine S., McQualter K., Mueller T., Muller B., Muneza A., O'Connor D., Olivier A.J., Rabeil T., Seager S., Stacy-Dawes J., van Schalkwyk L., Stabach J. (2023) Ranging behaviours across ecological and anthropogenic disturbance gradients: A pan-African perspective of giraffe (*Giraffa* spp.) space use. *Proceedings of the Royal Society B* 290(2001): 20230912. doi:10.1098/rspb.2023.0912

Burger A.L., Hartig J., Dierkes P.W. (2021) Biological and environmental factors as sources of variation in nocturnal behavior of giraffe. *Zoo Biology* 40(3): 171–181. doi:10.1002/zoo.21596

Burgess A. (2004) *The Giraffe Husbandry Resource Manual.* AZA Antelope and Giraffe TAG.

Carmona C.P., Tamme R., Pärtel M., de Bello F., Brosse S., Capdevila P., González M.R., González-Suárez M., Salguero-Gómez R., Vásquez-Valderrama M., Toussaint A. (2021) Erosion of global functional diversity across the tree of life. *Science Advances* 7: eabf2675. doi:10.1126/sciadv.abf2675

Casares M., Bernhard A., Gerique C., Malo E., Carbonell D. (2012) Hand-rearing Rothschild or Baringo giraffe *Giraffa camelopardalis rothschildi* calves at Bioparc Valencia, Spain, and Leipzig Zoo, Germany. *International Zoo Yearbook* 46(1): 221–231. doi:10.1111/j.1748-1090.2012.00174.x

Clauss M., Dierenfeld E.S. (2008) The nutrition of browsers. In: Fowler M.E., Miller R.E. (eds.). *Zoo and Wild Animal Medicine. Current Therapy 6*. St. Louis, Missouri: Saunders Elsevier, 444–454.

Clauss M., Lechner-Doll M., Flach E.J., Tack C., Hatt J.M. (2001) Comparative use of four different marker systems for the estimation of digestibility, and low food intake in a group of captive giraffes (*Giraffa camelopardalis*). *Zoo Biology* 20(4): 315–329. doi:10.1002/zoo.1031

Clauss M., Rose P., Hummel J., Hatt J.M. (2006) Serous fat atrophy and other nutrition-related health problems in captive giraffe (*Giraffa camelopardalis*). An evaluation of 83 necropsy reports. *Proceedings of the European Association of Zoo and Wildlife Veterinarians* 6: 233–

235.
Clauss M., Franz-Odendaal T.A., Brasch J., Castell J.C., Kaiser T. (2007) Tooth wear in captive giraffes (*Giraffa camelopardalis*): Mesowear analysis classifies free-ranging specimens as browsers but captive ones as grazers. *Journal of Zoo and Wildlife Medicine* 38(3): 433–445.
Clavadetscher I., Bond M.., Martin L., Schiffmann C., Hatt J.M., Clauss M. (2021) Development of an image-based body condition score for giraffes *Giraffa camelopardalis* and a comparison of zoo-housed and free-ranging individuals. *Journal of Zoo and Aquarium Research* 9(3): 170–185. doi:10.19227/jzar.v9i3.615
Clayton A. (2023) "That ancient and modern wonder": Giraffes, imperialism, and the making of the American menagerie, 1830–1840. *Atlantic Studies* 21(1): 30–52. doi:10.1080/14788810.2023.2240011
Cohen E., Fennell D. (2016) The elimination of Marius, the giraffe: Humanitarian act or callous management decision? *Tourism Recreation Research* 41(2): 168–176. doi:10.1080/02508281.2016.1147211
Coimbra R.T.F., Winter S., Kumar V., Koepfli K.P., Gooley R.M., Dobrynin P., Fennessy J., Janke A. (2021) Whole-genome analysis of giraffe supports four distinct species. *Current Biology* 31: 2929–2938. doi:10.1016/j.cub.2021.04.033
Colchero F., Rau R., Jones O.R., Barthold J.A., Conde D.A., Lenart A., Nemeth L., Scheuerlein A., Schoeley J., Torres C., Zarulli V., Altmann J., Brockman D.K., Bronikowski A.M., Fedigan L.M., Pusey A.E., Stoinski T.S., Strier K.B., Baudisch A., Alberts S.C., Vaupel J.W. (2016) The emergence of longevous populations. *Proceedings of the National Academy of Sciences* 113(48): 7681–7690. doi:10.1073/pnas.1612191113
Colchero F., Aburto J.M., Archie E.A., Boesch C., Breuer T., Campos F.A., Collins A., Conde D.A., Cords M., Crockford C., Thompson M.E., Fedigan L.M., Fichtel C., Groenenberg M., Hobaiter C., Kappeler P.M., Lawler R.R., Lewis R.J., Machanda Z.P., Manguette M.L., Muller M.N., Packer C., Parnell R.J., Perry S., Pusey A.E., Robbins M.M., Seyfarth R.M., Silk J.B., Staerk J., Stoinski T.S., Stokes E.J., Strier K.B., Strum S.C., Tung J., Villavicencio F., Wittig R.M., Wrangham R.W., Zuberbühler K., Vaupel J.W., Alberts S.C. (2021) The long lives of primates and the 'invariant rate of ageing'hypothesis. *Nature Communications* 12: 3666. doi:10.1038/s41467-021-23894-3
Dadone L.I., Schilz A., Friedman S.G., Bredahl J., Foxworth S., Chastain B. (2016) Training giraffe (*Giraffa camelopardalis reticulata*) for front foot radiographs and hoof care. *Zoo Biology* 35(3): 228–236.
Depauw S., Verbist L., Stevens J.M.G., Salas M. (2023) Feeding management of giraffe towards positive welfare. *Journal of Zoo and Aquarium Research* 11(4): 400–413. doi:10.19227/jzar.v11i4.769
Dixon C.E., Bedenice D., Restifo M., Mazan M., Brewer P., Knafo S.E. (2021) Neonatal intensive care of 10 hospitalized giraffe calves (*Giraffa camelopardalis*) requiring hand-rearing. *Journal of Zoo and Wildlife Medicine* 52(1): 57–66. doi:10.1638/2019-0021
Doden G., Garner M.M., Mangus L.M., Sander S. (2021) A retrospective survey of neoplasia in managed giraffes (*Giraffa camelopardalis*). *Journal of Zoo and Wildlife Medicine* 52(1): 332–336.
Duggan G., Burn C.C., Clauss M. (2016) Nocturnal behaviour in captive giraffe (*Giraffa camelopardalis*) – A pilot study. *Zoo Biology* 35(1): 14–18. doi:10.1002/zoo.21248
EAZA (2006) *EAZA Husbandry and Management Guidelines for* Giraffa camelopardalis. Arnhem, Belgium: Burgers' Zoo.
EAZA (2023) *Position Statement on Management Euthanasia/Culling.* Amsterdam, Netherlands: European Association of Zoos and Aquaria. Available online at https://www.eaza.net/assets/Uploads/Position-statements/2023/2023-04-EAZA-Management-Euthanasia-Culling-Statement.pdf
Farhadinia M.S., Johnson P.J., Zimmermann A., McGowan P.J.K., Meijaard E., Stanley-Price M., Macdonald D.W. (2020) Ex situ management as insurance against extinction of mammalian megafauna in an uncertain world. *Conservation Biology* 34(4): 988–996. doi:10.1111/cobi.13496
Foster J.B. (1966) The giraffe of Nairobi National Park: Home range, sex ratios, the herd, and food. *African Journal of Ecology* 4(1): 139–148. doi:10.1111/j.1365-2028.1966.tb00889.x
Foster J.B., Dagg, A.I. (1972) Notes on the biology of the giraffe. *African Journal of Ecology* 10(1): 1–16. doi:10.1111/j.1365-2028.1972.tb00855.x
Gage L.J. (2019) Giraffe husbandry and welfare. In: Miller R.E., Lamberski N., Calle P. (eds.). *Fowler's Zoo and Wild Animal Medicine Vol. 9*. St. Louis, Missouri: Elsevier, 619–622.
Gloneková M., Brandlová K., Pluháček J. (2016) Stealing milk by young and reciprocal mothers: High incidence of allonursing in giraffes, *Giraffa camelopardalis. Animal Behaviour* 113: 113–123. doi:10.1016/j.anbehav.2015.11.026
Gloneková M., Brandlová K., Pluháček J. (2020) Higher maternal care and tolerance in more experienced giraffe mothers. *Acta Ethologica* 23: 1–7. doi:10.1007/s10211-019-00328-4
Gussek I., Hirsch S., Hartmann M., Südekum K.H., Hummel J. (2017) Feeding practices for captive giraffes (*Giraffa camelopardalis*) in Europe: A survey in EEP zoos. *Journal of Zoo and Aquarium Research* 5(1): 62–70. doi:10.19227/jzar.v5i1.152
Gussek I., Große-Brinkhaus C., Südekum K.H., Hummel J. (2018) Influence of ration composition on nutritive and digestive variables in captive giraffes (*Giraffa camelopardalis*) indicating the appropriateness of feeding practice. *Journal of Animal Physiology and Animal Nutrition* 102(2): e513–e524. doi:10.1111/jpn.12790
Hatt J.M., Schaub D., Wanner M., Wettstein H.R., Flach E.J., Tack C., Hässig M., Ortmann S., Hummel J., Clauss M. (2005) Energy and fibre intake in a group of captive giraffe (*Giraffa camelopardalis*) offered increasing amounts of browse. *Journal of Veterinary Medicine Series A* 52(10): 485–490. doi:10.1111/j.1439-0442.2005.00769.x
Havercamp K., Watanuki K., Tomonaga M., Matsuzawa T., Hirata S. (2019) Longevity and mortality of captive chimpanzees in Japan from 1921 to 2018. *Primates* 60: 525–535. doi:10.1007/s10329-019-00755-8
Hofman S., Simonsen K., Zimmermann M., van der Meer R., Hausen M., Leus K. (2022) *Regional Collection Plan for the EAZA Antelope and Giraffid Taxon Advisory Group*. Amsterdam, Netherlands: EAZA Executive Office.
Hummel J., Clauss M. (2006) Feeding. In: *EAZA Husbandry and Management Guidelines for* Giraffa camelopardalis. Arnhem, Belgium: Burger's Zoo, 29–61.
Hummel J., Zimmermann W., Langenhorst T., Schleussner G., Damen M., Clauss M. (2006) Giraffe husbandry and feeding practices in Europe. Results of an EEP survey. *Proceedings of the European Association of Zoo and Wildlife Veterinarians* 6: 71–74.
Jett J., Ventre J. (2015) Captive killer whale (*Orcinus orca*) survival. *Marine Mammal Science* 31(4): 1362–1377. doi:10.1111/mms.12225
Jolly L. (2003) Giraffe Husbandry Manual. Australasian Society of Zoo Keeping.
Junge R.E., Bradley T.A. (1993) Peracute mortality syndrome of giraffes. In: Fowler M.E. (ed.). *Zoo and Wild Animal Medicine, Vol 3*. Philadelphia, Pennsylvania: W.B. Saunders Co., 547–549.
Kauffels T. (2008) New keeping of giraffes at Opel Zoo Kronberg. *Der Zoologische Garten* 77: 191–206.
Kearney C. (2005) *Effects of Dietary Physical Form and Carbohydrate Profile on Captive Giraffe.* Gainsville, Florida: University of Florida Doctoral dissertation.
Lagueux O. (2003) Geoffroy's giraffe: The hagiography of a charismatic mammal. *Journal of the History of Biology* 36: 225–247. doi:10.1023/A:1024435232569
Lamarck J.B. (1809) Philosophie Zoologique. Paris, France: JB Baillière.
Langman V.A. (1977) Cow-calf relationships in giraffe (*Giraffa camelopardalis giraffa*). *Zeitschrift fur Tierpsychologie* 43(3): 264–286. doi:10.1111/j.1439-0310.1977.tb00074.x
Lavista Ferres J.M., Lee D.E., Nasir M., Chen Y.C., Bijral A.S., Bercovitch F.B., Bond M.L. (2021) Social connectedness and movements among communities of giraffes vary by sex and age class. *Animal Behaviour* 180: 315–328. doi:10.1016/j.anbehav.2021.08.008
Lebleu O. (2020) *In the Footsteps of Zarafa, First Giraffe in France: A Chronicle of Giraffomania*, 1826–1845. London, UK: Rowman and Littlefield.
Ledgard J.M. (2006) *Giraffe*. London, UK: Jonathan Cape.
Lee D.E., Bond M.L. (2022) Giraffe metapopulation demography. In: Kiffner C., Bond M.L., Lee E.L. (eds.). *Tarangire: Human-Wildlife Coexistence in a Fragmented Ecosystem.* Cham, Switzerland: Springer, 189–207.
Lee D.E., Kissui B.M., Kiwango Y.A., Bond M.L. (2016a) Migratory herds of wildebeests and zebras indirectly affect calf survival of giraffes. *Ecology and Evolution* 6(23): 8402–8411. doi:10.1002/ece3.2561
Lee D.E., Bond M.L., Kissui B.M., Kiwango Y.A., Bolger D.T. (2016b) Spatial variation in giraffe demography: A test of two paradigms. *Journal of Mammalogy* 97(4): 1015–1025. doi:10.1093/jmammal/gyw086
Lee D.E., Cavener D.R., Bond M.L. (2018) Seeing spots: Quantifying mother-offspring similarity and assessing fitness consequences of coat pattern traits in a wild population of giraffes (*Giraffa camelopardalis*). *PeerJ* 6: e5690. doi:10.7717/peerj.5690
Lee D.E., Lohay G.G., Cavener D.R., Bond M.L. (2022) Using spot pattern recognition to examine population biology, evolutionary ecology, sociality, and movements of giraffes: A 70-year retrospective. *Mammalian Biology* 102: 1055–1071. doi:10.1007/s42991-022-00261-3
Leuthold B.M., Leuthold W. (1978) Ecology of the giraffe in Tsavo East National Park, Kenya. *African Journal of Ecology* 16(1): 1–20.

doi:10.1111/j.1365-2028.1978.tb00419.x

Mellor D.J., Hunt S., Gusset M. (2015) *Caring for Wildlife: The World Zoo and Aquarium Animal Welfare Strategy*. Gland, Switzerland: WAZA Executive Office.

Meuffels J., Ververs C., Pootoolal J., van Zijll Langhout M., Govaere J. (2019) Growth, husbandry, and diets of five successfully hand-reared orphaned giraffe calves (*Giraffa camelopardalis rothschildi* and *Giraffa camelopardalis reticulata*). *Journal of Zoo and Wildlife Medicine* 50(1): 205–218. doi:10.1638/2018-0016

Mitchell G., Van Sittert S., Skinner J.D. (2010) The demography of giraffe deaths in a drought. *Transactions of the Royal Society of South Africa* 65(3): 165–168. doi:10.1080/0035919X.2010.509153

Monson M.L., Dennis P.M., Lukas K.E., Krynak K.L., Carrino-Kyker S.R., Burke D.J., Schook M.W. (2018) The effects of increased hay-to-grain ratio on behavior, metabolic health measures, and fecal bacterial communities in four Masai giraffe (*Giraffa camelopardalis tippelskirchi*) at Cleveland Metroparks Zoo. *Zoo Biology* 37(5): 320–331. doi:10.1002/zoo.21434

Müller D.W.H., Zerbe P., Codron D., Clauss M., Hatt J.M. (2011a) A long life among ruminants: giraffids and other special cases. *Schweizer Archiv für Tierheilkunde* 153(11): 515–519.

Müller D.W.H., Bingaman Lackey L., Streich W.J., Fickel J., Hatt J.M., Clauss M. (2011b) Mating system, feeding type and ex-situ conservation effort determine life expectancy in captive ruminants. *Proceedings of the Royal Society B* 278(1714): 2076–2080. doi:10.1098/rspb.2010.2275

Muller Z. (2018) Population structure of giraffes is affected by management in the Great Rift Valley, Kenya. *PLoS ONE* 13(1): e0189678.

Muller Z., Bercovitch F., Brand R., Brown D., Brown M., Bolger D., Carter K., Deacon F., Doherty J.B., Fennessy J., Fennessy S., Hussein A.A., Lee D., Marais A., Strauss M., Tutchings A., Wube T. (2018) Giraffa camelopardalis (amended version of 2016 assessment). *The IUCN Red List of Threatened Species 2018*. e.T9194A136266699. doi:10.2305/IUCN.UK.2016-3.RLTS.T9194A136266699.en

Muller Z., Harris S. (2022) A review of the social behaviour of the giraffe Giraffa camelopardalis: A misunderstood but socially complex species. *Mammal Review* 52(1): 1–15. doi:10.1111/mam.12268

Okabe K., Fukuizumi H., Kawamura A., Kase C., Uetake K. (2023) An investigation of browsing enrichment, especially non-leaf foraging, on giraffes (*Giraffa camelopardalis reticulata*) at Kyoto City Zoo in Japan. *Zoo Biology* 42(1): 157–161. doi:10.1002/zoo.21726

Pellew R.A. (1983) The giraffe and its food resource in the Serengeti. II. Response of the giraffe ppopulation to changes in the food supply. *African Journal of Ecology* 21(4): 269–283.

Penfold L.M., Powell D., Traylor-Holzer K., Asa C.S. (2014) "Use it or lose it": Characterization, implications, and mitigation of female infertility in captive wildlife. *Zoo Biology* 33(1): 20–28. doi:10.1002/zoo.21104

Petzold A., Magnant A.S., Edderai D., Chardonnet B., Rigoulet J., Saint-Jalme M., Hassanin A. (2020) First insights into past biodiversity of giraffes based on mitochondrial sequences from museum specimens. *European Journal of Taxonomy* 703: 1–33. doi:10.5852/ejt.2020.703

Pizzutto C.S., Colbachini H., Jorge-Neto P.N. (2021) One Conservation: The integrated view of biodiversity conservation. *Animal Reproduction* 18(2): e20210024. doi:10.1590/1984-3143-AR2021-0024

Porton I., Niebruegge K. (2006) The changing role of hand rearing in zoo-based primate breeding programs. In: Sackett G.P., Ruppentahal G.C., Elias K. (eds.). *Nursery Rearing of Nonhuman Primates in the 21st Century*. Boston, Massachusetts: Springer, 21–31.

Potter J.S., Clauss M. (2005) Mortality of captive giraffe (Giraffa camelopardalis) associated with serous fat atrophy: A review of five cases at Auckland Zoo. *Journal of Zoo and Wildlife Medicine* 36(2): 301–307. doi:10.1638/03-097.1

Powell D.M., Ardaiolo M. (2016) Survey of US zoo and aquarium animal care staff attitudes regarding humane euthanasia for population management. *Zoo Biology* 35(3): 187–200. doi:10.1002/zoo.21278

Powell D.M., Dorsey C.L., Faust L.J. (2019) Advancing the science behind animal program sustainability: An overview of the special issue. *Zoo Biology* 38(1): 5–11. doi:10.1002/zoo.21474

Powell D.M., Lan J., Eng C. (2018) Survey of US-based zoo veterinarians' attitudes on population management euthanasia. *Zoo Biology* 37(6): 478–487. doi:10.1002/zoo.21447

Pratt D.M., Anderson V.H. (1985) Giraffe social behaviour. *Journal of Natural History* 19(4): 771–781. doi:10.1080/00222938500770471

R Core Team (2023) *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org

Razal C., Bryant J., Miller L. (2024) Assessing giraffe welfare during seasonal habitat changes in northern US zoos. *Journal of Zoo and Aquarium Research* 12(1): 9–15. doi:10.19227/jzar.v12i1.762

Remport L., Sós-Koroknai V., Hoitsy M., Sós E. (2022) Mandibular fractures in giraffes (*Giraffa camelopardalis*) in European zoos. *Journal of Zoo and Wildlife Medicine* 53(2): 448–454. doi:10.1638/2021-0007

Ringmar E. (2006) Audience for a giraffe: European expansionism and the quest for the exotic. *Journal of World History* 17(4): 375–397.

Roller M., Müller D.W.H., Bertelsen M.F., Bingaman Lackey L., Hatt J.M., Clauss M. (2021) The historical development of juvenile mortality and adult longevity in zoo-kept carnivores. *Zoo Biology* 40(6): 588–595.

Rose P. (2023) Identifying essential elements of good giraffe welfare — Can we use knowledge of a species' fundamental needs to develop welfare-focussed husbandry? *Journal of Zoological and Botanical Gardens* 4(3): 549–566. doi:10.3390/jzbg4030039

Rose P.E., Riley L.M. (2022) Expanding the role of the future zoo: Wellbeing should become the fifth aim for modern zoos. *Frontiers in Psychology* 13: 1018722. doi:10.3389/fpsyg.2022.1018722

Saroha J. (2018) Types and significance of population pyramids. *World Wide Journal of Multidisciplinary Research and Development* 4(4): 59–69.

Sauer C., Bertelsen M.F., Lund P., Weisbjerg M.R., Clauss M. (2016) Quantitative macroscopic anatomy of the giraffe (*Giraffa camelopardalis*) digestive tract. *Anatomia Histologia Embryologia* 45(5): 338–349. doi:10.1111/ahe.12201

Savoy J.C. (1966) Breeding and hand-rearing of the giraffe *Giraffa camelopardalis* at Columbus Zoo. *International Zoo Yearbook* 6(1): 202–204. doi:10.1111/j.1748-1090.1966.tb01755.x

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(2): 328–338. doi:10.1002/zoo.21733

Schüßler D., Gürtler W.D., Greven H. (2015) Aktivitätsbudgets von Rothschildgiraffen (*Giraffa camelopardalis rothschildi* Lydekker, 1903) in der „Zoom Erlebniswelt Gelsenkirchen". *Der Zoologische Garten* 84(1–2): 61–74. doi:10.1016/j.zoolgart.2015.01.002

Schüßler D., Gürtler W.D., Keyser S., Greven H. (2017) Einflüsse des Nahrungsangebotes auf Aktivitätsbudgets und mittlere Partikelgrößen im Kot von Rothschildgiraffen (*Giraffa camelopardalis rothschildi*, Lydekker 1903) in der ZOOM Erlebniswelt Gelsenkirchen. *Der Zoologische Garten* 86(1–6): 167–175.

Schwarzenberger F., Krawinkel P., Jeserschek S.M., Schauerte N., Geiger C., Balfanz F., Knauf-Witzens T., Sicks F., Martinez Nevado E., Anfray G., Hein A., Kaandorp-Huber C., Marcordes S., Venshøj B. (2022) Immunocontraception of male and female giraffes using the GnRH vaccine Improvac®. *Zoo Biology* 41(1): 50–64. doi:10.1002/zoo.21651

Siler W. (1979) A competing-risk model for animal mortality. *Ecology* 60(4): 750–757. doi:10.2307/1936612

Strauss M.K.L., Kilewo M., Rentsch D., Packer C. (2015) Food supply and poaching limit giraffe abundance in the Serengeti. *Population Ecology* 57: 505–516. doi:10.1007/s10144-015-0499-9

Strauss M.K.L., Packer C. (2013) Using claw marks to study lion predation on giraffes of the Serengeti. *Journal of Zoology* 289(2): 134–142. doi:10.1111/j.1469-7998.2012.00972.x

Sullivan K., van Heutgen E., Ange-van Heutgen K., Poore M.H., Dierenfeld E.S., Wolfe B. (2010a) Analysis of nutrient concentrations in the diet, serum, and urine of giraffe from surveyed North American zoological institutions. *Zoo Biology* 29(4): 457–469. doi:10.1002/zoo.20278

Therneau T. (2022) *A package for survival analysis in R.* R package version 3.3-1. https://CRAN.R-project.org/package=survival

Thomas S. (2020) *Social Change for Conservation: The World Zoo and Aquarium Conservation Education Strategy.* Barcelona, Spain: WAZA Executive Office.

Tidière M., Colchero F., Staerk J., Adkesson M.J., Andersen D.H., Bland L., Böye M., Brando S., Clegg I., Cubaynes S., Cutting A., De Man D., Derocher A.E., Dorsey C., Elgar W., Gaglione E., Anderson Hansen K., Jungheim A., Kok J., Laule G., Lopez Goya A., Miller L., Monreal-Pawlowsky T., Mucha K., Owen M.A., Petersen S.D., Pilfold N., Richardson D., Richardson E.S., Sabo D., Sato N., Shellabarger W., Skovlund C.R., Tomisawa K., Trautwein S.E., Van Bonn W., Van Elk C., Von Fersen L., Wahlberg M., Zhang P., Zhang X., Conde D.A. (2023) Survival improvements of marine mammals in zoological institutions mirror historical advances in human longevity. *Proceedings of the Royal Society B* 290(2009): 20231895. doi:10.1098/rspb.2023.1895

Tidière M., Gaillard J.M., Müller D.W.H., Bingaman Lackey L., Gimenez O., Clauss M., Lemaître J.F. (2015) Does sexual selection shape sex differences in longevity and senescence patterns across vertebrates? A review and new insights from captive ruminants. *Evolution* 69(12): 3123–3140. doi:10.1111/evo.12801

Valdes E.V., Schlegel M. (2012) Advances in giraffe nutrition. In: Miller R.E.,

Fowler M.E. (eds.). *Fowler's Zoo and Wild Animal Medicine, Vol 7*. Current Therapy. St. Louis, Missouri: Elsevier Saunders, 612–618.

VanderWaal K.L., Wang H., McCowan B., Fushing H., Isbell L.A. (2014) Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). *Behavioral Ecology* 25(1): 17–26. doi:10.1093/beheco/art061

Veasey J.S., Waran N.K., Young R.J. (1996) On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator, using the giraffe (*Giraffa camelopardalis*) as a model. *Animal Welfare* 5(2): 139–153. doi:10.1017/S0962728600018571

Vesterberg H. (2014) *Årets København: Bengt Holst passer på the wildest place in town [Copenhagener of the Year: Bengt Holst looks after the wildest place in town]*. Politiken, 30. May 2014. https://politiken.dk/kultur/art5518609/Bengt-Holst-passer-p%C5518603%A5518605-the-wildest-place-in-town

Walker B.H., Emslie R.H., Owen-Smith R.N., Scholes R.J. (1987) To cull or not to cull: Lessons from a Southern African drought. *Journal of Applied Ecology* 24(2): 381–401. doi:10.2307/2403882

Walldén W. (2023) Giraffe (*Giraffa camelopardalis*) feeding: How stereotypies and other behaviours changed at Kolmårdens djurpark in Sweden. *Journal of Zoo and Aquarium Research* 11(4): 393–399. doi:10.19227/jzar.v11i4.789

WAZA (2020) *Protecting our Planet: Sustainability Strategy 2020–2030.* Barcelona, Spain: WAZA Executive Office.

Weitkamp M. (2016) Reconstruction of the giraffe exhibit at Osnabrück Zoo to improve the quality of hooves. *Der Zoologische Garten* 85(3–4): 121–130.

Wich S.A., Shumaker R.W., Perkins L., De Vries H. (2009) Captive and wild orangutan (*Pongo* sp.) survivorship: A comparison and the influence of management. *American Journal of Primatology* 71(8): 680–686. doi:10.1002/ajp.20704

Wiese R.J., Willis K. (2004) Calculation of longevity and life expectancy in captive elephants. *Zoo Biology* 23(4): 365–373. doi:10.1002/zoo.20011

Wittwer A., Roller M., Müller D.W.H., Bertelsen M.F., Bingaman Lackey L., Steck B., Biddle R., Versteege L., Clauss M. (2023) Historical development of the survivorship of zoo rhinoceroses – A comparative historical analysis. *Zoo Biology* 42(6): 797–810. doi:10.1002/zoo.21793

Zellmer G. (1961) Hand-rearing of giraffe at Bristol Zoo. *International Zoo Yearbook* 2(1): 90–93. doi:10.1111/j.1748-1090.1960.tb02759.x

Zimmerman C., Chen Y., Hardt D., Vatrapu R. (2014) Marius, the giraffe: A comparative informatics case study of linguistic features of the social media discourse. *Proceedings of the 5th ACM International Conference on Collaboration across Boundaries: Culture, Distance and Technology,* 5: 131–140. doi:10.1145/2631488.2631501