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Aging populations threaten conservation goals of zoos

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Improvements in wildlife husbandry mean that many zoo animals are living longer. This has put pressure on the finite holding capacity of zoos, which has often been addressed through a curtailing of reproduction to reduce population growth rates. Here, we explore how such actions have impacted the demographic trends of 774 mammal populations in European and North American zoo populations between 1970 and 2023. Irrespective of whether the data are clustered by region, taxonomic group, conservation status, or breeding program type, the proportion of old individuals has increased continuously, mirrored by a decrease in juveniles and actively reproducing adults. This aging demographic trend compromises the long-term sustainability of zoo populations and thus the ability of zoos to meet ex situ conservation goals. As the observed trends do not show signs of abating, reflection on current zoo population management is required.

zoological gardens | species conservation | population management | demography | reproduction

Significance

Zoos play an important role for global biodiversity through education, ex situ conservation, and reintroduction programs. For wildlife species currently threatened in their natural habitats or predicted to decline under future global change, it is essential that self-supporting ex situ populations are managed sustainably. However, due to limited space for placing new offspring, current management practices often curtail animal reproduction. Here, we show that by following this approach, zoo mammal populations in North America and Europe have, on average, become older and less reproductively active, with no end to these trajectories in sight. This makes a number of current zoo populations vulnerable to aging demographics. For zoos to fulfill their conservation mandate, these trends must be stopped or possibly reversed.

Modern zoos play an important role in the conservation of endangered wildlife species. Zoos have a history of successful reintroduction programs (1, 2), they educate the public about conservation (3), and many of the populations they harbor represent endangered species as insurance, rescue, restoration, research, education, or long-term ex situ populations (3–6). In the on-going biodiversity crisis, zoos have therefore been conceptualized as the "Millennium Ark" (7). This is reflected in the IUCN's guidelines and position on the mandate of zoos (6, 8) including their recommendation that more than 2,700 animal species require ex situ (outside of their natural habitat, e.g., in zoos) conservation action (9). While zoos also hold nonthreatened species, they globally self-imposed the mission of ex situ conservation in 1993 (10), which also led to a public mandate by the European Union for European zoos as centers for ex situ species conservation since 1999 (11). However, the long-term sustainability of zoo populations—"sustaining the ark"—has been a persistent challenge, with problems arising from small populations, uncontrolled mortality, limited genetic diversity, and the logistical and financial challenges of animal exchange between institutions (12–17). In 2014, this led to the warning that "the Millennium Ark is sinking" (18).

In recent decades, however, progress in zoo animal husbandry and management has alleviated some of these challenges (19–22) to the extent that most animals in zoos are now likely to live beyond the natural longevity of their wild counterparts (23). Ironically, such progress has created a new challenge: pressure on the finite holding capacity of zoos as well-cared-for older individuals are occupying the space needed for new births. Additional space to house more individuals is not foreseeable in the near future as most zoos cannot expand, and few new zoos are being created. As a result, many zoos have resorted to reducing reproduction by means of hormonal contraception, castration, or physical segregation of sexes (16). Over time, this is altering the shape of population pyramids in a way that resembles the "demographic transition" in humans (24). Populations of a wide-variety of species—from ungulates to primates and carnivores—are changing from bottom-heavy pyramid-shapes with many juvenile individuals into top-heavy, diamond-shaped "pyramids" with more older individuals (22, 25) (Fig. 1). With their high reproductive activity, pyramid-shaped populations are well-equipped to buffer unforeseen crises, such as disease outbreaks, impairment of animal exchange by epidemics, or a several-year-streak of plain bad luck in breeding success. In contrast, diamond-shaped populations, especially when consisting of a low number of individuals, are less resilient to these stochastic events, which may compromise the long-term sustainability and ex situ conservation goals of zoos (26, 27).

Although the zoo community is generally aware of this development, its full scope has not yet been quantified. Here, we collected data for 361 North American and 413 European mammal populations housed in zoos between 1970 and 2023, to analyze the

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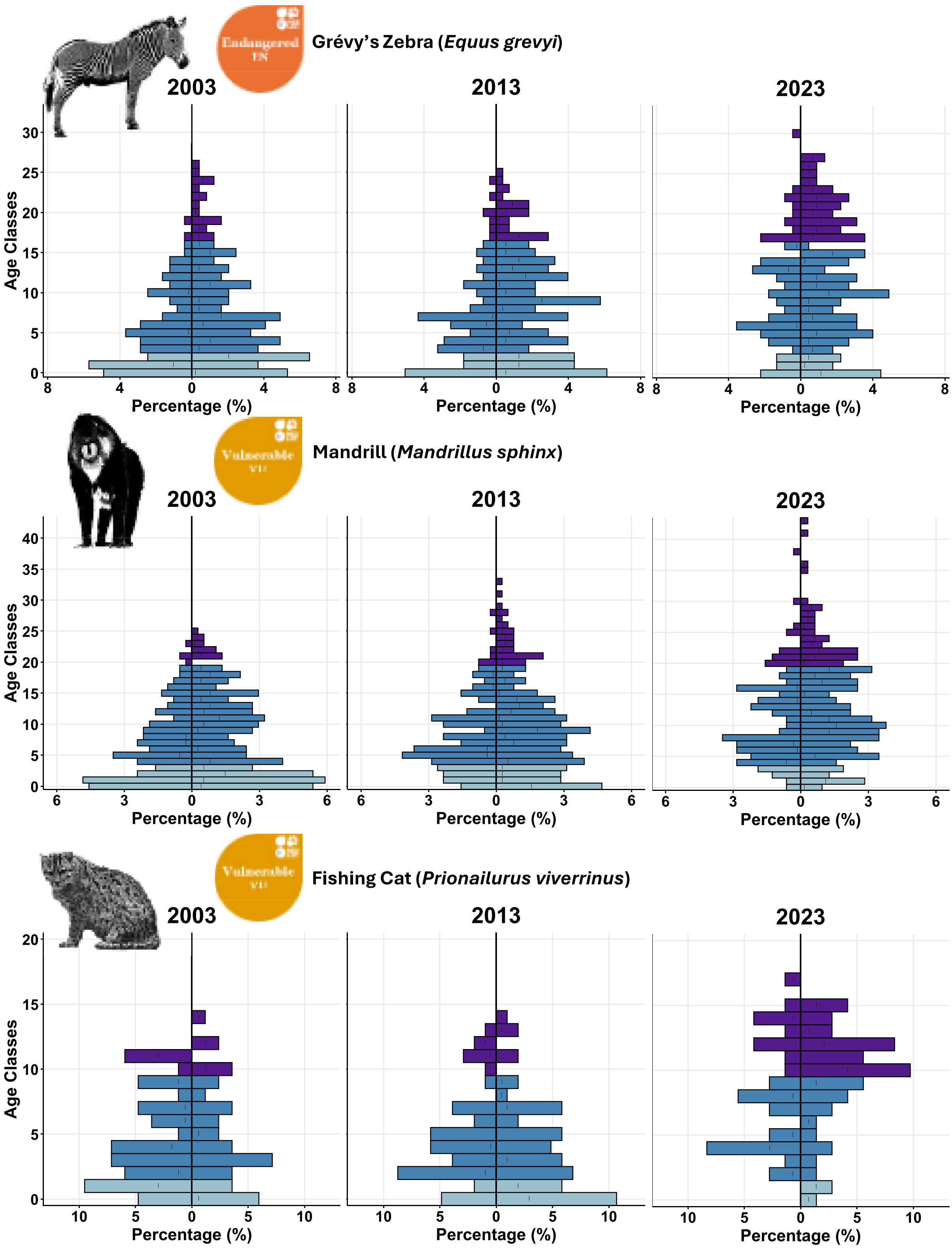

Fig. 1. Three examples of age structure development in European zoo populations across 20 y. All three populations had a "pyramidal" population structure typical of a resilient, breeding population in 2003 but have rapidly shifted to a narrow-bottom ("diamond") shape typical of aging populations following restricted breeding. IUCN status as of 2025 (9). Bar colors represent juveniles (light blue), adults (blue) and seniors (purple).

underlying demographic trends of these populations. We determined the shapes of the population pyramids (per sex), the proportion of juvenile, adult and senior individuals (the latter being defined as above the age threshold for reproductive senescence), the proportion of reproductively active individuals, and birth rates for each year. Temporal trends were depicted graphically for various subsets based on region (North American or European zoos), taxonomic groups, IUCN conservation status, or management strategies: both the American Association of Zoos and Aquariums (AZA) and the European Association of Zoos and Aquaria (EAZA) have populations managed as "high-priority" or "low-priority" (for details, see *SI Appendix*). We analyzed historical trends (of individual populations as well as subset averages) with Bayesian "changepoint detection."

Results and Discussion

Zoo Populations are Consistently Aging over Time. Between 1970 and 2023, there was a consistent decrease in the proportion of "pyramid"-shaped populations, and a concomitant increase of "diamond"-shaped populations; correspondingly, the average proportion of seniors increased, that of juveniles decreased (Fig. 2), and the median population age increased (*SI Appendix*, Fig. S2). Although some shift from juveniles to adults and seniors is expected as growing populations transition to more stable ones, no leveling-off of this trend is evident over the last 50 y (Fig. 2). Moreover, these trends occurred irrespective of whether the data were split by region, taxonomic group, IUCN conservation status, or management strategy (i.e., whether a species is managed by a dedicated plan, designated to be phased out by the regional zoo community, etc.) (*SI Appendix*, Figs. S3–S6). Generally, the observed trends started earlier in North America compared to Europe, possibly because of larger holding capacities in the more numerous European zoos. Alternative explanations include systematic differences in the founding populations and hence genetic diversity between continents. Only in North America was there an intermittent increase in "pyramid"-shapes between 2010 and 2015 (that occurred in both high- and low-priority populations; *SI Appendix*, Fig. S5), possibly linked to the introduction of a variety of animal population management strategies in this region in 2010 (28). In Europe, the acceleration of aging in the most recent years could in part be a consequence of a restriction of animal exchange between zoos due to both Brexit and the COVID pandemic.

Of the 361 populations from North America and 413 from Europe that were part of the dataset in 1970, 14 and 3% no longer remained (zero individuals left) in the respective region by 2023. Of the remaining 310 and 403 populations, 40 and 63% of the North American and European populations had increasing trends for the proportion of seniors; on average, these trends had been present for the last 14 ± 13 and 17 ± 13 y, respectively (*SI Appendix*, Table S2). Concomitantly, 29 and 47% of the North American and European populations had decreasing trends for the proportion of juveniles, with average historical trend lengths of 26 ± 18 and 25 ± 16 y, respectively (*SI Appendix*, Table S2). 53 and 42% had stabilized at an average proportion of juveniles of 14 ± 8% and 14 ± 9%. These trends will partly reflect the increased survival of adult individuals due to improved husbandry practices in zoos. However, another 15 and 6% of these populations had reached a proportion of zero juveniles before 2023 (being excluded from the "stabilization" category), indicating that reduced reproductive activity was a contributing factor. Again, these trends were similar across all subsets (*SI Appendix*, Tables S3–S6).

Zoo Populations Increasingly Underuse Their Reproductive Potential. The contribution of curtailed reproduction to these trends is evident when assessing birth rates or the proportion of reproductively active females over time (Fig. 3). Reproductive activity was, on average, higher in Europe than in North America, but overall trends were similar. 49 and 68% of the North American and European populations showed decreasing trends for the proportion of actively reproducing females, with average historical

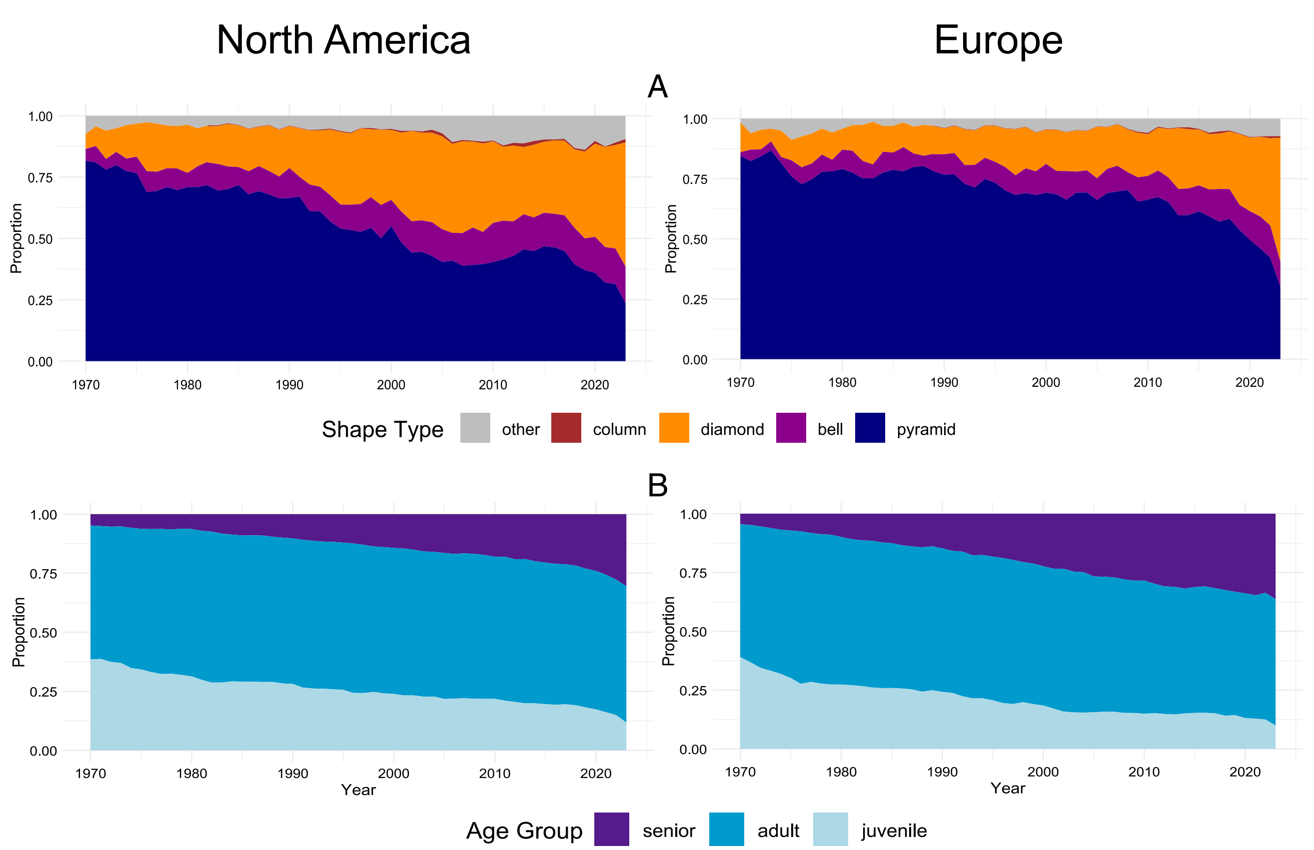

Fig. 2. Development of population age structure in zoo populations in Europe and North America. (*A*) Comparison of all mammal populations between North America and Europe, indicating the trend in population structure over time (for pyramid and diamond shapes see Fig. 1; other shapes explained in the *Materials and Methods*); (*B*) and the average proportion of age groups (juveniles, adults and seniors) over time.

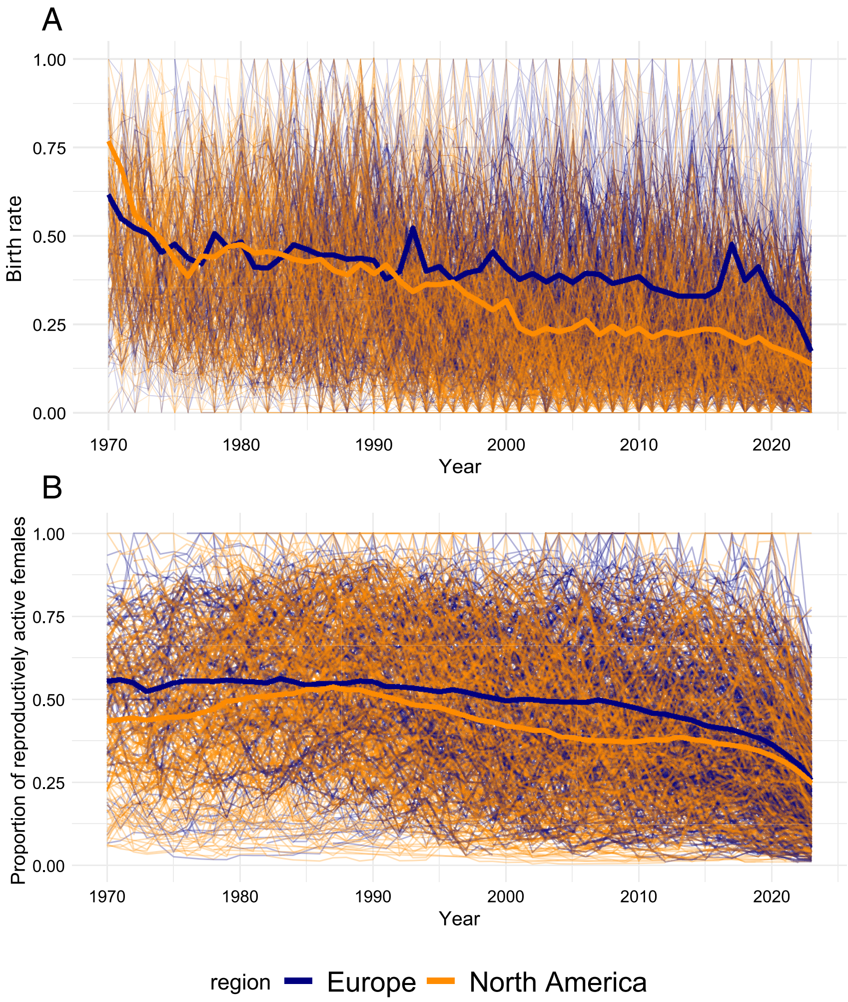

Fig. 3. Development of the breeding population and birth rates in zoo populations in Europe and North America. (*A*) Average birth rates over time for the cluster of all populations analyzed. Birth rate as $N_{\text{Births}}/N_{\text{females(adult+senior)}}$. Display capped at 1. (*B*) Average proportion of actively reproducing mature (adult + senior) females of the entire mature female population in zoo mammal populations in Europe and North America each year. This represents the count of proven breeder females alive at their reproductive prime (adult) and females that reproduced at each given year and are beyond their reproductive prime (senior). The thick lines indicate the total average per year; the thin lines represent individual populations.

trend lengths of 15 ± 13 and 18 ± 12 y, respectively (*SI Appendix*, Table S2); 15 and 7% of populations had already reached zero reproductively active females before 2023. These trends were also similar across all different subsets (*SI Appendix*, Tables S3–S6). For the high-priority populations, 76% in North America and 79% in Europe had decreasing trends for the proportion of actively reproducing females, with average historical trend lengths of 14 ± 11 and 18 ± 12 y (*SI Appendix*, Tables S5 and S6). In theory, the resilience of larger populations is less threatened by a low proportion of reproductively active individuals, because large populations have a greater capacity to initiate reproduction again and recover after stochastic events; however, the proportion of actively reproducing individuals was generally not inversely proportional to population size, irrespective of the regional, taxonomic, or management subsets (*SI Appendix*, Figs. S2–S6). If these trends of reduced reproduction were to continue into the future, many more zoo populations would vanish (Fig. 4). Clearly, for zoos to successfully reach their mandate of species conservation, measures to rectify these trajectories are required.

The Conservation Conundrum of Good Animal Husbandry and Limited Holding Capacity. Across the various animal groups, median age has increased consistently over time (*SI Appendix*, Figs. S2–S7). Indeed, there are now branches of veterinary care specifically devoted to caring for geriatric zoo animals (30). This stands in contrast to natural environments where predation, disease and density-dependent processes often cause premature mortality and keep population sizes in congruence with the available resources and space (31, 32). Such trends in zoos are a hallmark of collectively good animal husbandry across the community, with husbandry guidelines and international standards reducing uncontrolled zoo animal mortality (19–22); however, in the absence of self-regulation by natural mortality, proactive management is required.

Relying on old-aged individuals is an inherently risky management strategy. Although most mammals probably do not experience menopause (33), reproductive senescence is widespread (34) and was also detected in most species included in the present study (cf. *Materials and Methods*). Therefore, in continuously aging mammal populations, the likelihood of successful reproduction will necessarily decrease over time. Additionally, the prevention of reproduction by hormonal contraception or segregation of sexual partners can significantly curtail the chances of subsequent successful reproduction (16, 26, 35). On top of this, stochastic events such as mating partner incompatibility, infertility, miscarriage, accidents, diseases, birth of an individual of the other sex, or unpredictable litter sizes add another layer of risk when reproduction is managed for exact numerical replacement.

Zoos strive to overcome some of these obstacles through careful management that accounts for species-specific and even individual-specific characteristics. E.g., zoos have long used a dedicated software to support population management decisions that accounts for genetic relatedness, population-specific average mortality, and the age-specific reproductive potential of individuals (36). But

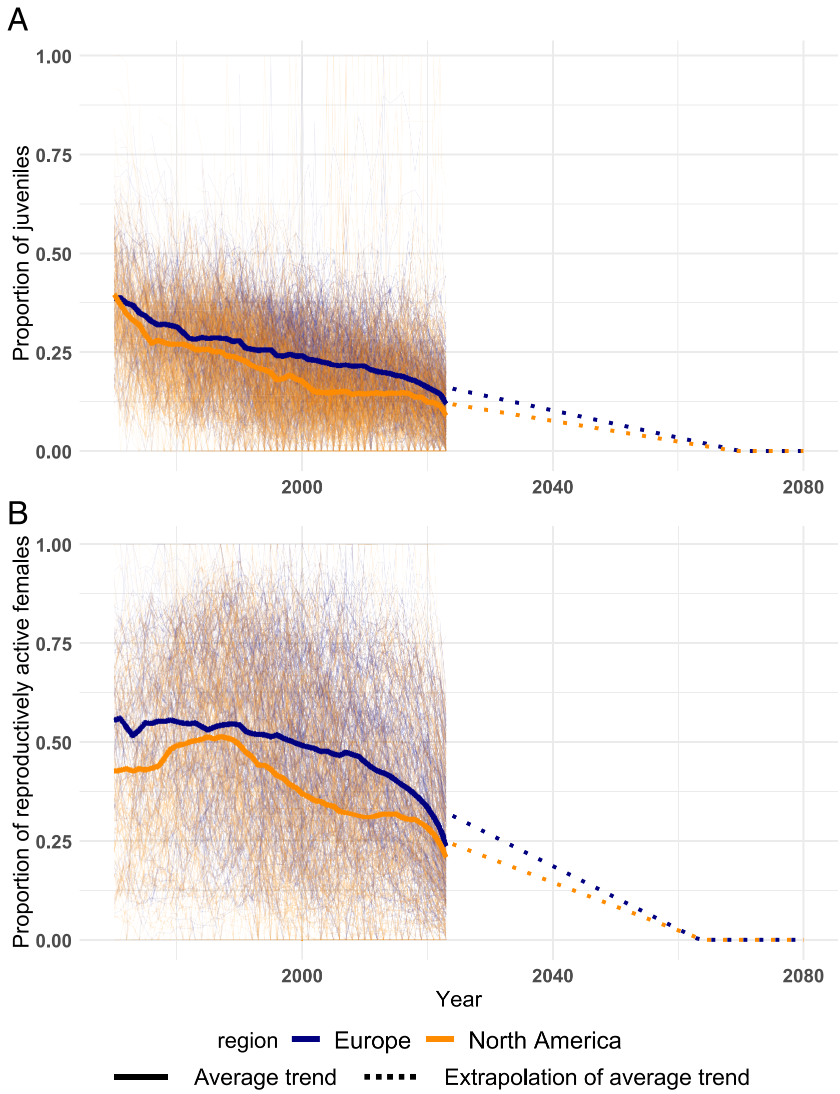

Fig. 4. Hypothetical extrapolation of the average trends of developments of (*A*) the proportion of juveniles and (*B*) the proportion of actively reproducing females based on the last 30 y by "Gaussian Point Process"(29) under the assumption that no corrective measures are taken.

under high-quality husbandry and finite space capacity, curtailing reproduction inevitably leads to older populations which over time jeopardizes their sustainability. Instead, management strategies that promote reproduction in prime breeding-age individuals and the future reproductive capacity of the population offer a more robust solution and important safety buffer. Inevitably, however, under conditions of high reproduction, strategies must also be designed for the overabundance of individuals through either increased space availability, transfer of animals out of the zoo community, or controlled mortality.

Increasing Holding Space for at-risk Species. Space itself has become a most critical resource for zoos (37, 38). Across zoos, absolute population sizes are generally stable or in decline (*SI Appendix*, Figs. S2–S6), indicating that holding space capacity has been reached. Population peaks were historically reached at different times for populations ascribed low- or high-priority for zoo management in North America (*SI Appendix*, Fig. S5) or Europe (*SI Appendix*, Fig. S6), being more recent in the high-priority populations. This leads to the double-edged interpretation that either more space is allocated to priority populations or that priority labels are given to large populations. In either case, the historical trends of reproductive activity of high-priority populations do not indicate that zoos have managed their reproduction differently from nonpriority populations in the recent past.

Increasing the available space for small zoo populations can offer temporary, but—due to the general finiteness of resources—never substantive relief. When populations are only managed by adjusting reproduction to the available space without actively removing individuals, then a somewhat stable age composition fluctuating around an average can probably only be achieved at a sufficiently large size, not by exactly replacing individuals that die with new ones each year, but by judiciously allowing moderate boom-and-bust cycles over time. Small populations, by contrast, can accidentally be pushed to the verge of extinction by such cycles. There is no clear cut-off to define "large" and "small" populations (14); among the currently existing populations, 79% in North America and 63% in Europe had fewer than 150 living individuals in 2023, likely representing "small" populations.

Calls for more holding space have a long tradition in the zoo community and can be achieved in two ways. First, more zoos could be built or existing zoos expanded [the request for dedicated "retirement sanctuaries" (39) belongs to this category]. Second, existing space can be reallocated, for example, to allow more holding space for endangered species only, leading to an overall reduction in the number of species kept (40). This approach is reflected in ongoing assessments of which species to maintain or phase out as zoo populations (41), which can partially be interpreted as a continuous reduction of species considered in recent years (42). For example, in our data, a number of populations have vanished from zoos since 1970 (59 in North America and 10 in Europe, *SI Appendix*, Fig. S2). This approach, however, does not reflect the increasing number of species that are becoming threatened in their natural habitats (43) and hence would benefit from ex situ conservation in the future (8, 9). Yet, this phasing out of certain species will most likely go unnoticed by the general public and not attract negative attention. It can be perceived as simply abandoning ex situ responsibility for species after species over time due to resource limitations, and the question arises how to balance the number of populations to maintain and the space required for populations of safe sizes (44). Aiming for more capacity and discussing which species to prioritize, e.g., as part of Regional Collection Plans or Regional Species Plans (17, 40, 41, 45), are important aspects of conservation planning; however, these solutions take long timescales to implement and may not provide sufficient help in the coming decade. More immediate solutions may well be required.

Strategies That Promote Robust Population Pyramids. A healthy demographic structure can be achieved by facilitating constant reproduction and maintaining the population size by either transfer of "surplus" animals out of the managed zoo population or by applying controlled mortality through deliberate, respectful, and humane killing (46–49). Arguably, both of these approaches apply more to smaller populations, which are more vulnerable to stochastic events when reproduction is curtailed. Applied judiciously, removal from the zoo population by out-transfer or controlled mortality can keep the population within holding space constraints, without aging and compromising its reproductive potential.

In some cases, "surplus" individuals may be transferred outside of the zoo community; for example, to the private sector (50) or through carefully planned reintroduction programs (2). When appropriate, such transfers can bolster the global population size and diversify conservation efforts. However, in many cases, transfers of animals outside of the zoo community are not feasible. While the transfer of animals to the private sector is more accepted in North America (50), there is little tradition of this practice in Europe, where the transfer of ungulates, carnivores, and primates to private entities is met with skepticism (45), due to concerns for husbandry and welfare of the animals as well as traceability. And releasing animals into the wild requires species-specific restoration and expansion of a natural habitat (to ensure they have the resources they need), including strategies for their protection and the avoidance of human-wildlife conflict (to ensure they are not directly targets of attack), as well as preparation of the release animals, which all makes this option unsuitable as a constant buffer for surplus.

Controlled mortality, on the other hand, offers a practical, long-term solution. Such an approach is in our experience not an issue of public dispute when applied to fish, amphibians, reptiles, and even birds; it is, however, debated in mammals, with clear differences in the application between different mammal groups (*SI Appendix*, Text) (51). Yet, such an approach can assist in the production of food resources for zoo predator species (i.e., there would be no net change in the total number of animals that must be culled as predators are always fed culled animals) and has been suggested to promote public education and animal welfare (48). In our data, ungulates had the lowest proportion of seniors and the highest proportion of reproductively active females (*SI Appendix*, Fig. S7), maintained a high (though also decreasing) proportion of pyramid-shaped populations (*SI Appendix*, Fig. S3) and their nearly even sex ratio at birth differed most distinctively from the female-biased one among adult individuals (*SI Appendix*, Fig. S8). One possible explanation is that in hoofstock, transfer of surplus individuals to the private sector and controlled mortality may be more accepted and hence practiced compared to other mammal taxa (50, 51).

The zoo community has realized the relevance of controlled mortality for population management for a long time (46–49, 52) and included it as an option in management strategies for zoo populations (45, 53). But faced with public pressure from urban societies dissociated from nature, that equate deaths with poor animal welfare, many zoos are finding it risky to employ this tool (48). Indeed, in some countries, euthanasia for zoo population management is even illegal (45).

We are not aware of research on the detailed motivations and decisions involved in the planning behind the trends depicted in our study. Therefore, considering the limited transfer options for offspring and a suspected reluctance to cull zoo mammals before a geriatric stage, we hypothesize that the trends we observe are the outcome of a two-level tragedy of the commons: (i) At the level of the individual studbook, where studbook managers might avoid recommending controlled mortality—and where individual studbooks lead to the overall depicted trends not because of an overarching plan, but because of the sum of individual-studbook reluctance to allow safety buffer breeding in the absence of holding space to avoid the challenges of surplus animals. (ii) At the level of the individual zoo, where the managers might not want to cull, or might be prevented from culling individuals in their care by (perceived) societal pressure or legal restrictions, and hence curtail reproduction—and where individual zoos managing a given species thus might add to a trend that imperils the conservation mandate of zoos, not because of a species-specific overarching plan, but due to the sum of individual-zoo decisions against controlled mortality.

Possibly, and most importantly, not all zoos keeping a given species would need to adopt the same strategies of population management. A studbook coordinator could, in consensus with the institutions participating in the specific program, distribute tasks between institutions in the sense of true teamwork; as long as a certain proportion of zoos would apply controlled mortality with the clear support of the others, the logical aim of attaining a constant (and not decreasing) proportion of juveniles and maintaining reproductive activity at population level is a realistic target. In some species, species-specific solutions to delay reproduction and increase interbirth intervals without negative side-effects and to apply truly reversible contraception can complement controlled mortality. We stress that the potential, hypothetical outlook of a higher reliance on nonlethal management options in the future should not be used as an excuse to let populations today become less sustainable.

Zoos: Entertainment Entities or Public Service Providers. Zoos operate as recreational entertainment entities, generating revenue to finance themselves (54). At the same time, they act to fulfill a societal mandate or a self-imposed mission as a link between urban societies and nature, to promote and support nature conservation, and to conserve species (7, 8, 11). As part of their core expertise, zoos are leading authorities in ex situ animal care. The dilemma of increasing pressure on the finite holding capacities of zoos should not be understood as a failure inherent in a business model. Rather, it is a challenge for long-term species conservation generated as a result of institutional excellence that zoos and the public must now address.

Our data highlight that zoo mammal populations in Europe and North America are aging. This fundamentally jeopardizes the long-term capacity of zoos to harbor insurance populations, facilitate reintroductions of threatened species, and simply maintain a variety of self-sustaining species programs. Zoos must be empowered to collectively manage for long-term population sustainability to protect wildlife species. This will require continuous, engaged communication within the respective societies, sometimes including alterations to current legislation. It had best start now.

Materials and Methods

The records of all individuals for the class Mammalia were obtained under license agreement 103210 from Species360 (ZIMS for Husbandry), an online database platform currently used by more than 1,200 institutions worldwide to manage their animal data. The dataset included information on the sex, dates of birth and death, whether the animal was wild or zoo-born, parentship data including an estimate of the reliability of parentship information, region of occurrence, and its current status at the time of download (dead or alive). We considered only populations that had at least reached an arbitrary threshold of 150 individuals recorded between January 1, 1970, and December 31, 2023, yielding a final number of 774 mammal populations [361 (sub)species in North America and 413 in Europe]. Before analyses, data were submitted to series of validation and curation steps (*SI Appendix*). For each species, the age categories "juvenile," "adult," and "senior" were defined based on species-specific information, and for adults and seniors, it was noted whether they were listed as sires or dams (i.e., reproductively active) (*SI Appendix*).

"Population pyramids" were created for every year based on data from males and females separately. "Pyramid" shape types and their definitions are in *SI Appendix*, Table S1. The classification process, as well as tests for its plausibility by assessing changes between "pyramid" shapes, are described in detail elsewhere (55), and the corresponding code is publicly available (56).

In addition to the pyramid shape and the proportion of juveniles, adults and seniors, we calculated the following for each population in each year: The median age of all the individuals of the population [expressed as a proportion of the species' maximum lifespan, to ensure comparability between species of different absolute lifespans (57, 58)], the proportion of proven breeders in the population, the proportion of actively reproducing individuals of all adults and for each sex [defined as the number of proven breeders among adults plus the seniors that had been a parent in the respective year, divided by the sum of adults and seniors (the mature population)], the sex ratios (males:females) at birth and of adults, birth rates (number of births divided by the number of mature females at a given year), and the population size relative to the population's peak. Coding was done in the Python 3.10 programming language (59), using the pandas package (60) for data curation and the scikit-learn package (61) for statistical analysis and modeling. Bayesian statistics were used to assess trends and their historical duration, by using RBeast in Python (62). This was applied to the proportion of juveniles, the proportion of seniors, and the proportion of reproductively active females.

All procedures were applied to individual populations. Subsequently, we aggregated the results by different groups, averaging the measures across all populations per year to display historical trends for the respective groups. Additionally, because zoos do not manage averages but individual populations, we also counted the number of individual populations for the respective groups that went "extinct" (i.e., between 1970 and 2023, at least 150 individual animals were recorded, but no living individuals existed in 2023 or earlier), populations that had in 2023 an increasing, decreasing, or stabilizing trend (including the trend length and the proportion of the respective animal category in 2023), populations in which the respective animal category had reached a proportion of 1 (mainly applicable to the "senior" category) or a proportion of 0 (mainly applicable to the "juvenile" and "actively reproducing female" categories) prior to 2023—these were not included in the "stabilizing trends"—and the populations for which the trend models did not yield a result with a certainty ≥ 0.5 or for which the model could not be applied due to data peculiarities.

The analyses were conducted separately for North America and Europe, on all mammal populations aggregated, for six large taxonomic subgroups, by IUCN conservation status, and by the priority status of North American or European zoo population management (see *SI Appendix* for details).

The major limitations of our analyses are the purely demographic approach that is not informed by reasons of death (uncontrolled vs. controlled), actual knowledge of taxon-specific holding capacities, or genetics. Also, the fact that management approaches to specific taxa changed—possibly repeatedly—over time is not reflected in the categorization by current management priorities (see *SI Appendix* for more details).

Data, Materials, and Software Availability. Raw data used for the analysis of demographic population patterns (Species360 Data Use Approval # 103210) cannot be publicly shared, as Species360 is the custodian (not the owner) of their members' data. Raw data are accessible through Research Request applications (quoting # 103210) at https://conservation.species360.org/data-sharing/ (63) (contact support@species360.org for more information).

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