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Global and regional patterns in distribution and threat status of zoo collections of turtles and tortoises

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Turtles are a globally threatened group of reptiles. Zoo populations may contribute to the conservation of species, including turtles, but collection composition may not align with conservation needs. We combined data from the Zoological Information Management System (ZIMS), EDGE of Existence, the IUCN Red List and the Reptile Database to investigate zoo turtle holdings on global and regional scales. Globally, zoo collections were representative of turtle diversity, regional species distributions and threat statuses, indicating no bias towards threatened species and no taxonomic or distribution blind spots. Species kept in zoos had significantly lower EDGE scores than those not represented, and threatened species were no more likely to have been bred in the year prior to data collection (before March 2022) or have non-viable populations, but were more likely to have a larger population size. Although Africa, Asia and South America have the smallest turtle holdings in terms of species, allowing for regional capacity, these regions hold more, while Europe holds fewer than expected turtle species – North American and Asian holdings do not differ from expected. African, Asian, North and South American regions significantly bias their collections towards native species. We found evidence for significant increases in turtle populations at the genus level following the EAZA Shellshock campaign in Europe. ZIMS data are limited by taxonomy, membership and accuracy of records but provide the best window into patterns of zoo turtle collections. While holding a species in a zoo does not equate to conservation value, based on these data, we recommend that conservation prioritisation exercises are developed for all turtle species, holding institutions or regional taxonomic advisory address population viability and support for institutions working with significant turtle populations in captivity to join ZIMS is provided.

Keywords: chelonia, ex-situ, zoos, conservation, ZIMS

INTRODUCTION

Turtles and tortoises (order Testudines; henceforth ‘turtles’) have an almost global distribution outside of the poles. Representatives of the group occur in most habitats, from desert to rainforest to coral reef (Ihlow et al., 2012). The group is also deeply connected to human cultures across the globe (Lovich et al., 2018) and performs important ecosystem services (e.g. Falcón & Hansen, 2018).

However, turtles are in the midst of a global conservation crisis; nearly half of the > 350 recognised species of Testudines are threatened with extinction (Ersnt & Lovich, 2009; Stanford et al., 2020). Despite this, and the relatively small size of the group as a whole, approximately one third of all turtle species are yet to be assessed for the IUCN Red List, and many existing assessments are out of date, meaning that threat levels may be higher than current data suggest (Böhm et al., 2013; Rhodin et al., 2018).

Population declines and extirpation are being driven by illegal and legal trade, habitat destruction and degradation, emerging infectious diseases and climate change (reviewed by Stanford et al., 2020). Over-exploitation for pet, meat and traditional medicine trades are probably the greatest specific threat to freshwater turtles and tortoises, which represent all but seven species of Testudines (Schlaepfer et al., 2005), with millions of animals traded both legally and illegally on a global scale (IUCN TFTSG, 2011; Mărginean et al., 2018; Cheung et al., 2006; Chow et al., 2014; Shamsur et al., 2013; Sihombing et al., 2021). The Chinese market for turtles is particularly large (Gong et al., 2009) and demand there has placed particular collection pressure on turtle populations, primarily across Asia, but also beginning to reach into North America (Lau & Shi, 2000).

Finally, at the level of species, turtles represent a significant amount of phylogenetic diversity relative to other tetrapod groups (Gumbs et al., 2020) and many turtle species have been identified as global priorities for conservation by the EDGE of Existence programme by using a combined score of evolutionary distinctiveness and extinction risk taken from the IUCN Red List.

Zoos, aquariums and similar organisations holding captive populations of wild animals (henceforth ‘zoos’, for convenience, with the explicit acknowledgement that

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zoological gardens sensu stricto may differ importantly from other animal holding organisations included in ZIMS) can form pivotal components of conservation initiatives, especially as part of the IUCN One Plan Approach (Traylor-Holzer et al., 2019) and have had positive impacts on conservation in both ex- and in-situ contexts (Robovský et al., 2020). Zoos are almost unique in their capacity to use ex-situ approaches to contribute to conservation goals, through engaging with the public to raise funds and awareness, holding so-called Ark populations, breeding for conservation translocation, acting as rehabilitation centres for injured wild animals, using captive population research species biology and to trial field methods under controlled conditions. However, zoos can struggle to strike the (albeit difficult) balance between the animal husbandry requirements, impacts on visitor appeal, distribution relative to the location of a given zoo, and threat status of focal groups of ectothermic vertebrates to align collection plans with global conservation needs (Tapley et al., 2015; Dawson et al., 2016; Harding et al., 2016; Biega et al., 2017; Biega & Martin, 2018; Jacken et al., 2020; Wahle et al., 2021).

These competing factors may lead zoo collections to misalign with the conservation needs of particular groups. Information concerning global patterns of collection holdings is useful to inform the zoo community's allocation of resources and collection plan design to more effectively support conservation. However, there is currently a poor understanding of global patterns in turtle species holdings in zoos, and how well they address conservation needs (Horne et al., 2012). Despite this, turtles have been the focus of specific zoo campaigns designed to improve conservation impact. The European Association of Zoos and Aquarium (EAZA) Shellshock campaign of 2004–5 was the largest of these, and raised awareness and funds aimed at supporting turtle conservation through the creation of 'turtle Arks' and collaboration with field programmes. The campaign was specifically associated with a push to increase holdings of threatened turtle taxa in European zoos, with a particular focus on Asian species, where conservation needs were deemed highest due to human consumption of turtles (Buley, 2005; Shellshock, EAZA.net, 2022).

In the present work, we aimed to appraise global patterns in turtle species holdings in zoos via the utilisation of the Zoological Information Management Software (ZIMS) database (Species360, 2022). More specifically, we aimed to investigate phylogenetic representation, the distribution of individuals, breeding success and the relative distribution of individuals and species holdings based on their IUCN Red List status, as well as to identify regional trends in collection composition. We also investigated how the Shellshock campaign affected European zoo holdings of freshwater turtles and tortoises.

METHODS

Zoo holding and geographic data

A list of all currently recognised turtle species (i.e. all taxa within order Testudines) was downloaded from the Reptile Database (Uetz et al., 2022), on 18 March 2022. The available data for turtle holdings in the Zoological Information Management Software (Species360 Zoological Information Management Software (ZIMS), 2022) were then downloaded via the Species Holdings tool as of 19 March 2022. This dataset included, for each species, the number of individuals kept (male, female, other), number of holding institutions, the continental regions (as defined by Species360) in which these institutions resided (Africa, Asia, Europe, North America, South America, Oceania), the number of individuals held in each of these regions and the number of births globally in the last 12 months. Species were allocated to global captive population size categories (N < 10, 11–50, 51–100, 101–200, 201–1000, > 1000), following Wahle et al. (2021). The native presence of each species in each of the continental regions was recorded by comparison with the range data according to the IUCN Red List (IUCN, 2022) and the Reptile Database for each species. Numbers of ZIMS registered animal collection holding institutions by region were provided by Species360 as Europe (586), Asia (114), North America (367), South America (32), Oceania [=Australia in older versions] (83) and Africa (24), as of 6 April 2022. Additional ZIMS registered institutions exist, but these do not hold animal collections and were excluded from analysis.

Taxonomy was aligned with the Reptile Database. Subspecies and obsolete taxa were collapsed into their respective species and recognised senior synonyms by additively combining holding data. Species that appeared on the Reptile Database but not in ZIMS Species holdings records were assigned as 'not in zoos' and all above records recorded as '0' or 'NA'. The Galapagos giant tortoises presented a unique problem in that multiple species are recognised by some authorities (see Kehlmaier et al., 2021), with some (including *Chelonoidis nigra* sensu stricto, under which the other species were considered subspecies) being assessed as Extinct by the IUCN. Many ZIMS records, however, are still assigned to *C. nigra* as subspecific status is not recorded, and consequently numerous individuals of an Extinct species are apparently extant in ZIMS. In order to address this problem, we collapsed all Galapagos giant tortoise species into *C. nigra* sensu lato. This is aligned with recent genetic work indicating shallow divergence and subspecific status of evolutionarily distinct units in this group (Kehlmaier et al., 2021).

The total number of individuals held in European zoos for ten years (1 January 1994–1 January 2004) prior to and ten years following (1 January 2006–1 January 2016) the EAZA Shellshock campaign (2004–5 inclusive) was counted for each turtle genus from the ZIMS database. These large time windows were selected to allow for the time taken for collection planning, species acquisition and breeding to respond to the Shellshock campaign, and to account for annual fluctuations due to breeding or death events. *Trachemys*, *Centrochelys* and *Testudo* were excluded from this analysis due to the huge number of individuals involved and inaccuracy and lack of clarity of records resulting from large numbers of rescued and customs-seized animals moving through collections. Genera with a population count of zero in both time windows were also excluded.

Table 1. Hypotheses, null hypotheses (where relevant) addressed, with datasets and statistical approaches used to test them

H_1	H_0	Variables	Test
Global species holdings do not differ in proportion from described diversity at the family level.	NA	Number of species represented in each family in zoos; numbers of species in each family of Testudines.	Chi-squared analysis for goodness of fit, with p-value simulation (2,000 iterations).
Species holdings are evenly distributed across continental regions.	NA	Number of species held by region; number of institutions per region; total number of Testudines species globally.	Chi-squared analysis for goodness of fit, with p-value simulation (2,000 iterations).
Zoo collections reflect global distribution of species between regions. There is no difference in distribution between global holdings of species by native region and the number of species native to each region.	NA	Global species holding counts, split by species-native region; proportions of number of all turtle species native to each region.	Chi-squared analysis for goodness of fit, with p-value simulation (2,000 iterations).
Regional zoo collections prioritise local faunas, in line with IUCN guidelines for ex-situ conservation.	Species holdings for zoos within each region, split by native region, do not differ from global distribution of species by region.	Regional species holding counts split between species native regions; proportions of number of all Testudines species native to each region.	Chi-squared analysis for goodness of fit with p-value simulation (2,000 iterations), with pairwise proportion post-hoc test with Bonferroni correction.
Global zoo species holdings are biased towards higher IUCN Red List categories.	Species holdings do not differ in distribution from species numbers across IUCN Red List categories.	Counts of species in captivity, split by IUCN Red List category of species; total numbers of species in each IUCN Red List status category.	Chi-squared analysis for goodness of fit, with p-value simulation (2,000 iterations), with post-hoc test. Post-hoc two proportions test with continuity correction.
European zoo species holdings are biased towards higher IUCN Red List categories.	Species holdings do not differ in distribution from species numbers across IUCN Red List categories.	Counts of species in captivity, split by IUCN Red List category of species; total numbers of species in each IUCN Red List status category.	Chi-squared analysis for goodness of fit, with p-value simulation (2,000 iterations), with post-hoc test. Post-hoc two proportions test with continuity correction.
Species in zoos are more likely to be threatened than not threatened.	Threat status of species in zoos, in terms of numbers present in each category, do not differ in distribution from threat status of species not in zoos.	Counts of species in and not in zoos, split by IUCN Red List category of species.	Chi-squared analysis for independence with p-value simulation (2,000 iterations), with pairwise proportion post-hoc test with Bonferroni correction.
Species held in zoos have higher average EDGE scores than species not held in zoos	There is no difference in EDGE scores between species held in zoos.	EDGE scores of species in and not in zoos.	Mann-Whitney U Test (following Shapiro Wilks test showing that data did not conform to a normal distribution).
Among species held in zoos, population sizes are larger for threatened species.	There is no difference in population size distribution between threatened and not threatened species.	Counts of species with global populations in each population size category, split by threatened and not threatened categories.	Chi-squared analysis for independence with p-value simulation (2,000 iterations).
Threatened species are bred more than not threatened species.	There is no difference in proportions bred between threatened and not threatened species.	Numbers of species where breeding was recorded in the last twelve months, split by threatened or not threatened categories.	Two proportions test with continuity correction.
The proportion of threatened and not-threatened species where only a single sex is present in holding institutions differs.	There is no difference in the proportions of threatened and not threatened species represented by a single sex.	Numbers of threatened and not threatened species, numbers of species with only single sex reported in each category.	Two proportions test with continuity correction.
European zoos increased the size of turtle collections after the EAZA Shellshock campaign.	There is no difference in turtle population sizes in European zoos before and after the Shellshock campaign.	Total numbers of individuals in European zoos before and after the campaign, split by genus.	Paired samples Wilcoxon test.

Conservation status

The IUCN Red List of Threatened Species (IUCN, 2022) was accessed on 20 March 2022 and the threat status of all species was recorded; those with no Red List assessment were recorded as 'Not Assessed'. For some analyses, those assessed as Critically Endangered, Endangered or Vulnerable were classed as 'threatened', those assessed as Near Threatened or Least Concern were classed as 'not threatened', and Not Assessed and Data Deficient taxa were assigned to the threat group 'Unknown'. The EDGE score for each species was also accessed from the EDGE of Existence list for reptiles (Gross, 2018; Gumbs et al., 2018). Where EDGE scores did not exist for a given taxa, the record was recorded as NA.

Statistical analysis

Alternative and Null hypotheses and analyses used to test them are presented in Table 1. We sought to test whether zoos, at both global and regional levels, prioritise threatened and region-native turtle taxa in terms of species presence, institutional species holding numbers, population sizes and reproductive output. Analyses were conducted in R 4.2.0 (R Core Team, 2021), using the stats (R Core Team, 2021) and chisquare.posthoc.test packages (Ebert, 2019). Where appropriate, expected values were calculated under the null hypothesis of random distribution of counts. P values were corrected to account for false discovery rate, using the Benjamini-Hochberg method (Benjamini & Hochberg, 1995). P value simulation via Monte Carlo test with 2,000 iterations was used for chi-squared tests where expected values fell below 5 for at least one cell (Hope, 1968). Post-hoc tests, where appropriate, were conducted following the method of Beasley & Schumacker (1995) with Bonferroni corrections.

RESULTS

Full raw data are available at https://github.com/CJMichaels/Turtle-zoo-holdings.git. Reported p values are Benjamini-Hochberg adjusted p values corrected for false discovery rate (see Methods).

Phylogenetic representation

Cross-referencing of the Reptile Database, IUCN Red List and ZIMS yielded a total number of 357 Testudines species in 96 genera and 14 families, of which 248 species in 87 genera were present (captive population > 0) in zoos globally. All families of turtle were represented in zoos, and the family-level composition of the global captive population in terms of species numbers did not differ significantly from that of all recognised Testudines species (X^2 = 10.365, p = 0.6727; Fig. 1), although Geomydidae and Testudinidae were markedly over-represented, and Trionychidae, Kinosternidae and Pelomedusidae were markedly under-represented.

Geographic distribution of captive Testudines

Regional species holdings by region were North America (188), Europe (174), Asia (119), South America (45), Oceania (46) and Africa (32). Total populations by species ranged from 1 (fifteen species) to 7,390 (*Trachemys scripta*) with a median population size of 41 individuals and an interquartile range of 9–174.75 individuals. The number of species native to each zoo region was North America (101), Europe (15), Asia (107), South America (63), Oceania (49) and Africa (68).

Global proportions of holdings of species native to each region did not differ from the proportions of all species native to each region (X^2_5 = 3.4052, p = 0.6869, Fig. 2a). Species holdings by zoo regions were not proportionate to the number of institutions within each region. Zoo holdings of each region were not distributed proportionately to the number of zoos within them (X^2_5 = 201.93, p < 0.0001; Fig. 2b); Europe held significantly fewer species than proportionate to the number of institutions within the region (post-hoc p < 0.001), while South America, Africa and Asia (all post-hoc p values < 0.001) held significantly more; other regions were proportionately represented (all post-hoc p values > 0.05). At a regional level, South American (X^2_5 = 66.242, p = 0.0023), Asian (X^2_5 = 39.824, p = 0.00175), African (X^2_5 = 47.681, p = 0.0014), North

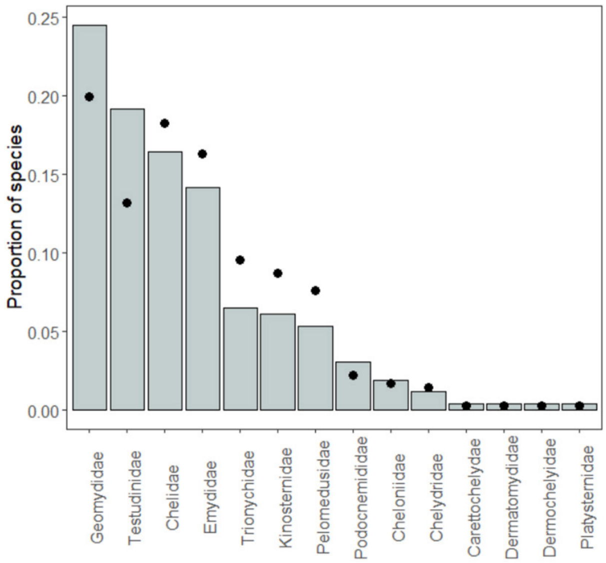

Figure 1. Proportions of species in global zoo holdings split by family (grey bars) against expected proportions derived from known diversity of turtles (black points)

Table 2. Post-hoc p values for comparisons of distributions of zoo holdings in each global zoo region of turtles native to each global zoo region. Significant p values are in bold.

Species Native Region	Zoo Region					
	Africa	Asia	Europe	N. America	Oceania	S. America
Africa	**0.000**	>0.999	>0.999	>0.999	>0.999	>0.999
Asia	0.071	**0.000**	>0.999	>0.999	>0.999	**0.002**
Europe	0.551	>0.999	>0.999	>0.999	>0.999	>0.999
N. America	>0.999	0.118	>0.999	**0.017**	>0.999	>0.999
Oceania	>0.999	>0.999	>0.999	>0.999	**<0.001**	>0.999
S. America	>0.999	0.872	>0.999	>0.999	>0.999	**<0.001**

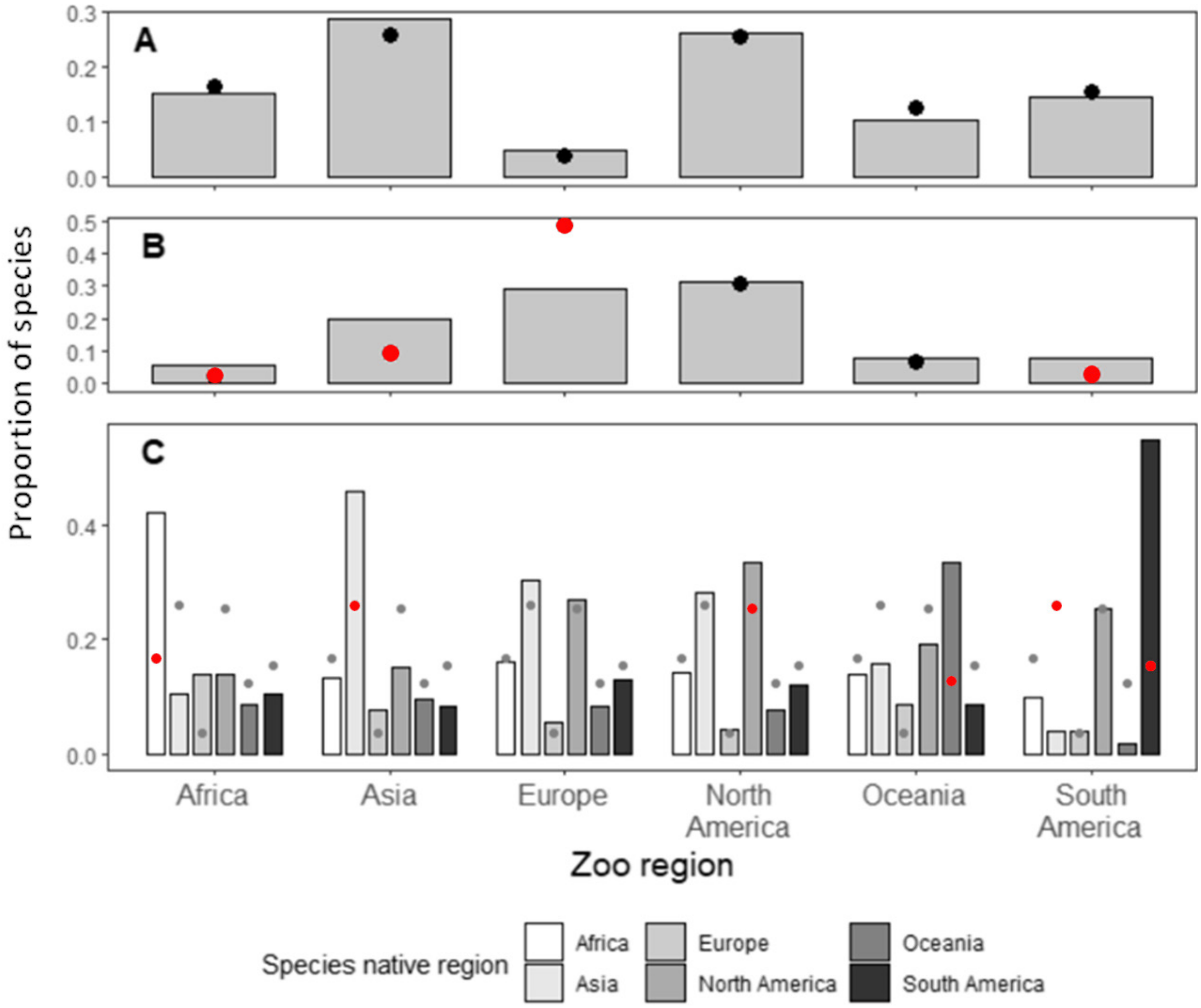

Figure 2. **A**. Proportions of globally zoo-held species split by species native region (grey bars) against expected numbers derived from distributions of total global turtle diversity (black points), which do not differ significantly. **B**. Proportionate species holdings by zoo region (grey bars) vs. expected numbers derived from total global species and numbers of ZIMS registered collections per region (points), which differ significantly (red points) such that Europe holds fewer species than predicted by numbers of institutions (post-hoc p < 0.001), while South America (post-hoc p = 0.003) and Asia (post-hoc p = 0.001) held significantly more. **C**. Proportionate zoo holdings of turtle species in each zoo region (x axis) split by species native range of held taxa (bars), against expected proportions (points) derived from global turtle diversity. Distributions of holdings differ from expected distributions for all regions other than Europe, with red points indicating those categories which differed significantly from expected. See Table 2 for post-hoc p values. The legend pertains only to panel C.

American (X^2_5 = 12.028, p = 0.0448) and Oceanian (X^2_5 = 28.501, p = 0.0017) zoo species holdings were primarily skewed towards native regional faunas (Fig. 2c), while European (X^2_5 = 7.0296, p = 0.3044) collections were not significantly different in composition to global proportions (see Table 2).

Threat status, species holdings and breeding success

Of the 248 turtle species represented in zoos, 125 were listed as 'threatened', 62 as 'not threatened' and 61 as 'Unknown'. Distribution across IUCN Red List categories was Not Assessed (57), Data Deficient (4), Least Concern (38), Near Threatened (24), Vulnerable (40), Endangered (35), Critically Endangered (50). Proportions of species in captivity in IUCN Red List Category did not differ significantly from proportions of all recognised species in Red List category (X^2 = 5.7872, p = 0.5133; Fig. 3a). In European collections specifically, which were subject to the Shellshock campaign, there was a significant difference (X^2 = 13.801, p = 0.03148), which was caused by lower-than-expected holdings of Not Assessed species (post-hoc p = 0.002438).

Comparing species numbers in each IUCN Red List category between species in and species not in zoos, distributions were not equal (X^2 = 54.42, p = 0.0007; Fig. 3b), such that the former were significantly more likely to be Least Concern (post-hoc p = 0.008) and less likely to be Not Assessed (NOA) (post-hoc p < 0.0001). Median (range) EDGE scores were 25.16 (6.54–149.70) for species in zoos, and 41.20 (9.63–52.63) for species not represented in zoos. Species in zoos had lower EDGE scores on average than species not represented in zoos (W = 12545, p = 0.0007).

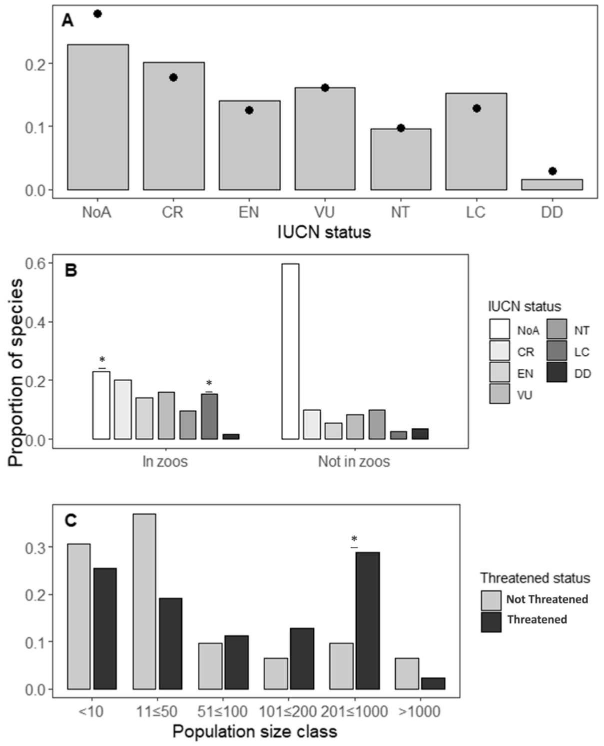

Figure 3. **A**. Proportions of global zoo turtle species holdings split by IUCN Red List threat category (bars) against expected proportions of species derived from all turtle Red List assessments (black points), which do not differ significantly. **B**. Proportions of species split by IUCN Red List threat category in zoo holdings (left) and not in zoos (right). Asterisks indicate categories where proportions of species in zoos differ significantly from their corresponding categories not in zoos. **C**. Proportions of species held in zoos globally split by populations size class and threatened/not threatened status. The asterisk indicates the category where there is a significant difference between threat categories.

Populations of threatened species were disproportionately more likely to comprise population sizes of 201–1000 individuals than were not threatened species, but there were no other differences in distributions between threatened and not threatened taxa (X^2 = 15.885, p = 0.001, post-hoc p value = 0.038; Fig. 3c). Three not threatened and six threatened species were represented by only a single animal in zoos globally, hence representing non-viable populations; these proportions did not differ significantly between threatened and not threatened groups (z = 0.0116, p = 0.99202); i.e. threatened species were no more or less likely to comprise non-viable breeding populations. All species with at least two individuals reported either at least one male and one female, or reported individuals of unknown sex, and are therefore here considered at least potentially viable in the loosest sense of being able to produce offspring. 48,091 individuals were held in ZIMS institutions, of which 10,231 were recorded as being male, 11,700 as female and 26,160 recorded as ‘Other’ (meaning unknown sex). Threatened (46 %) and not threatened (34 %) species did not significantly differ in whether breeding occurred in the last twelve months (X^2_1 = 1.89, p = 0.2644).

Shellshock campaign

Seventy-two genera were present in zoos in at least one time period. There was a significant increase in turtle populations by genus in European zoos between the ten years immediately preceding and the decade immediately following the Shellshock campaign (V_{71} = 1797.5.5, p = 0.01). The median (Q1, Q3) percentage change in population size by genus was 29.65(-17.74, 108.58) % with a range of -100 to 1350 % change. No genera were lost from zoos between time periods, and only one genus (*Dogania*) was gained with representation of a single animal.

DISCUSSION

Our analysis of the ZIMS database and subsequent analyses show that global zoo holdings of turtles proportionately represent family-level diversity and regional distribution, but that at a regional level institutions (with the exception of Europe) tend to bias turtle collections towards region-native faunas. Globally, species held did not differ proportionately in IUCN Red List threat status from listings of all turtle species. These data suggest that, at a global level, zoo collections represent a random cross-section through turtle species with no evidence for selectivity towards threatened species, regions of origin or particular taxonomic groups (although the Geomydidae and Testudinidae are somewhat over-represented, this is not significantly different from expected). Conversely, Dawson et al. (2016) found that North American, European and Oceanian threatened species of amphibian were proportionately better represented in zoos globally, partly as a result of the sheer numbers of threatened taxa found in other regions.

The tendency to bias collections towards native faunas may align with IUCN (McGowan et al., 2017) and the Convention of Biological Diversity (Glowka et al., 1994) guidance to focus ex-situ activities on local species. However, it is likely that this may be incidental, and the trend actually reflect local availability of species, especially given that a large proportion of turtle taxa are included on an appendix of CITES (CITES, 2022), which increases the complexities in the international move of animals. This may also be the reason for the absence of some genera from zoos; no capacity for, or focus on ex-situ turtle conservation may exist in range, with no logistic or legal ability to move animals outside of range. Collaboration with range states to build capacity in range could address this and provide an avenue to ex-situ conservation without requiring export of animals from range states. Questionnaire-based research might determine whether this is the case. These results align with those of Wahle et al. (2021) for Australian zoos, which typically held regionally native skink species, and for European zoos, which held cosmopolitan collections, but not for North American or Asian collections, which were more cosmopolitan for skinks than we found to be the case for turtles.

As well as assessing turtle holdings in zoos, we also performed analyses comparing species held in zoos with those not held in zoos. This approach can provide additional insight into the selection of species by zoos globally, and the potential conservation value thereof. Species in zoos were more likely to be assessed as Least Concern and less likely to be Not Assessed than those not held in zoos, and had a lower average EDGE score. These findings reinforce the fact that zoos, at a global level, do not bias collections towards threatened or phylogenetically important turtle species. Indeed, the few genera with no species representation in zoos at all (*Cyclanorbis*, *Natator*, *Palea*, *Psammobates*, *Rafetus*, *Rheodytes*, *Rhinemys*, *Vijayachelys*) are mostly small or monotypic, threatened groups. The under-representation of Not Assessed taxa in zoos, compared with those not in zoos, is probably an artefact of lag between species description and IUCN Red List assessment. Tapley et al. (2018) showed that, for amphibians, recently described species are likely to remain unassessed for some time, and this is likely the same for turtles. Zoos are less likely to have access to recently described species due to the length of time involved in sustainably procuring species that are not currently in captivity already, and lack of IUCN Red List assessment may also de-prioritise these taxa in institutional and regional collection planning processes, as well as for funding organisations that may be necessary to initiate ex-situ projects. Additionally, in the case of taxonomic splits, ZIMS records may be slow to be updated accordingly. In amphibians, as a comparison, Biega et al. (2017) showed in a paired approach that there was no difference in threat status between amphibians kept in zoos and closely related species not held in zoos. This indicates a similar situation with regard to threatened species representation, but without bias towards non threatened taxa.

Despite holding one of the highest numbers of turtle species once regional institution numbers are accounted for, European collections hold fewer than expected turtle species, and collections in South America, Asia and Africa hold more than expected species. In their study on skink holdings in zoos, Wahle et al. (2021) also reported the lowest absolute species numbers in African and South American institutions, which they linked to available resources and infrastructure as well as historic circumstances, but do not present an analysis allowing for regional numbers of institutions. Similarly, Ziegler et al. (2016) and Jacken et al. (2020) showed that European and North American collections held large proportions of varanid lizards and amphibian species, respectively, which they attribute to greater resources and historical factors, but also did not correct for numbers of collections in these regions.

For skinks, varanid lizards, amphibians, and turtles alike (where substantial technical knowledge is required for successful husbandry), European zoos are in the unusual position of having a large expertise and resource capacity for maintaining the animals in question, but a relatively small (or in the case of varanids, a total absence of) native fauna on which to practice this expertise. This may contribute to the under-representation of turtles in European collections, but may also be linked to a number of other factors, including public preferences and relative costs of maintenance.

As well as holding fewer species of turtle than predicted by numbers of institutions, Europe specifically did not show bias towards more threatened species (only a tendency to under-represent Not Assessed species, likely for the same reasons as outlined above on the global scale), despite the Shellshock campaign of 2004–5. European collections may over-represent Asian species as a factor of the Shellshock campaign, which had a strong focus on the Asian turtle crisis, the international pet trade of the 1980s and 1990s – which created conditions of ready availability of many Asian turtle species in Europe – and the relatively small number (15 species) of native European species available to provide local focus.

A comparison of turtle populations in European zoos before and after the Shellshock campaign suggests that the campaign is associated with an increase in numbers of turtles held, but no meaningful increase in representation of genera. Data from ZIMS were from the European region, which imperfectly overlaps with EAZA members, as some EAZA members fall outside the ZIMS European region, and some European zoos are not EAZA members. Additionally, the identified link is circumstantial and further research, outside the scope of this study, would be needed to better understand the impact of the Shellshock campaign. If the Shellshock campaign did cause this population increase in zoos, then this would bolster its established success in raising funds for turtle conservation, although the lack of focus on threatened species may dilute the intended impact. The failure to increase diversity of holdings at the genus level may also limit the success of Shellshock in that aspects of phylogenetic diversity still lack captive populations in zoos. In-depth analysis of conservation impact would be needed to understand how the campaign addressed its ultimate goal of addressing the global turtle conservation crisis.

Within those species that are held in zoos globally, we did find evidence of a tendency to afford larger captive population sizes to threatened turtle species. These data align with those presented by Dawson et al. (2016) and Jacken et al. (2020), who showed that threatened amphibian species were afforded increasingly large captive population sizes in zoos. Although the few species that fall into the highest population size category of > 1000 are not threatened, these are represented by taxa that are very common within the pet trade. *Trachemys scripta* (> 7,000 individuals) and *Centrochelys sulcata* (> 2,000 individuals) represent the species with the two highest population sizes and both are commonly rescued or abandoned pet species, as are five others of the nine species in this population size category (Petrozzi et al., 2018; Valdez, 2021).These species are often housed in great numbers by zoos as part of responses to pet welfare and alien species crises. It is unclear if the tendency to afford threatened species with a higher captive population size is related to conservation breeding programmes, but several threatened species with large population sizes include substantial subpopulations registered in range-country institutions that are part of direct conservation breeding initiatives. For example, more than 90 % of ZIMS-registered *Astrochelys yniphora* (Critically Endangered) are housed in a breeding centre in Madagascar. Despite larger populations sizes for threatened species, we found no evidence of higher breeding success, with no difference in proportions of species bred in the last twelve months between threatened and not threatened species. Indeed, across both categories, only about half of all held species had been recently bred. It is possible that this reflects the long lifespan of turtles and finite holding capacity, which necessitates little recruitment in captive populations, but alternatively could reflect the difficulty of successfully breeding many turtle species in captivity.

When considering the trends described here, as well as those presented for other taxa such as skinks (Wahle et al., 2021), monitor lizards (Ziegler et al., 2016) and amphibians (Dawson et al., 2016; Biega et al., 2017; Biega & Martin, 2018; Jacken et al., 2020), it is important to critically appraise several assumptions. These are that a) holding a threatened species in zoos is reflective of conservation value, and b) that, conversely, holding not threatened taxa has lesser, nil or even negative conservation value. Put in another way, does it matter if zoos are not biasing collections towards threatened species? Zoos and similar captive institutions have played key roles in the conservation of a number of species globally (Robovský et al., 2020), and specifically for turtle species (Raghavan et al., 2015; Murphy, 2016a; 2016b). The Ark concept of keeping threatened species safe in captivity only brings long-term conservation value if such populations are eventually able to provide animals to return to the wild. This requires both successful husbandry (and reproduction in most cases) and the mitigation of threats in the field. The vast majority of threatened turtles in captivity are not part of formal or active conservation projects and, beyond safeguarding individuals in captivity, little direct conservation benefit is gained from holding them. For example, Vyas (2006) surveyed holdings of the threatened Indian star tortoise *Geochelone elegans* in Indian zoos and questioned the conservation impact of the sector in that the substantial captive population resulted in no reproduction and that, in many cases, holding institutions had little knowledge about their animals. From our dataset, this may still be the case, as from a population of nearly 750 animals globally, a third are unsexed, and from 260 females only 13 offspring were born in the last 12 months from a species capable of producing multiple clutches of up to ten eggs each annually (Vyas, 2005).

Beyond the Ark, zoo conservation contribution comes not only in the provision of animals for translocation, but includes research to inform on species biology, husbandry requirements and to test field techniques, and engagement with the public to raise awareness and funds. The latter remits are not dependent on holding threatened taxa as they can be conducted using representative not threatened taxa. Recently, there have been some encouraging developments aligned with the one plan approach to conservation (Byers et al., 2013) with the aim of greater collaboration between zoos, aquariums and range state counterparts to further both direct and indirect conservation roles for threatened turtles (e.g. Goetz et al., 2019). However, the approach of looking at zoos as a collective entity, either at global and regional levels, implicitly assumes aligned goals and working practices causing institutions to collaborate – for example, treating captive turtles of a given species as a metapopulation. In reality, varying standards of care, institutional goals, resources and collection plans, and international -, institutional- and individual- level politics prevent this from being a reality and, indeed, zoos may actually act more as competitors than collaborators (Maynard et al., 2020). All this means that species holding data are not a perfect proxy for the conservation value of collections, and the data presented here should be considered just one dimension in estimating the impact of zoos on turtle conservation.

ZIMS is the best available database to understand global and regional trends in holdings of captive turtles, as well as other exotic taxa. However, limitations exist in terms of its comprehensiveness and accuracy. Not all institutions maintaining living collections are registered on ZIMS; among other reasons, the subscription is not free and many institutions may be unable or unwilling to provide the necessary funds. For turtles specifically, there are notable exceptions – for example, the Turtle Conservation Centre in Cuc Phuong National Park is a singularly important turtle collection for conservation in Vietnam, involved in ongoing conservation projects for threatened turtles (e.g. Hoang et al., 2021), but is not registered on ZIMS. Similarly, the Charles Darwin Research Station, which has undertaken decades of captive breeding and conservation work to restore Galapagos Giant Tortoises, is also absent from ZIMS. Moreover, for collections that are registered on ZIMS, taxonomic confusion, difficulty in identification of individuals and incomplete or outdated records are a virtual certainty, although impossible to detect without a fine scale survey of individual zoos at a global level. ZIMS, although rich in information content, is also difficult to extract data from and there are limited options to filter results. This makes finer scale investigations of holding trends logistically impossible. These factors must be taken into consideration while interpreting the data presented here. However, despite these limitations, the sheer scale of the ZIMS database provides an insight into global turtle holdings that would otherwise be impossible to gain.

We suggest the following set of actions that could be adopted by the zoo community in order to have a greater impact from their turtle holdings:

i) conservation prioritisation exercises such as regional collection plans are developed for all turtle species in the near future, so that institutions have more direction with regard to which species they should hold;
ii) holding institutions or regional taxonomic advisory groups should phase out the species with non-viable populations or work with other institutions or regional associations to acquire additional stock to make populations viable;
iii) support for non ZIMS member organisations that maintain turtles for conservation purposes, particularly in low to middle income countries, should be offered, so that the conservation community has a more detailed overview of global turtle holdings;

iv) international collaboration both between zoos and between in-situ conservation organisations to align collection plans with conservation needs and to maximise conservation impact.

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