Continuous enhancement in management, care, and welfare in great apes in zoological institutions as evidenced by survival summary metrics

Lowland gorilla (*Gorilla gorilla*); Chimpanzee (*Pan troglodytes*); Sumatran orangutan (*Pongo abelii*); Bornean orangutan (*Pongo pygmaeus*)

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Introduction

This report endeavours to investigate trends in life expectancy and lifespan equality in great apes under human care from the early 1800s to 2023 in zoological institutions and contextualise these trends in relation to contemporary *ex situ* animal management practices.

The last decades (i.e., since the 1990s) revealed that *ex situ* measures have become more and more relevant in species conservation because of the accelerating loss of habitats and animal species (Ceballos et al. 2015; IUCN SSC 2023). Even charismatic species like African wild ass (*Equus africanus*) or Philippine spotted deer (*Rusa alfredi*) may be lost without *ex situ* assurance populations in zoological institutions. The major role of zoological institutions in *ex situ* conservation efforts for more and more species comes with a growing responsibility and an increased need for goal-oriented and scientifically-evaluated husbandry and population management. To play a relevant role in the frame of the One Plan Approach (Byers et al. 2013) for great ape conservation, zoological institutions need to define the key features of population management under excellent husbandry conditions for these species. This requires the objective analysis of previous and present management practices. This report is a first step towards closing the gap between experience-based expertise and societal debates about great apes in captivity by analysing populations survival parameters to evaluate husbandry success, using objective data sets.

Historically, zoological institutions have shifted their role from museums with living animal collections to institutions where conservation is at the centre of their focus, therefore, dedicating significant time, energy, resources, and research to animal welfare (see Beer et al. 2023 and Vincelette 2024 for review). Individual institutions do not represent isolated entities, but they are linked in regional, continental and global organisations, which also set standards in terms of husbandry, collection plans and population management, and who exert control about adherence to commonly decided policies and practices via accreditation programs (Hutchins and Smith 2003; Hutchins et al. 2016). Although problematic establishments still exist, and welfare standards continue to evolve, accredited zoological institutions are transforming, or already have completely transformed, into institutions serving conservation, education, and research activities (Coe 1996; Grow et al. 2024).

Animal welfare in zoological institutions is also paramount for broader conservation goals in order to ensure behaviourally competent, disease-free, and genetically suitable individuals. Poor welfare can lead to distress, compromised immune function, behavioural inflexibility, reduced breeding success, and decreased survival rates (Wingfield and Sapolsky 2003; Morgan and Tromborg 2007; Walker et al. 2012). Furthermore, observing healthy animals engaging in natural behaviours is essential for gathering valuable insights into the biology of their counterparts in the wild and for educating the public about their natural habits (Fernandez et al. 2009).

Despite ethical concerns regarding the care and welfare of animals under human care, widespread public interest remains in visiting zoos and aquariums. Indeed, people seek to reconnect with nature and experience positive emotions through interactions with animals, and conservation of species has indirect values to society (McNally et al. 2024). Over the recent decades, this public has also become more interested in, and aware of, the welfare of zoo animals. Changes in societies' perception of animals – wild or domestic – have been an important driver for this transformation. This shift is exemplified by the establishment of non-governmental organisations dedicated to protecting wildlife from human activities and by various domestic and global legislations enacted throughout the 20th

century to govern the treatment of captive great apes. A prevailing argument against zoological institutions posits that animals under human care experience shorter life expectancies than their wild counterparts, leading to claims that zoological institutions offer substandard living conditions for their animals (e.g., in elephants, Clubb et al. 2008; Atkinson and Lindsay 2022). Accredited zoological institutions recognize the importance of animal welfare and put significant effort into animal welfare research and implementation.

All species within the great ape family are classified as either ***Endangered*** or ***Critically Endangered*** on the Red List of Threatened Species, by the International Union for Conservation for Nature (IUCN 2023), underscoring the urgency of conservation efforts. Furthermore, in November 2023, the IUCN Species Survival Commission (SSC) has acknowledged "*the significant contributions that botanical gardens, aquariums, and zoos can, and do, bring to conserving wild animals, fungi and plants*" (IUCN SSC 2023). Banning species from accredited zoological institutions may represent missed opportunities to ***(i)*** acquire species-specific knowledge to support conservation efforts (Loh et al. 2018; Conde et al. 2019), ***(ii)*** care for confiscated animals or serve as a temporary home for rescued individuals (IUCN SSC 2023), ***(iii)*** maintain assurance populations that help preserve species as well as their genetic and behavioural diversity until threats in the wild are abated and allow potential reintroduction into the wild (Ballou et al. 2010), and ***(iv)*** promoting public engagement and behaviour change through education (McNally et al. 2024).

Survival-related metrics are commonly used as a proxy of population-level welfare as happier and healthier individuals tend to live longer (Diener and Chan 2011; Weiss et al. 2011; Walker et al. 2012). Here, we studied the change in two key survival summary metrics – shown to be a reliable proxy of population welfare in human and non-human animals (Colchero et al. 2016, 2021; Aburto et al. 2020; Tidière et al. 2023) – for four great ape species living in zoological institutions between 1835 and 2023: the **lowland gorilla** (*Gorilla gorilla*), **chimpanzee** (*Pan troglodytes*), **Sumatran orangutan** (*Pongo abelii*), and **Bornean orangutan** (*Pongo pygmaeus*). The other great ape species, such as the bonobos (*Pan paniscus*), were not included here due to lack of adequate data to perform the analyses. **Our findings support the mounting evidence that modern zoological institutions have progressively enhanced and improved the quality of life for these four species under managed care** (Courtenay and Santow 2008; Wich et al. 2009). The average life expectancy of the four species at birth has increased by 14 years in the past century. This improvement is particularly impressive for the **chimpanzees**, which had a life expectancy of approximately 7 years at the beginning of the 20th century, while individuals born in zoological institutions today have a life expectancy of around 30 years, a 4.3-fold improvement in 100 years. Next, we reviewed scientific literature detailing the various efforts made by accredited zoological institutions to improve the care and welfare of great apes under their care to contextualise the observed survival improvements. Criticisms of animal captivity are relatively recent, while literature reviews and expert knowledge show that accredited zoological institutions began focusing on husbandry and welfare as early as the beginning of the 20th century (see Young 2003; Hosey et al. 2020; Vincelette 2024). These efforts underscore the proactive behaviour of accredited zoological institutions in constantly improving their management practices, striving to provide for the wellbeing of great apes.

This research contributes to the ongoing discourse on animal welfare in zoological institutions and may inform future policy decisions. It also underscores the importance of biology-informed husbandry, resource investment, and scientific research in enhancing the lives of animals in zoological institutions.

I. Study of population welfare based on survival parameters for great apes kept at zoological institutions between 1835 and 2023

We conducted a temporal analysis of survival of great apes in zoological institutions worldwide since 1835. We estimated changes in population welfare by defining two-summary metrics related to the distribution of age at death in the population: the **life expectancy** and **lifespan equality** (see Box 1). The combination of these two metrics has been proved as a measure of a population's welfare in humans and non-human animals (Colchero et al. 2016; Tidière et al. 2023, see Box 1 for more details).

Box 1. Life Expectancy & Lifespan Equality: an indicator of societal and well-being improvements in human populations.

What is Life Expectancy?
It is a statistical measure of the average time an organism is expected to live, based on the year of its birth, current age, and other demographic factors like sex. The life expectancy is given in units of time (e.g., years).

What is Lifespan Equality?
This metric is comparable to the inverse of the coefficient of variation of age at death in a population, encompassing two components: (1) how similar are lifespans of individuals from a given population: homogeneous across ages or concentrated; and (2) whether the probability of death in this population is higher early or late in life. Therefore, in a population, the higher the concentration of deaths at older ages, the higher the equality. The lifespan equality is a metric without units nor boundaries. It is not used on its own but for comparison.

Why are these measures an indicator of well-being in a population?
Research in animals and humans has shown that increases in the quality of the environment of life, and thus indirectly welfare, are associated with higher survival rates and longer lifespans through direct mechanisms (i.e., interventions directly preventing deaths; NHTSA) and indirect mechanisms (i.e., the long-lasting cumulative effects of factors degrading or improving health conditions, such as nutrition, medical care, and happiness; Mishra 2016). Mortality rates (and thus survival) are common indicators of well-being used in humans and other species (Walker et al. 2012; Aburto et al. 2020). Indeed, **happier and healthier individuals live longer** (Diener and Chan 2011; Weiss et al. 2011; Walker et al. 2012).

What can the relationship between life expectancy and lifespan equality tell us about changes in well-being in a population?
Studies have found that, in humans, life expectancy and lifespan equality are highest in modern industrialised societies due to the concentration of deaths at old ages and a steep reduction in infant and juvenile mortality. Both measures are lower in non-industrialised populations, due to higher mortality at young ages and higher environmental causes of mortality (Colchero et al. 2016; Aburto et al. 2020). The increase in life expectancy and lifespan equality in tandem across time reflects improvements in societal welfare across different human populations, and the decrease of one or both is directly related to a degradation in the population conditions of life (Aburto and Beltrán-Sánchez 2019). Likewise, studies on non-human primates (Colchero et al. 2021) and four marine mammal species (Tidière et al. 2023) have shown that the same pattern occurs when comparing wild populations and animals living in zoos. While changes in this indicator reflect the changes in terms of conditions of life and welfare of a population, it cannot be used to assess the welfare of the individual.

ESTIMATING LIFE EXPECTANCY AND LIFESPAN EQUALITY

Records were obtained from the Zoological Information Management System (ZIMS) managed by Species360, a non-profit organisation with over 1,300 current members all around the world, including zoos, aquariums, rescue centres, and wildlife sanctuaries (Species360 2023). Records included information on individuals of great ape species living in zoological institutions from the early 1800s to December 4th, 2023 (Data Use Agreement #95154). The **lowland gorilla** (*Gorilla gorilla*), **chimpanzee** (*Pan troglodytes*), **Sumatran orangutan** (*Pongo abelii*), and **Bornean orangutan** (*Pongo pygmaeus*) were retained for the study because the database contained at least 100 individuals per sex for each period and species, to ensure unbiased mortality estimates and minimise uncertainty (Colchero and Clark 2012). Less than 100 individuals per sex and per period where available for bonobos (*Pan paniscus*) and mountain gorillas (*Gorilla beringei*), excluding them for the analyses.

We analysed the data into three time periods of at least 20 years for the **lowland gorilla** and the two **orangutan** species, and five periods for **chimpanzees** (see Figure 1). To define mortality patterns, we fitted a Siler mortality model (Siler 1979) on age-specific mortality rates using the Bayesian survival trajectory analysis (BaSTA) package (Colchero and Clark 2012; Colchero et al. 2012) in R (R Core Team 2023). From the patterns of age-specific mortality we defined two means of summary statistics: the **life expectancy** and the **lifespan equality** (see Tidière et al. 2023 for more details on the methods).

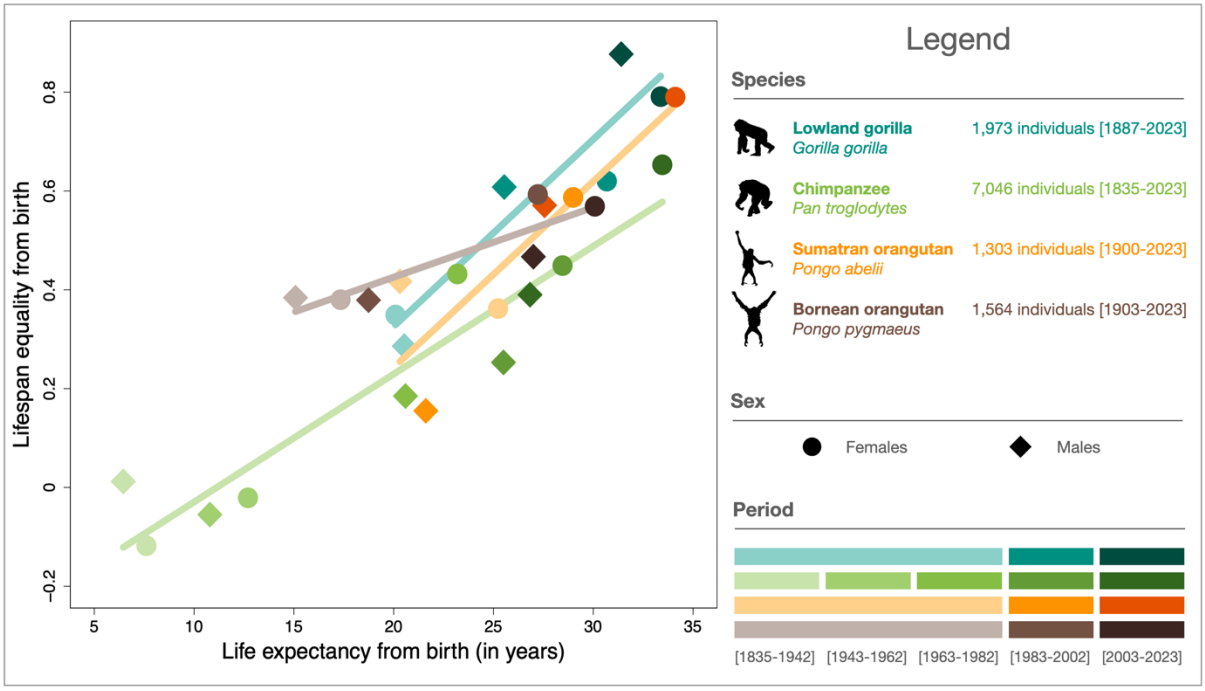

Figure 1. Increase in life expectancy and lifespan equality across time for females and males of four great ape species in zoological institutions within the last 200 years. The markers indicate the mean values obtained per sex, period, and species, while the line represents the species-specific trend.

ENHANCED LIFE EXPECTANCY AND LIFESPAN EQUALITY OF GREAT APES IN ZOOLOGICAL INSTITUTIONS OVER TIME

We found a global and progressive increase of the two-summary metrics for both sexes and the four species between the 1800s and 2023 (see Figure 1 and Table 1). During the studied period, life expectancy at birth has increased by 13.9 years on average (a 2.2-fold increase) for males and females of the four species, ranging from an increase of 7.3 years for **Sumatran orangutan** females to 24.6 years for **chimpanzee** females. For example, the life expectancy at birth of female **chimpanzees** born in a zoological institution before 1942 was 7.61±0.88 years (n=266 individuals) but changed to 33.46±1.04 years (n=1,814 individuals, 4.4-fold increase, Table 1) in the 2003-2023 period. Similarly, lifespan equality improved in all four species regardless of sex between the 1800s and 2021, with the smallest increase for **Bornean orangutan** males and the most impressive increase for **chimpanzee** females.

We observed an improvement in the life expectancy and the lifespan equality for the four species over time. However, for male **Sumatran orangutans**, a decrease of their lifespan equality is observed from before 1983 (0.417±0.106, n=201 individuals) to between 1983-2002 (0.155±0.138, n=235 individuals) while the life expectancy at birth remains similar (20.31±1.59 years to 21.61±2.15 years). In the 2003-2023 period, the two metrics increased again, with a life expectancy at birth of 27.56±1.67 years and a lifespan equality of 0.571±0.096 (n=416 individuals). Finally, the improvement of these two-summary metrics for **Bornean orangutans** seems slower than for the other species. The continuous improvement in survival metrics presented here for both **orangutan** species confirms previously published observations showing steady improvement of their survival rates in zoological institutions since the late 1800s until the 2000s (Jones 1982; Wich et al. 2009). Moreover, Wich et al. (2009) underscore that the survival rates of **orangutans** born in zoological institutions in the 2000s are comparable to those observed in wild populations.

Table 1. Summary of average life expectancy at birth changes between the early periods and 2003-2023.

Species	Sex	Compared periods	Increase in years	Factor of increase
Lowland gorilla *Gorilla gorilla*	Females	1887-1982 vs. 2003-2023 1983-2002 vs. 2003-2023	13.3 2.7	1.7 1.1
	Males	1887-1982 vs. 2003-2023 1983-2002 vs. 2003-2023	10.9 5.9	1.5 1.2
Chimpanzee *Pan troglodytes*	Females	1835-1942 vs. 2003-2023 1983-2002 vs. 2003-2023	25.9 5.0	4.4 1.2
	Males	1835-1942 vs. 2003-2023 1983-2002 vs. 2003-2023	20.4 1.3	4.2 1.1
Sumatran orangutan *Pongo abelii*	Females	1900-1982 vs. 2003-2023 1983-2002 vs. 2003-2023	8.9 5.1	1.4 1.2
	Males	1900-1982 vs. 2003-2023 1983-2002 vs. 2003-2023	7.3 6.0	1.4 1.3
Bornean orangutan *Pongo pygmaeus*	Females	1903-1982 vs. 2003-2023 1983-2002 vs. 2003-2023	12.7 2.9	1.7 1.1
	Males	1903-1982 vs. 2003-2023 1983-2002 vs. 2003-2023	11.9 8.3	1.8 1.4

Our results demonstrate an overall improvement on a population level in parameters related to survival. These results do not provide a direct indicator of individuals' welfare within those populations. Nevertheless, this population-level welfare indicator can still provide evidence of progress already made as well as further opportunities for continuous improvement in animal welfare.

COMPARISON WITH WILD POPULATIONS

In the case of **gorillas** and **chimpanzees**, a recent study compared the life expectancy and lifespan equality of various wild populations with those of populations living in zoological institutions in the last decades (Colchero et al. 2021). The authors emphasised that zoo populations exhibit longer life expectancies and greater lifespan equality than any of the other wild populations studied, for both sexes and both species. This study confirms similar results obtained for **chimpanzee** populations living 40 to 60 years earlier (Courtenay and Santow 2008).

The findings from these studies (Jones 1982; Courtenay and Santow 2008; Wich et al. 2009; Colchero et al. 2021), in conjunction with those presented in this report, indicate that changes in zoo management practices have significantly increased the survivorship of great apes in captivity, enabling them to demonstrate similar or even higher survival rates than their wild counterparts. Consequently, these results challenge the commonly held notion that great apes living in accredited zoological institutions have shorter lifespans than those in the wild.

II. Population survival improvement is tied to the continuous advances made by accredited zoological institutions

The rise in life expectancy and lifespan equality of great apes over time can be attributed to various factors, many of which may have interacted synergistically. Notably transitioning zoological institutions from menageries to accredited institutions committed to animal conservation and welfare, research, and public education, underscores the steady improvement in survival metrics for great apes. In this section, we examine the diverse factors that might have positively influenced the survival of great apes in zoological institutions, drawing support from scientific literature and accumulated knowledge and experience of experts of these species.

CHANGE IN PERCEPTION AND LEGISLATION

Our perception of great apes has undergone a significant transformation over the past two centuries. Once regarded as formidable wild creatures evoking both fear and awe, they are now viewed in a more holistic light, recognized for their sensitivity, intelligence, and cognitive needs. However, they also serve as poignant reminders of the detrimental effects of human activities on their natural habitats (Estrada et al. 2017; IUCN 2023). This shift in perspective has been facilitated by advancements in our

understanding of great ape biology and ethology. Therefore, as our comprehension deepens regarding their biology and needs, both at the species and individual levels, we observe a corresponding enhancement in their welfare and survival.

In 2023, the World Association of Zoos and Aquariums (WAZA) made welfare assessments mandatory for all accredited zoological institutions (WAZA 2023), marking the culmination of years with increased focus on the well-being of animals under human care. This will not only advance research but also fundamentally change how we perceive and assess animal welfare and well-being in the future.

Establishment of international organisations

Changes in perception of wildlife are exemplified by the establishment of non-governmental organisations dedicated to protecting wildlife from human activities. For instance, the International Primate Protection League (IPPL) that aims to safeguard primates globally was founded in 1973. Concomitantly, the IUCN spearheaded in 1973 an agreement among over 80 Parties to regulate wildlife trade. This agreement resulted in the establishment of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which took effect in 1975. This agreement placed all great ape species under CITES Appendix I (since 1975, **chimpanzees** since 1977), restricting their international trade to protect wild populations. Consequently, zoological institutions could no longer source wild-born individuals. This prompted institutions to focus on breeding programs, expert exchanges, and cooperation, to build self-sustaining and genetically diverse populations. These regulatory changes in animal transfers and wild capture, particularly impactful in the 1980s, likely spurred comprehensive efforts to improve great apes' physical health and survival.

Regulation through laws and policies

Various legislations were enacted both domestically and globally to govern the treatment of captive great apes throughout the 20th century (e.g., Pruetz and McGrew 2001). Notably, the USA Animal Welfare Act of 1966 (AWA) established minimum standards for the treatment of animals in research, teaching, exhibition, transport, and by dealers. Similarly, European nations introduced their own regulations, such as the Danish Act for Animal Welfare in 1916 and the UK Zoo Licensing Act of 1981, before the European Union implemented the Directive 1999/22/EC. This European directive on the keeping of wild animals in zoological settings sets the minimally acceptable frame for zoological institutions such as "*accomodat[ing] their animals under conditions that satisfy the biological and conservation requirements of the individual species*". However, determining these minimum standards remains challenging, leading to variations between countries.

These regulations embody the collective concern of zoo professionals, governmental agencies, and the public for the humane and enhanced care of great apes managed under human care. Therefore, the progressive implementation of regulations throughout the 20th century has contributed to the global advancement of care and management practices in accredited zoological institutions, and to the observed reduced mortality rates among *ex situ* great apes.

PROFESSIONALISATION AND ORGANISATION

Professionalisation

Accredited zoological institutions have undergone significant transformation, especially marked by increased professionalisation of their staff. Notably, biologists and veterinarians have been increasingly hired as permanent employees in zoological institutions (Fowler 1977, 2006), and they have enhanced their expertise in wildlife biology and medicine through education and research (as detailed in the *Veterinary medicine and health care* section). Furthermore, the establishment of specialised training programs, like the first French school for zookeepers opening in the 1990s, illustrates this commitment to professional development. This overall professionalisation has revolutionised zoological disease prevention and treatment as well as animal care and welfare programs resulting in improved survival rates among zoo inhabitants as highlighted for instance by the significant change in the causes of death in great apes over time (Ross et al. 2022).

Data-based management

The professionalisation of zoological institutions has been accompanied by the systematic enhancement of data recording efforts. One pivotal development in this regard is the establishment of the non-profit organisation Species360, formerly known as the International Species Information System, in 1974 (Seal et al. 1976; Earnhardt et al. 1995; Flesness 2003). Today, the Zoological Information Management System (ZIMS), from Species360, serves as a comprehensive repository for individual animal (and plants since 2022, Hortis) data pertaining to husbandry, medical, welfare and population management records, with some dating back to the early-1800s.

By systematically documenting information, zoological institutions can monitor the daily health and welfare of their animals while also aggregating data to enable age-, sex-, and species-specific analyses, thereby facilitating progressive improvements in practices. Furthermore, these data not only inform evidence-based husbandry practices and management decisions, but are also used in scientific research, enriching our understanding of species. The accumulation and analysis of standardised data continues to be used to refine husbandry practices (Earnhardt et al. 1995; Che-Castaldo et al. 2019) and ultimately enhances the survival and welfare of great apes living in human care.

Organisation into Regional Associations

Promoting international collaborations

During the 20th century, zoological institutions structured themselves into different regional associations, to organise the cooperation between the different institutions. Many associations exist today at different levels (world, continent, regional, national, etc...), such as:

- AZA: (American) Association of Zoo and Aquariums (1924)
- WAZA: World Association of Zoos and Aquariums (1935)
- EAZA: European Association of Zoos and Aquaria (1985)
- PAAZA: Pan-African Association of Zoo and Aquaria (1989)
- ALPZA: Latin American Zoo and Aquarium Association (1990)
- SEAZA: SouthEast Asian Zoos and Aquariums Association (1990)

- ZAA: Zoo and Aquarium Association Australasia (1990)

These associations facilitate information exchange between institutions, establish accreditation protocols that define acceptable standards of animal care and welfare, and promote the different goals of accredited zoological institutions (i.e., education, research, and conservation). These regional associations encourage and promote high standards for the husbandry of zoo and aquarium animals.

Animal care guidelines

The progressive increase in survivorship for great apes in zoological institutions across the last century is very likely the result of a range of factors that have changed in zoo management. These changes have been stimulated by the development of guidelines and care manuals published by various regional zoo associations. Indeed, within these regional associations, specialised groups of experts, such as Taxon Advisory Groups (TAG), have played a pivotal role since the 1980s in fostering collaboration among diverse institutions to establish comprehensive guidelines for the care of great apes in human care.

Best practices guidelines represent the culmination of decades of collective experience and scientific insights leading to the implementation of these guidelines (e.g., Carlsen et al. 2022). This has led to improved husbandry standards for great apes and has delineated expectations for member institutions to ensure inclusion of robust welfare programs and expertise. These guidelines are also informed by scientific research. By harnessing this wealth of knowledge, these guidelines facilitate continuous enhancements in the living conditions of great apes within accredited institutions, with the overarching objective of bolstering their survival and welfare. They constantly support evidence-based progression of modern zoos approaches. Accessible through the websites of various regional associations, these guidelines serve as invaluable resources for caretakers and zoological institutions.

META-POPULATION MANAGEMENT

Given the endangered status of great apes and the threats facing wild populations, conserving them through captive populations is imperative. Therefore, over the past 35 years, collaboration among zoological institutions has intensified to enhance species management (Becker 1998), particularly aimed at improving breeding outcomes and ensuring future species survival. The focus is on maintaining demographically stable and genetically diverse populations of great apes, crucial for future potential reintroduction efforts if required, while upholding high standards of animal welfare (Boer 1991; EAZA 2021). For nearly two decades, WAZA "*strongly recommends that all breeding programmes should be based on sound science and management using the latest available knowledge on population management, reproductive biology, genetics, animal behaviour, nutrition, veterinary care and husbandry standards*" (WAZA 2015, website).

Population management programs

Following the establishment of CITES regulations, thereby limiting the import of wild-caught animals, regional associations and zoological institutions have spearheaded initiatives to establish collaborative management plans and breeding programs. The establishment of international and regional studbooks in the 1960s underscores the commitment to coordinated breeding efforts recommending management and breeding strategies based on genetic and demographic analyses. Institutions that

house a particular species collaborate in *ex situ* breeding programs aimed at managing small populations within zoological institutions as part of a larger collective encompassing all zoo animals, operating at regional and/or global scales. These breeding programs are an integral part of the One Plan Approach as defined by the IUCN, which aims to unite *in situ* and *ex situ* actions to develop relevant conservation strategies that mitigate the biodiversity crisis (Byers et al. 2013). Indeed, regional breeding programs like the Species Survival Plan (SSP) in North America, the EAZA Ex-situ Programme (EEP, formerly named European Endangered species Programme) within the EAZA region, or the Species Management Program (SMP) in the Australasia, have been instrumental in conserving genetically diverse captive populations over the long term. A basic concept of these breeding programs is that they are self-sustainable without import of individuals from natural habitats.

These breeding programs aim to manage populations through genetics to prevent individuals from being inbred, since they might suffer from reduced reproductive and survival parameters (Ballou et al. 2010), and overall to preserve the genetic diversity (Becker 1998). They recommend breeding only pure species and subspecies, and as a result, the number of hybrid births has decreased dramatically in recent years. For instance, efforts to identify pure subspecies of **chimpanzees** in European facilities have been ongoing since 1995: *P. troglodytes* has four recognised subspecies, the genetics of which are managed separately (Carlsen et al. 2022). Similarly, an important step taken in the 1970s was the distinction of two **orangutan** species, and the first attempts to stop producing hybrids. Fifty years later, the population size, age structure, and genetic variation of the two species of **orangutan** in Europe are considered healthy.

Survival and hand-raising of infants

Between the 1950s and 1980s, hand-raising of great ape infants was common practice in zoological institutions (Mallinson et al. 1976) to enhance survival rates by ensuring veterinary care due to a lack of knowledge about the importance of their social structure, for example, as these species exhibit late weaning and prolonged maternal dependence (Harvey and Clutton-Brock 1985; Martin 1995). However, in some cases, this practice induced behavioural issues such as impaired breeding behaviour, inadequate infant care, increased aggression, and social dysfunction (Harcourt 1987; Carlsen 2002; Abello and Colell 2006). Effective maternal skills in female great apes are now considered best developed through being reared by their mothers and observing maternal behaviour within a social group of adults and infants, significantly improving breeding success, a key survival indicator (Abello and Colell 2006). Consequently, since the 1990s, mother-rearing has been recommended (Fulk et al. 1992) despite potential increased infant mortality risks, as it substantially enhances the social and reproductive capabilities of adult great apes (Pryce 1995).

Box 2. Species-specific management history

Lowland gorilla: This species has been globally managed since 1967 with the creation of an international studbook by WAZA. Fourteen years later, AZA started its SSP in North America. The history of lowland gorilla EEPs is somewhat complex (EAZA 2021), as studbooks and breeding programs existed well before the official EEP structure was established. The EAZA EEP for the Western lowland gorilla began in 1987. In the late 1980s and early 1990s, the ZAA joined the EEP to facilitate gorilla transfers. A formal ZAA SMP was established around 2001, with their regional ZAA population managed as a subset of the EEP.

Chimpanzee: Structured management of chimpanzee populations in zoological institutions began to take shape in the late 20th century. The SSP for chimpanzees was established by AZA in 1989, and the SMP by ZAA

in 1988, with prior studbook and management plans in place. In 1994, the EAZA Primate TAG, Ape Subgroup, recognized the urgent need for structured management of the European chimpanzee population. In 2002, the EEP for western chimpanzees (*P. t. verus*) was established and by 2007, a generic studbook provided an overview of the population, and a comprehensive management strategy was developed. This management plan extended outside of Europe including now institutions from the middle east, Africa, Asia and South Africa. Their strategy was revised in 2014, and the Long-Term Management Plan (LTMP) was published in 2018, guiding current management practices (see Carlsen et al. 2022 for more details and references).

Orangutan species: An important milestone in the 1970s was recognizing Sumatran (*Pongo abelii*) and Bornean (*P. pygmaeus*) orangutans as distinct species, which led to efforts to stop hybrid breeding. This distinction necessitated significant rearrangements and testing, causing potential stress and challenges in population management. In 1967, WAZA initiated International Studbooks for orangutans, and AZA established their SSPs in 1982. The management of orangutans in the ZAA region dates back to the 1980s, with studbooks and management plans in place before 1988. Separate SMPs for Sumatran and Bornean orangutans were established in 1989 following the discovery of some biological and genetic differences between the two orangutan species. For example, the Bornean species is considered to live more solitary in the natural habitat, potentially experiencing higher levels of stress when kept in groups in zoological institutions, in contrast to the Sumatran species where group size does not correlate to measured stress levels (Weingrill et al. 2011). This is also reflected in a higher susceptibility of Bornean species to certain diseases (Zimmermann et al. 2011). The European studbooks for orangutans were created in 1982 by EAZA, followed by the approval of their EEPs in 1989 for Sumatran orangutans and 1990 for Bornean orangutans.

VETERINARY MEDICINE AND HEALTH CARE

The progress in veterinary medicine closely follows human medicine, often incorporating knowledge, tools and treatments used in human health care (Gutierrez et al. 2023). The evolving patterns in causes of death (i.e., the decrease in infectious disease over time, the increase in chronic/non-communicable diseases such as heart diseases; Ross et al. 2022), align with the steady enhancement of survival metrics among great apes in zoological settings. These patterns underscore the dynamic nature of the continuous progress made in management and veterinary practices of great apes in zoological institutions.

Veterinarians in zoological institutions

Throughout history, zoo veterinarians have played a pivotal role in the care of zoo animals. The profession traces back to the appointment of the first zoo veterinarian in the UK in 1829, followed by the establishment of similar roles in the USA from the early 1900s. By the 1970s, most zoological institutions housing great apes typically employed full-time veterinarians. In some instances, zoo directors also held veterinary qualifications, although they may not have practised veterinary medicine while serving in administrative roles. As early as 1902, the New York Zoological Society aimed to formalise veterinary care by establishing a permanent medical department (Osborn 1903). This initiative aimed to advance understanding of wildlife health in captivity, identify disease causes, and develop preventive measures.

Organisation and professionalisation

The evolution of zoo veterinary advisory groups has been ongoing for nearly 50 years growing in capacity and expertise over time. Specialised organisations like the American College of Zoological

Medicine (ACZM) or the European College of Zoological Medicine (ECZM) have further professionalised the field since the 1980s. These bodies offer formal training and certification for zoo veterinarians, shaping the present and future of zoo animal medicine. Key developments to improve breeding success and long-term viability include the establishment of professional bodies such as the American Association of Zoo Veterinarians (AAZV) in 1946 and the British Veterinary Zoological Society (BVZS) in 1961 (see Fowler 1977 for more details). The World Association of Wildlife Veterinarians (WAWV) emerged from the World Veterinary Association in 1991, followed by the formation of the European Association of Zoo and Wildlife Veterinarians (EAZWV) in 1996.

These associations facilitate knowledge exchange and provide training for future zoo veterinarians. Notably, university-based training programs in zoo animal medicine were non-existent globally until 1968. Zoo veterinarians, in close collaboration with biologists, have been instrumental in setting standards for the care of wildlife, including enclosure and pool sizes, environmental conditions, and dietary requirements. Their involvement in accreditation programs, such as the AZA accreditation, underscores their commitment to ensuring the humane treatment of animals and compliance with regulatory standards, including the USA Federal Animal Welfare Act (Schroeder 1976). Finally, platforms, like the module *ZIMS for Medical* from Species360, are used by veterinarians to exchange diagnostic insights among a network of peers, facilitating collaborative problem-solving and knowledge-sharing within the profession. This exemplifies the modern approach to veterinary care in zoological settings, emphasising collaboration and access to collective expertise.

Veterinary research

Since the 1970s, there has been a notable advancement in veterinary research, marked by the creation of the Journal of Zoo Animal Medicine in 1970. The number of scientific articles published by zoological institutions has steadily increased since then (Loh et al. 2018; Hvilsom et al. 2020; Kögler et al. 2020).

The focus on cardiovascular health in great apes started in the early 1990s and has prompted the establishment of initiatives such as the Great Ape Heart Project™ (GAHP) in 2010, alongside parallel efforts like the Ape Heart Project in Europe and the International Primate Heart Project. These projects, involving collaborations between zoological institutions and research organisations, aim to address cardiovascular health concerns regarding great apes under human care, contributing to their overall survival, welfare, and conservation. Research has revealed a significant prevalence of cardiovascular disease related to death in great apes under human care (Murphy et al. 2018). The fact that these diseases have emerged as relevant in recent decades is likely a direct effect of the increased life expectancy in zoological institutions. In general, the advancements in zoo medicine have led to increased survival rates and longer lifespans in great apes, also resulting in a rise in age-related diseases such as cancer (Lombard and Witte 1959; Vincze et al. 2022). In addition, the development of diagnostic techniques and treatments, facilitated by initiatives like the GAHP, has enabled the diagnosis and management of cardiovascular conditions in affected individuals. As a result, advances in understanding and treating cardiovascular disease in great apes have emerged, while also enhancing veterinary practices related to anaesthesia and medical care in these populations, evidently contributing to the recent increase of these species' survival and longevity in zoological institutions.

Training to facilitate medical procedures

The integration of medical training, particularly through operant conditioning techniques, has surged since the 1960s in zoological institutions. Notably, a 2000 conference presentation emphasised the efficacy of operant conditioning in facilitating medical procedures and immobilizations for apes, reducing reliance on anaesthesia (Seiver et al. 2001). This approach, exemplified by Disney Animal Kingdom's daily medical training with **gorillas** since its founding in 1998, has demonstrated decreased anaesthesia requirements and enhanced safety and quality of medical care. From the 2000s onwards, there has been a notable increase in utilising training to support various medical procedures such as blood draws and ultrasounds, reflecting a proactive approach to healthcare (Thompson H., Pers. Comm.). Animal training, a practice with roots dating back to the early 20th century, has seen renewed interest among veterinarians, particularly for its benefits in promoting regular health assessments and minimising stress during interventions, thereby potentially extending longevity. For instance, evidence suggests that training for anaesthesia induction provides a better anaesthesia quality and reduces stress-related changes in samples collected (Lambeth et al. 2006; Burrows et al. 2021).

While great apes can be trained for basic medical procedures like tooth checks, special consideration is required to ensure that training protocols do not disrupt their social dynamics. Even though training can be valuable for certain medical interventions, its implementation should be judicious, considering its potential impact on group dynamics and individual welfare. Training should serve as a tool to enhance healthcare and enrichment, rather than a goal itself, with careful consideration given to maintaining the individual's social interactions.

Medical practices

The advent of modern drugs since the 1980s has greatly improved disease prevention and treatment, further enhancing the health and well-being of captive great apes. These changes, in interaction with the progress in management practices and nutrition, resulted in the first increase in longevity in great apes (see Coe 1996, and Figure 1). Moreover, one transformative change was exposing great apes to natural environments, including ground, plants, dirt, and weather. These management changes significantly enhanced their immune systems, making them resilient to many infections over the long term. Adapting to and building immunity against numerous human infections was undoubtedly crucial for their longevity in human care (Encke D., Pers. Comm.).

As advances in medical knowledge and aseptic technology occurred, great ape longevity greatly increased. Indeed, earlier and more aggressive treatments, particularly for chronic respiratory diseases, have contributed to increased survival rates. Furthermore, the implementation of quarantine and vaccination protocols, along with improvements in anaesthetic practices, has led to reduced mortality rates (e.g., Wich et al. 2009). Clear medical guidelines have been established, emphasising techniques such as voluntary blood draws to minimise the need for total sedation. Enhanced monitoring capabilities during procedures and the ability to conduct blood tests onsite have further improved diagnostic and treatment processes.

Access to human specialists and specialised medical equipment has also expanded, allowing for more tailored and effective treatments. Additionally, the integration of specialised databases like ZIMS has provided valuable information on drug safety and species-specific reference ranges, facilitating more personalised care. The evolution of medical care has enhanced the health and welfare of great apes,

as well as minimised stress associated with medical interventions. These developments have revolutionised great apes' healthcare, for instance, resulting in the progressive improvement of their survival and longevity (Wich et al. 2009).

Orangutans exemplify the benefits of diagnostic and preventive measures in veterinary care. For instance, the use of CT scans has enabled the diagnosis of conditions like sinusitis, which were previously undetectable with conventional X-rays (Steinmetz and Zimmermann 2012). Early diagnosis and intervention, including surgical procedures, have alleviated suffering and improved the welfare of orangutans. These advancements underscore the importance of utilising improved technologies and veterinary expertise to enhance the health and survival of great apes in human care.

Management of elderly populations

As observed in modern human populations with increasing longevity, modern zoological institutions face a similar challenge with the ageing of animals, leading to significant geriatric issues. The progressive increase in animal longevity necessitates a shift in focus from merely extending lifespan to enhancing the quality of life. Geriatric management is now a critical component of animal welfare, emphasising care at the end of life. Veterinary practices have evolved, yet equating longevity with good welfare is increasingly scrutinised. Advances in veterinary care and rising public expectations have prompted zoological institutions to adopt more supportive therapies for aged animals (Nieuwland and Meijboom 2023). These interventions include pain management, nutritional adjustments, and habitat modifications to accommodate reduced mobility and other age-related challenges (Brando and Chapman 2023). The shift is supported by research focusing on the specific needs of ageing animal populations (Brando and Chapman 2023), leading to specialised care plans that ensure older animals maintain a good quality of life. Public perception of geriatric management has also evolved, with greater acceptance and understanding of the need for humane end-of-life care (Chapman et al. 2023). However, differences between institutions persist, influenced by varying legal frameworks, public opinions, and institutional policies. Consequently, while some zoological institutions may strive to keep the oldest animals alive, others recognize that longevity alone is not necessarily indicative of good welfare, balancing the decision to euthanize with the welfare of the individual and consideration of social group dynamics.

NUTRITION

As a fundamental aspect of animal management, nutrition is essential for reproduction, growth, disease prevention, and therefore longevity (Dierenfeld 1997). Proper feeding management of wild animals under human care requires both husbandry skills and applied nutritional sciences.

Historically, zoo animals have faced various health issues, including under- or over-nourishment. Diet-related diseases include obesity, diabetes, nutritional deficiencies such as rickets (Dierenfeld 1997), and abnormal behaviours like regurgitation and reingestion (Lukas et al. 1999; Cabana et al. 2018). However, the nutrition of great apes in modern zoological institutions has improved significantly over the past century. This transition has been influenced by the establishment of organisations like the Nutrition Advisory Group in North America (1994) and the European Zoo Nutrition Group (1999). These

organisations, along with recommendations from regional associations and evolving practices in zoological institutions, have driven nutritional advancements for captive animals over the last 50 years.

Significant improvements have resulted from incorporating research on the feeding ecology of free-ranging populations into the diets of their captive counterparts. Moreover, changes have occurred not only in the *what* is provided to great apes but also in the *how*, along with evolving perceptions and definitions of a healthy body weight.

Changes in diet composition

Throughout the 20th century, the diet composition for great apes in zoological institutions has evolved significantly to better reflect their natural diets and improve their health and therefore their longevity. Initially, apes' diet primarily consisted of human foods such as pasta, bread, domesticated fruit, or milk. For example, the first captive **lowland gorilla** at London Zoo in 1887 was fed sausages, cheese sandwiches, boiled potatoes, mutton, and beer, surviving only a few weeks (Blunt 1976). Such diets were prone to trigger deficiencies, in particular calcium deficiency and hence metabolic bone disease (Corson-White 1931; Fiennes 1974). To address in particular mineral deficiencies, 'complete' diets were developed that were adequately supplemented in minerals and vitamins (Ratcliffe 1966). This change drastically improved survival rates, reducing the overall annual mortality of mammals and birds from 20% to 10% (Wackernagel 1966). The use of such diets was not commonplace, and there was a heated debate on whether zoo animals, including primates, should be fed such complete diets or rather on individual diet items (Hediger 1966).

In the 1980s, multiple daily feedings, dietary enrichment, and combinations of complete (commercial) pelleted or extruded diets (as safety delivery for minerals and vitamins) together with whole diet items became common practice. In 1995, the need to increase dietary fibre levels when feeding folivorous primates was highlighted (Edwards 1995). At this time, the realisation that domestic fruit differs dramatically in nutrient composition than fruits consumed by 'frugivorous' species, including great apes in natural habitats, was first pronounced (Oftedal and Allen 1996).

A critical milestone was the publication of the *Nutrient Requirements for Nonhuman Primates* by the National Research Council (NRC, USA) in 2003, providing information on natural diets, including their nutrient composition, for all primate species (NRC 2003). Notably, the trend not to mimic natural diets is still prevalent in that work (NRC 2003, chapter 3). Moreover, from 2010 onwards, there was a shift towards individualised diets based on the specific needs of each species but also each individual, based on different criteria such as age, weight, or reproductive status (e.g., lactation, contraception). Two trends are particularly important: the reduction of dietary sugar and starch levels, and an increase in dietary fibre (Oftedal and Allen 1996; Schmidt et al. 2005; Cabana et al. 2018). Diets of higher fibre and lower sugar have been shown to have a variety of health benefits, including a reduction of obesity, caries, undesirable behaviour such as regurgitation and reingestion, and intraspecific aggression (Schmidt et al. 2000; NRC 2003; Plowman 2013; Britt et al. 2015; Cabana et al. 2018). Some zoological institutions even now collect and dry leaves and branches in summer to supplement winter diets, ensuring a more natural fibre intake for their primates. Therefore, these dietary improvements, such as a significant improvement in nutrient profiles (Smith et al. 2014), have enhanced the health and welfare of captive apes, contributing to better health outcomes and longevity.

Changes in diet presentation

At the beginning of the 20th century, great apes were fed 1-2 meals per day with a uniform diet for all individuals and species. By the 1990s, this shifted to multiple feeds per day with species-specific diets. Currently, there is a focus on increasing foraging time and overall activity to promote natural behaviours by scattering or hiding food, as well as increasing processing time such as providing whole fruits rather than pre-chopped fruits (Brereton 2020). In addition, seasonal feeding patterns enhance nutrition and enrichment, fostering resilience. These approaches have been shown to improve welfare (Isbell 1991; Young 1998), such as enhancing dental health. Some modern enclosures, such as in Apenheul Zoo in the Netherlands, incorporate various feeding systems that would traditionally have been called 'enrichment devices' for the everyday feeding of the majority of the diet, shifting the perception of enrichment from something supplementary to something done on a daily basis.

These progressive changes reflect a deeper understanding of the importance of nutrition, feeding behaviour, and enrichment, in promoting the health and welfare of great apes, therefore progressively increasing their overall survival. By adopting naturalistic feeding strategies, zoological institutions can better meet the nutritional and psychological needs of these animals, significantly improving their quality of life.

Changes in body condition perception

The body condition in great apes in zoological institutions has shifted, with an emphasis on managing optimal body mass for physical health and longevity (Obanda et al. 2014). Body condition scoring and improved diets have led to reduced body weight, addressing, for example, obesity-associated comorbidities in captive **chimpanzees**, including hypertension, insulin resistance, cardiovascular disease, and inflammatory diseases (Curry et al. 2023). **Gorillas** and **orangutans**, as hindgut fermenters, are particularly prone to obesity, and their body weight has historically been challenging to manage. For example, historically, lax dietary guidelines for **orangutans** in captivity led to obesity (Jones 1982) and has been linked to increased mortality through diabetes, heart disease, high blood pressure, and other diseases in humans (Hensrud et al. 2002; Cocks 2007). Appropriate diet changes have shown potential for increasing longevity in other species (e.g., in humans, Ekmekcioglu 2020). Therefore, managing body mass is critical for the overall health and longevity of great apes in human care.

ENVIRONMENT

Historical changes in great ape exhibits

Due to their size, intelligence, life history and behavioural requirements, great apes present significant challenges in designing effective captive environments. The evolution of great ape enclosure design illustrates a shift from early misunderstandings to a more empathetic and ecologically focused approach (Coe and Maple 1984; Coe 1989b,a, 1996).

By the 1880s, criticisms of bars and barren cages in American zoos began a transition towards naturalistic enclosures, marking a shift to living museums emphasising animal habitats. By the mid-1900s, significant advancements in health and hygiene led to facilities designed for easy cleaning and

durability (Coe 1996). Notably, the Frankfurt Zoo had already implemented measures to protect apes from infections by installing glass windows in front of the ape cages as early as 1871. However, many great apes' enclosures still lacked outdoor exhibits, little access to sunlight, and often had only concrete as floor substrate. Therefore, in the 1960s, a re-evaluation of great ape exhibit design emerged in the Netherlands (van Bemmel 1960; van den Bergh 1960). By the mid-1970s, a paradigm shift recognized great apes as ecological beings (Maple and Stine 1982), leading to naturalistic habitats with increased opportunities for occupation and choice. The 1970s saw ape houses with open exhibits, moats, and grassed areas, housing multiple ape species in individual enclosures within a larger complex. In the 1980s, species-specific more spacious and diverse enclosures were built, incorporating natural substrates and novel items to stimulate ape curiosity. These designs aimed to maximise choice and diversity, addressing both the known and unknown needs of the animals. This period also saw a transition from concrete-based housing to larger, more naturalistic habitats with flexible climbing structures, fostering more physical activity and potentially improving welfare and lifespan. Subsequent decades saw further improvements, including enrichment programs in the 1990s, prioritising climbing opportunities and 24-hours access to indoor and outdoor enclosures, enhancing the welfare of captive great apes. Climbing opportunities began to mimic the wild. While several design aspects for great apes' enclosures have been known since the 1970s, it was around the 2000s that an international consensus was made on guidelines (Encke D., Pers. Comm.).

Great apes' housing has also been improved by increasing environmental opportunities, such as sunlight access, indoor/outdoor areas, or interactions with humans (Ross and Lukas 2006). Access to sunlight is crucial for positive welfare outcomes, and **chimpanzees** with unlimited outdoor access were found to have significantly higher blood vitamin D levels (Moittié et al. 2022). However, since some great apes in the wild live in habitats with dense canopy and have been seen actively seeking shade during hot period of the day in zoos (Duncan and Pillay 2013), zoological institutions should consider incorporating shaded areas into their outdoor enclosures. Finally, temperature manipulation can also modify activity levels, with higher temperatures correlating with increased inactivity (Kosheleff and Anderson 2009).

Recent studies have suggested these changes have potentially led to outcomes such as increased activity, reduced disease transfer and improved health that are potential factors related to the increase in great apes' longevity. Notably, a decrease in accidental deaths attributed to advancements in exhibit design and management have been shown (Ross et al. 2022). Moreover, rigorous examination of enclosure design and efficacy are now performed (Ross and Lukas 2006; Kelling and Gaalema 2011; Duncan et al. 2022). For example, European zoological institutions that would like to exhibit great apes are highly encouraged to discuss their plans with the EEP coordinator of the species before building a new facility, to ensure it meets accreditation standards, before obtaining animals. Overall, the development of great ape enclosures reflects a continuous commitment to meeting the complex physical, behavioural, social, and psychological needs of these species.

Complexity, opportunities and enrichment

Providing appropriate housing is essential for good animal welfare, yet spatial restriction is inherent in captivity. As explained above, in the last decades, zoological institutions worldwide have been replacing small, barren enclosures with larger, naturalistic ones to cater to animals' behavioural and psychological needs, which have had demonstrated welfare benefits (Ross et al. 2011). Another difficulty inherent to great apes is that space must be developed in three dimensions. Providing habitat

complexity, in addition to providing opportunities, have been shown to be critical among captive primates: the complexity of the environment promotes locomotion more effectively than enclosure size alone (Jensvold et al. 2001; de Azevedo et al. 2023), and enlarging enclosure size without adding complexity does not reduce stereotypic behaviours (Honess and Marin 2006). Complexity can be enhanced by incorporating structures that support highly motivated, natural behaviours, including arboreal travel, foraging, and social interactions including rest; these structures are ideally designed in a way that their arrangement can be changed repeatedly.

Since the 1970s, researchers have recognized that zoological environments significantly influence the development of primate behaviour. Enrichment for great apes includes food variety (i.e., what, how, and how often, see *Nutrition* section), timed opportunities for natural behaviours (e.g., UV lamps), random objects (e.g., soap bubbles, fabric), and interactions, including medical training with humans. Appropriate enrichment by species, sex, age, and background can reduce aggression, eliminate abnormal behaviour, and greatly improve primate welfare in zoological institutions (Honess and Marin 2006). Furthermore, expanded and enriched environments can increase and homogenise space use in managed great apes (Duncan et al. 2022) as well as stimulating exploration and problem-solving (Mcdonald 1994). Moreover, cognitive enrichment is crucial for the well-being of great apes, helping them to develop their capabilities and maintain their mental health. Effective habitat design plays a key role in providing a platform for enrichment, such as incorporating puzzle feeders or climbing ropes, and creating opportunities to reconfigure furnishings within the habitat. Additionally, offering great apes choice and control over their environment, like the ability to turn heating and lighting on or off or to move between indoor and outdoor spaces, further enhances their quality of life. Enrichment can also be provided by access to multiple habitats and rotating between them, which can offer positive experiences for some individuals, although it may be less beneficial for others. Due to its crucial role in animal welfare, enrichment plans have been mandated by several regional associations for more than 20 years (e.g., AZA 2022).

SOCIAL MANAGEMENT

In the latter half of the 20th century, many wild-born infant great apes were captured, resulting in early maternal loss, social isolation, and lack of peers. These traumatic conditions during transport and captivity significantly increased developmental problems (see Pascual et al. 2023 for references and more details). This might explain the low life expectancy and lifespan equality values obtained in the earliest periods studied here (see Figure 1).

Initially, all great apes were managed similarly in captivity, with one male paired with one or several females and uniform diets and conditions for all species. Over time, it became evident that each species possesses unique social systems, necessitating tailored management approaches (Nadler 1984; Box 3). Providing an adequate social environment is crucial for the well-being of captive great apes, as species with naturally large group sizes and extensive ranges are more prone to develop stereotypical behaviours in captivity (Mcdonald 1994; Lehmann et al. 2007; Pomerantz et al. 2013). For example, early social deprivation can have lifelong impacts on the immune system, profoundly affecting primates' survival (Lewis et al. 2000).

In the 1980s, zoo management practices shifted towards emphasising family units over breeding pairs (Coe and Maple 1984). In addition, regulatory changes in this period led to a more holistic approach to great ape care, potentially improving physical health and survival but raising concerns about behavioural opportunities and optimal social groupings. By the 1990s, recommendations emerged to manage captive great apes according to their wild social structures (e.g., Harcourt 1987). In the 2000s, a nuanced approach considering individual preferences, including mate choice, became prevalent. Wich et al. (2009) suggest that appropriate social settings, in combination with improved physical housing conditions, reduced stress and enhanced health in captive **orangutans**, thereby increasing survival. Effective social management likely has a direct and indirect impact on the health, welfare, and longevity of great apes in zoological institutions.

Box 3. Species-specific social management history

Gorilla: The social organisation of gorillas typically involves a single adult male, or silverback, who dominates and protects the group (Watts 1996). In the 1990s, management practices began distinguishing between the two gorilla species, with lowland gorillas (*Gorilla gorilla*) starting to get managed according to their species-specific needs, different from the ones of the mountain gorillas (*G. beringei*). In the 2000s, zoological institutions housing gorillas started to consider bachelor groups for the management of males (Harcourt 1987). Also, some regions have moved to selecting older males as breeding males rather than younger males, as females prefer older and more experienced males in the wild. Exhibit design also evolved to ensure long-term well-being by providing an appropriate environmental and social context for all groups (Coe et al. 2009).

Chimpanzee: In the 1970s, chimpanzee management shifted from breeding pairs to family units to better reflect natural social structures. By the 2000s, a fission-fusion management system was adopted, enabling dynamic group compositions. The preferred method now involves multi-male, multi-female groups, mirroring their natural social behaviours. These changes aim to replicate the complexities of chimpanzee social dynamics, creating a more enriched and fulfilling environment for these social primates (Angley et al. 2024).

Orangutans: In the 2000s, zoological facilities moved from keeping orangutans in pairs (Coe and Maple 1984) to a fission-fusion management system, allowing for dynamic group compositions. At Perth Zoo (Australia), orangutans are housed semi-solitarily, reflecting their natural biology. Personal observations from caretakers suggest that orangutans thrive when they can choose their companions, pointing to the importance of considering individual preferences and social dynamics in their management for overall well-being (Thompson H., Pers. Comm.).

Animal Welfare

A focus on the animals' feelings

The study and perception of animal welfare in zoological institutions have evolved significantly, recognising its crucial role in enhancing the health, reproduction, and longevity of captive animals (Broom 1991; Wielebnowski et al. 2002). Animal welfare related scientific publications grew exponentially in recent years (Hosey et al. 2020), and great apes are one of the most studied taxa in zoo animal welfare (Freire and Nicol 2019; Hosey et al. 2020).

Ensuring optimal welfare involves more than just veterinary care, safe environments, and proper nutrition; it also encompasses the individual animal's overall sum of daily positive and negative experiences (Webb et al. 2019). In several species, there is evidence that individual affective state

influences health and therefore mortality and longevity (Walker et al. 2012), with happier individuals being shown to live longer in humans (Diener and Chan 2011) and **orangutans** (Weiss et al. 2011).

The concept of animal welfare gained prominence in the 1960s, initially focusing on intensive farming conditions (Veissier et al. 2008). Over time, its scope has expanded to include laboratory, companion, and zoo-housed animals (Webster 2005; Whitham and Wielebnowski 2009). While there is no single definition of animal welfare, it is generally accepted that welfare primarily concerns how the animal is *feeling* (Broom and Fraser 2015; Dawkins 2015) or how an individual is coping with the conditions in which it lives (Rose and O'Brien 2020; Jones et al. 2022). Recent advances include the concepts of the Five Domains and A Life Worth Living (Green and Mellor 2011; Mellor et al. 2020), or the concept of a meaningful life provided by solvable challenges (Clauss and Schiffmann 2022), yet many welfare aspects remain to be addressed by both scientists and animal care professionals (Ward et al. 2018). This progress in animal welfare science has notably been facilitated by the extensive data collected in systems like ZIMS (Species360 2023).

While foundational, this framework requires continual reassessment to encompass proactive welfare measures (McCulloch 2013). Therefore, in 2023, WAZA made welfare assessment plans mandatory for their member institutions (WAZA 2023). Ultimately, improving welfare in zoological institutions enhances reproductive potential and longevity, bolstering conservation, research, and education efforts.

Increased focus on positive reinforcement training

Positive reinforcement training in handling non-domestic animals became prominent in the 1970s, emphasising new methodologies and perspectives. This training enhances animal husbandry, such as during transportation, ensuring animal well-being, or daily care such as shifting between habitat spaces (Embury A.S., Pers. Comm.). Training can also provide opportunities to build resilience toward zoos specific factors such as proximity to visitors. Pomerantz and Terkel (2009) demonstrated that a training program significantly reduced abnormal and stress-related behaviours in a **chimpanzee** group, while increasing prosocial affiliative behaviours. The training notably benefited low-ranking individuals more than high-ranking ones. Additionally, these relationships created with the caretakers facilitate early detection of health issues, enabling timely medical intervention, improving treatment outcomes, and thus increasing animal survival and longevity.

Understanding stereotypical behaviours

Primate species which naturally live in large groups and have large ranges are particularly prone to exhibiting stereotypic behaviours in captivity (Pomerantz et al. 2013), and are widely considered as a sign of substandard welfare when animals develop them. Research increasingly focuses on understanding and mitigating these behaviours (Ross and Lukas 2006; Mellor et al. 2018), which persist as coping mechanisms and are, as in humans, challenging to eliminate without pharmacological intervention (Poulsen et al. 1996; Swaisgood and Shepherdson 2005; Bauer et al. 2013). Stereotypic behaviour can be triggered by current enclosure conditions or past experiences, complicating the identification of precise causes. Therefore, efforts are aimed at understanding the aetiology of stereotypic behaviour, using functional assessment to determine the timing and frequency of

undesired behaviours. It aims to better anticipate its onset and expedite elimination through improved housing and husbandry practices (Swaisgood and Shepherdson 2005; Pomerantz and Terkel 2009; Pomerantz et al. 2013).

Impact of the personality

Research in animal welfare is seeing a recent emphasis on an individual's personality. Personality traits can influence how animals cope with their environment and, therefore, impact health outcomes not only via stress, including morbidity and mortality (Deary et al. 2010). In humans and nonhuman primates, there is a relationship between immune response and personality, especially dimensions related to sociability, reactivity, and behavioural inhibition (Ironson et al. 2008; Capitanio 2011). This can directly apply to selecting individuals for breeding pairs, deciding on transfers, considering group structure, planning introductions, and determining how caregivers interact with individuals (Embury A.S., Pers. Comm.).

Providing choice and control

Converging evidence from animal research, clinical studies, and neuroimaging indicates that the need for control is a biological imperative for survival (Leotti et al. 2010). Primates, evolved to live in complex social groups, consume varied diets, and inhabit heterogeneous environments, are particularly sensitive to the availability of choice. While wild animals operate within environmental constraints, they retain freedom within their behavioural norms, a liberty still often absent in zoo animals.

Zoological institutions have increasingly emphasised providing animals with opportunities to express choices and preferences to enhance welfare and align with individual personalities (e.g., Coe 1998). Individual differences in preferences and personalities in great apes, such as shown in **chimpanzees** (Angley et al. 2024), underscore the emerging importance of providing choices to great apes in human care to help support positive welfare. Providing choice has shown promise in improving behavioural and physiological welfare indicators (Englund and Cronin 2023; Rust et al. 2024).

Conclusion

This report empirically and statistically demonstrates the increase in a population-level welfare indicator based on survival summary metrics and presents living standard improvements among the great apes within accredited zoological settings.

This report emphasises the advancements in husbandry and management practices made by accredited zoological institutions over the past century for four species of great apes: the **lowland gorilla** (*Gorilla gorilla*), **chimpanzee** (*Pan troglodytes*), **Sumatran orangutan** (*Pongo abelii*) and **Bornean orangutan** (*Pongo pygmaeus*). The efficacy of these improvements is made evident in the progressive and significant increase in life expectancy and lifespan equality of the *ex situ* populations of these species in zoological institutions. While the measure of a long life does not necessarily equate with a good (high-welfare) life, the use of survival-related metrics as a welfare indicator is intuitive: on the one hand, happier and healthier individuals live longer, as shown in humans and non-human primates (Diener and Chan 2011; Weiss et al. 2011). On the other hand, living conditions that accidentally induce premature death in a population cannot be reconciled with a high level of population welfare (Walker et al. 2012).

Great apes are increasingly threatened by human activities, including habitat destruction, poaching, and climate change (Estrada et al. 2017; IUCN 2023). As their numbers dwindle in the wild (IUCN 2023), zoological institutions have become crucial sanctuaries for the long-term survival and understanding of these species (Conde 2013; Hutchins et al. 2016). Accredited zoological institutions holding great apes are ***(i)*** key partners for species ***conservation*** such as by maintaining genetically diverse and healthy self-sustainable populations (IUCN SSC 2023), ***(ii)*** powerful ***educational platforms*** raising awareness about the plight of great apes and encouraging people to support conservation efforts and adopt more sustainable lifestyles that reduce human impact on the environment (Bruni et al. 2008; Conway 2011; Godinez and Fernandez 2019; McNally et al. 2024), and ***(iii) centres for scientific research*** that contributes to our understanding of great apes (Loh et al. 2018; Hvilsom et al. 2020; Kögler et al. 2020). By participating in breeding programs, supporting field conservation efforts, educating the public, and conducting vital research, accredited zoological institutions also contribute significantly to the global efforts to save great apes from extinction.

While improvements in life expectancy and lifespan equality reflect positive changes in the living conditions and overall welfare of great ape populations in zoological institutions, this metric alone cannot be used to assess individual welfare. Increasing the average lifespan indicates that, as a whole, the conditions are favourable for the species. However, it does not guarantee that every individual within the population is thriving under these improved conditions. Each animal's experience and personality are unique, and not all may cope equally well with the environment provided, challenging zoological institutions to adapt the management according to the individual needs. Therefore, while celebrating these advancements, it remains crucial to focus on the individual welfare of each animal to ensure that all are benefiting from the improved standards of care. To achieve this goal, rigorously capturing data on individual welfare, as done in the *Care & Welfare* module of ZIMS, is critical for enhancing not only the quantity but, more importantly, the quality of life of great apes in zoological institutions.

Ensuring the survival of these species requires a multifaceted approach, and accredited zoological institutions are at the forefront of this endeavour, bridging the gap between the wild and human society in the quest to preserve our planet's biodiversity.

Acronym list

AAZV	American Association of Zoo Veterinarians
ACZM	American College of Zoological Medicine
ALPZA:	Latin American Zoo and Aquarium Association (1990)
AWA:	USA Animal Welfare Act of 1966
AZA:	(North American) Association of Zoo and Aquariums (1924)
BaSTA:	Bayesian Survival Trajectory Analysis
BVZS:	British Veterinary Zoological Society
CITES:	Convention on International Trade in Endangered Species of Wild Fauna and Flora (1975)
EAZA:	European Association of Zoos and Aquaria (1985)
EAZWV:	European Association of Zoo and Wildlife Veterinarians
EEP:	EAZA Ex-situ Programme (previously European Endangered Species Programme)
ECZM:	European College of Zoological Medicine
GAHP:	Great Ape Heart Project
IPPL:	International Primate Protection League (1973)
IUCN:	International Union for Conservation of Nature
LTMP:	Long-Term Management Plan for EEP species
NRC:	USA National Research Council
PAAZA:	Pan-African Association of Zoo and Aquaria (1989)
SEAZA:	SouthEast Asian Zoos and Aquariums Association (1990)
SMP:	Species Management Program (ZAA)
SSC:	Species Survival Commission (IUCN)
SSP:	Species Survival Plan (AZA)
TAG:	Taxon Advisory Group
UK:	United Kingdom
USA:	United States of America
WAWV:	World Association of Wildlife Veterinarians
WAZA:	World Association of Zoos and Aquariums (1935)
ZAA:	Zoo and Aquarium Association Australasia (1990)
ZIMS:	Zoological Information Management System (Species360)

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