



Threatened turtles and tortoises (Testudines) in zoos: A ZIMS database analysis for improved One Plan Approach to Conservation actions

PHILIPP GINAL^{1,2}, JADE STAHLBERG³, ANNA RAUHAUS³, PHILIPP WAGNER⁴,
DENNIS RÖDDER¹ & THOMAS ZIEGLER³

¹ LIB, Museum Koenig Bonn, Leibniz Institute for the Analysis of Biodiversity Change, Adenauerallee 127, 53113 Bonn, Germany

² Aquazoo Löbbecke-Museum, Kaiserswerther Str. 380, 40474 Düsseldorf, Germany

³ AG Zoologischer Garten Köln, Riehler Str. 173, 50735 Köln, Germany

³ Institut für Zoologie, Universität zu Köln, Zùlpicher Str. 47b, 50674 Köln, Germany

⁴ Allwetterzoo, Sentruper Str. 315, 48161 Münster, Germany

Corresponding author: PHILIPP GINAL, e-mail: Philipp.ginal@gmx.de

Manuscript received: 24 January 2023

Accepted: 30 May 2023 by MELITA VAMBERGER

Abstract. Turtles and tortoises are one of the world's most threatened vertebrates; more than half of the 352 currently recognised species are threatened. To implement the IUCN CPSP's One Plan Approach to Conservation, we herein analyse the available information from the Zoological Information Management System (ZIMS) to provide an overview of the species already held in zoos. A total of 252 species (71.6%) are currently kept in ZIMS institutions, with 138 of them listed as threatened (76.7% of all threatened turtles). Additional 26 (15 threatened) species are listed in the database Zootierliste (Zoo Animal List). Zoos keep 152 (84.4%) of 180 threatened and 110 out of 150 not threatened species and show a preference for keeping threatened species. Concerning threatened turtle species, nine are represented with more than 500 individuals in zoo collections, while 25 are only kept as single individuals or in same-sex-groups. More than half of the held species are only represented in one to ten zoos. Most species are kept in North America, Europe and Asia, where most of the ZIMS institutions are located. A total of 92 (59 threatened) species (37.1% of all zoo-kept species) were successfully bred in 140 zoos (15.8% of 888 ZIMS-institutions keeping turtles) in the last 12 months. There already exists a tendency towards breeding threatened species. Still, zoos could improve both conservation breeding networking and establish further conservation breeding programs to create reserve populations, which would be in broad fulfilment with the IUCN's One Plan Approach to Conservation.

Key words. Conservation breeding, endangered turtles, ex situ, in situ, protection status, species conservation.

Introduction

Turtles and tortoises (Testudines; hereafter named turtles) are found on all continents (RHODIN et al. 2021) from 56° N to 42° S (STANFORD et al. 2020) where they occupy diverse ecological niches in terrestrial, limnic and marine ecosystems (THOMSON et al. 2021, D'ORTONA & MC-ROBERT 2018). They are a monophyletic order consisting of six superfamilies, 14 families, 97 genera, 352 species and 129 additional subspecies or 486 taxa (RHODIN et al. 2021). Of these, more than half (51.9%) are considered threatened under the IUCN (2022) Red List, making them one of the most vulnerable groups of vertebrates (Turtle Conservation Coalition 2011, LOVICH et al. 2018). Many of the threat statuses are now outdated, at least 35% of the species surveyed are now likely to be in a higher category (Cox et al.

2022) and various other turtle species have not yet been classified at all (RHODIN et al. 2021). Therefore, a recent assessment has even shown that about 60% of the species are threatened (COX et al. 2022)

Turtles are among the key components of many ecosystems (LOVICH et al. 2018, STANFORD et al. 2020), serve as ecosystem engineers (KINLAW & GRASMUECK 2012) and contribute to ecosystem services such as nutrient cycling (THOMPSON 1993, MOSS 2017, HASTINGS et al. 2014), seed dispersal (MOLL & JANSEN 1995, ELBERS & MOLL 2011) and soil quality improvement (HOLE 1981). However, 30.8% of all turtle species suffer massively from poaching by humans. This includes capturing animals and collecting eggs for consumption, for use in traditional medicine and for sale in the pet trade. The capture of adults, especially females, drastically impacts population sizes (PENALOZA et

al. 2013, D'ORTONA & McROBERT 2018, STANFORD et al. 2020). Additionally, only few juveniles survive to reach sexual maturity, which can take between five and 50 years, depending on the species. Moreover, other factors such as climate change (STANFORD et al. 2020), invasive species (CHESSMAN 2021), habitat loss through agricultural expansion and sand mining, habitat fragmentation, urbanisation and deforestation is putting additional pressure on turtle populations (COX et al. 2022). To safeguard turtle populations, many species have been placed under protection and both their poaching and consumption have been banned. Nevertheless, turtles are still frequently taken from the wild for these purposes (PENALOZA et al. 2013). Especially in Asia, demand is very high (HAITAO et al. 2007, 2008, Turtle Conservation Coalition 2018). Populations of highly sought-after species are now down to a few hundred animals and are on the brink of extinction (MANDIMBIHASINA et al. 2018, GONG et al. 2009).

We acknowledge conservation zoos as model zoo, with the zoo at the centre of a web of conservation, research and societal activities (SPOONER et al. 2023). Zoos and aquaria can play a central role in the conservation of turtles, according to the One Plan Approach to Conservation proposed by IUCN's Conservation Planning Specialist Group (CPSG) (BYERS et al. 2013). For instance, they can support on-site conservation measures and can function as modern arks for Critically Endangered species. Zoos and their ex situ approaches can greatly increase the survival rate of eggs and hatchlings (GIBBONS 1987) and surplus is available for release into the natural habitat whenever this should become required (ZIEGLER 2015). It is therefore essential to obtain an overview of the turtle species that have been kept in zoos to-date with focus on their breeding. That way, as was recently analysed, e.g., for amphibians, crocodiles and some lizard groups (ZIEGLER et al. 2016, 2017, JACKEN et al. 2020, WAHLE et al. 2021), potential gaps in ex situ conservation can be identified and new breeding programmes for rare, poorly researched or threatened species can be initiated.

We thus have examined which turtle species are already kept in zoos, which are not yet found in zoos, and how breeding within zoos is shaping up. Furthermore, we test if a global strategy is identifiable, i.e. if threatened species are more frequently kept than not threatened species. In addition, the different geographical ZIMS regions are compared with each other to test for geographic biases.

Material and methods

Species holding data

We obtained a list of all recognized turtle species from Reptile Database on April/08/2022 (UETZ et al. 2022). The species list was cross-checked and updated with RHODIN et al. (2021). Subsequently, the Zoological Information Management Software (ZIMS 2022) was utilized to access data on the turtle species kept in zoos, which comprised the number of individuals kept, the number of institutions, and the

offspring/number of breedings within the last 12 months (dates of access were April/18/2022 and April/19/2022). The ZIMS database does not claim to be up-to-date or complete, as some species are listed under outdated species names. Where available, the data was updated to the currently accepted taxonomy. The ZIMS database divides the origin of the institutes into the six continental regions Africa, Asia, Europe, North America, South America and Oceania. All obtained taxonomic data were analysed on species-level, while subspecies were not considered.

As ZIMS provides no free access and requires the necessary license to use it, the open-access website Zootierliste (Zoo Animal List) was used (ZTL 2022) to identify additional species/holdings. ZTL is a database that records current and past animal holdings of zoos and other public animal holding facilities, such as small private zoos or sanctuaries. The stock of facilities located inside and outside the European Union is entered and updated by registered users. ZTL provides more limited information than ZIMS and covers Europe only, with few exceptions. The data from ZTL thus were only used to evaluate the number of turtle species already kept in zoos and the number of turtle keepers. Further analyses were restricted to the dataset obtained from ZIMS.

Threat status

To determine the threat status for each turtle species, the IUCN Red List was accessed on April/14/2022 (IUCN 2022). Species were classified into three groups based on their IUCN (2022) Red List status: threatened, not threatened and unclassified. Species were considered threatened if they were classified as Vulnerable (VU), Endangered (EN) or Critically Endangered (CR). All species with the status (LC – Least Concern) or potentially endangered (NT – Near Threatened) were classified as not threatened. Species for which there is insufficient data (DD – Data Deficient), whose data have not been evaluated (NE – Not Evaluated) or for which no information has been provided (-) were classified as “Unclassifiable”. None of the species was classified as Extinct in the Wild (EW). However, one species, *Cuora zhoui*, is listed as CR but has never been found in the wild so far. Five species have been extinct since 1500 (EX – Extinct) (Cox et al. 2022) and were therefore not considered in this study.

For 62 species that have not yet been assigned a status according to IUCN Red List, the status could be completed with the support of the Turtle Taxonomy Working Group (TTWG), as they provided data in their taxonomy atlas (RHODIN et al. 2021) whose results have not yet been published. In addition, the status of a further 35 species was determined with the help of the Tortoise and Freshwater Turtle Specialist Group (TFTSG), which operates under the auspices of the IUCN Special Survival Commission (SSC). However, no threat status could be assigned to 22 remaining species and they were therefore excluded from further analyses.

Table 1. Overview of the number of turtle species listed as threatened (VU, EN, CR), not threatened (LC, NT) and “Unclassifiable” by IUCN Red List, and species kept by ZIMS and by ZTL institutions exclusively. Brackets represent percentage.

Database	UN	LC	NT	VU	EN	CR	Number of species total and [%]
ZIMS	4 (1.59)	82 (32.54)	28 (11.11)	48 (19.05)	37 (14.68)	52 (20.63)	252 (100)
ZTL exclusively species	0 (0.00)	8 (30.77)	4 (15.38)	5 (19.23)	5 (19.23)	4 (15.38)	26 (100)
Not in ZIMS	18 (18.00)	28 (28.00)	12 (12.00)	19 (19.00)	9 (9.00)	14 (14.00)	100 (100)
IUCN	22 (6.25)	110 (31.25)	40 (11.36)	67 (19.03)	46 (13.07)	67 (19.03)	352 (100)

Data analysis

Further data processing was carried out with the help of the statistical software IBM SPSS Statistics 28. The observed frequency distributions were checked for their significance by applying the Chi² test. Due to multiple testing, the significance level was adjusted by applying Bonferroni correction.

Results

Species holding data and threat statuses

Of the world’s 352 recent turtle species, over half (180 species, 51.14%) have been classified as threatened (as defined in this study) and 42.61% (150 species) are not threatened (Table 1). A low percentage of 7.07% (22 species) has no precise threat status (“Unclassifiable”) [0.57% (2 species); DD 5.4% (19 species); NE 0.28% (one species)]. Of the 352 turtle species, 252 species are held in 888 ZIMS institutions (see Supplementary document S1). Of these, 138 species (55.65%) are threatened, 110 species (44.35%) are not threatened and four species (1.57%) are “Unclassifiable” (Table 1). The “Unclassifiable” species were excluded from further analyses. According to the Chi² test, the threat status of turtle species kept in ZIMS institutions was not significantly different from the threat status of the recent turtle species (p = 0.114) and therefore ZIMS institutions seem not to focus on threatened or not threatened species concerning their turtle species kept.

According to ZTL, 26 additional species are kept in zoos (14 species threatened, 12 species not threatened). Together, the two databases list 278 species currently kept in zoological institutions. A total of 28 threatened turtle species are listed neither in ZIMS nor in ZTL (see Table 2). Again, the Chi² test revealed no significant difference between the distribution of species listed in IUCN and the species kept in ZIMS and ZTL institutions together (p = 0.094), which indicates that these institutions also seem not to be focussed on threatened or not threatened turtle species. For the following analyses, only species listed in ZIMS institutions were considered (unless otherwise stated).

Table 2. Threatened turtle species not kept in any zoo (ZIMS and ZTL) (n = 28). The population trend is indicated by “↓” as decreasing and by “?” as unknown.

Superfamily/ Species	IUCN status	Pop.-Trend
Cheloidea		
<i>Chelodina kuchlingi</i>	CR	?
<i>Chelodina pritchardi</i>	VU	↓
<i>Phrynops williamsi</i>	VU	↓
<i>Ranacephala hoguei</i>	CR	↓
<i>Rheodytes leukops</i>	VU	?
Chelydroidea		
<i>Kinosternon abaxillare</i>	VU	↓
<i>Kinosternon cora</i>	VU	?
<i>Kinosternon vogti</i>	CR	?
<i>Macrochelys suwanniensis</i>	VU	?
Testudinoidea		
<i>Chersobius solus</i>	VU	?
<i>Cuora yunnanensis</i>	CR	↓
<i>Gopherus evgoodei</i>	VU	↓
<i>Pseudemys alabamensis</i>	EN	?
<i>Trachemys adiutrix</i>	EN	?
<i>Trachemys hartwegi</i>	VU	?
<i>Trachemys medemi</i>	VU	?
<i>Trachemys taylori</i>	EN	↓
<i>Trachemys yaquia</i>	VU	↓
Trionychoidea		
<i>Amyda ornata</i>	VU	?
<i>Chitra vandijki</i>	CR	↓
<i>Cyclanorbis elegans</i>	CR	↓
<i>Cycloderma frenatum</i>	EN	↓
<i>Lissemys ceylonensis</i>	VU	↓
<i>Palea steindachneri</i>	CR	↓
<i>Pelochelys signifera</i>	VU	↓
<i>Pelodiscus variegatus</i>	CR	?
<i>Rafetus euphraticus</i>	EN	↓
<i>Rafetus swinhoi</i>	CR	↓

Frequency of individuals

A total of 27,641 turtles are kept in zoos, of which 7,710 individuals (27.89%) are male, 8,079 are female (29.23%) and 11,852 animals (42.88%) are unsexed. Of all individuals, 18,906 (68.40%) represent threatened turtle species and 8,735 individuals (31.6%) belong to not threatened species. The distribution of the number of individuals between threatened and not threatened species is not significant for all but one category. A significant difference (* $p = 0.003$) is found between the ratio of threatened and not threatened species represented with > 99 individuals in zoos (threatened: 56 species, not threatened: 21 species; Fig. 1B). Of these 77 species, 14 stand out with well over 500 individuals kept in zoos, nine species of which are threatened, and five species are not threatened. The threatened species are *As-*

trochelys radiata (1,429; CR), *A. yniphora* (714; CR), *Centrochelys sulcata* (2,436; EN), *Chelonia mydas* (956; EN), *Geochelone elegans* (738; VU), *Indotestudo elongata* (910; CR), *Malacochersus tornieri* (669; CR), *Testudo graeca* (730; VU), and *T. horsfieldii* (629; VU); the not threatened species are *Chelonoidis carbonarius* (1,559; LC), *Emys orbicularis* (1,684; NT), *Trachemys scripta* (2,065; LC), *Stigmochelys pardalis* (886; LC) and *Testudo hermanni* (1,724; NT).

Distribution across ZIMS institutions and geographic regions

In total, 1144 institutions are registered in ZIMS with 563 in Europe, 339 in North America, 117 in Asia, 71 in Oceania, 32 in South America and 22 in Africa. Across the 888 ZIMS

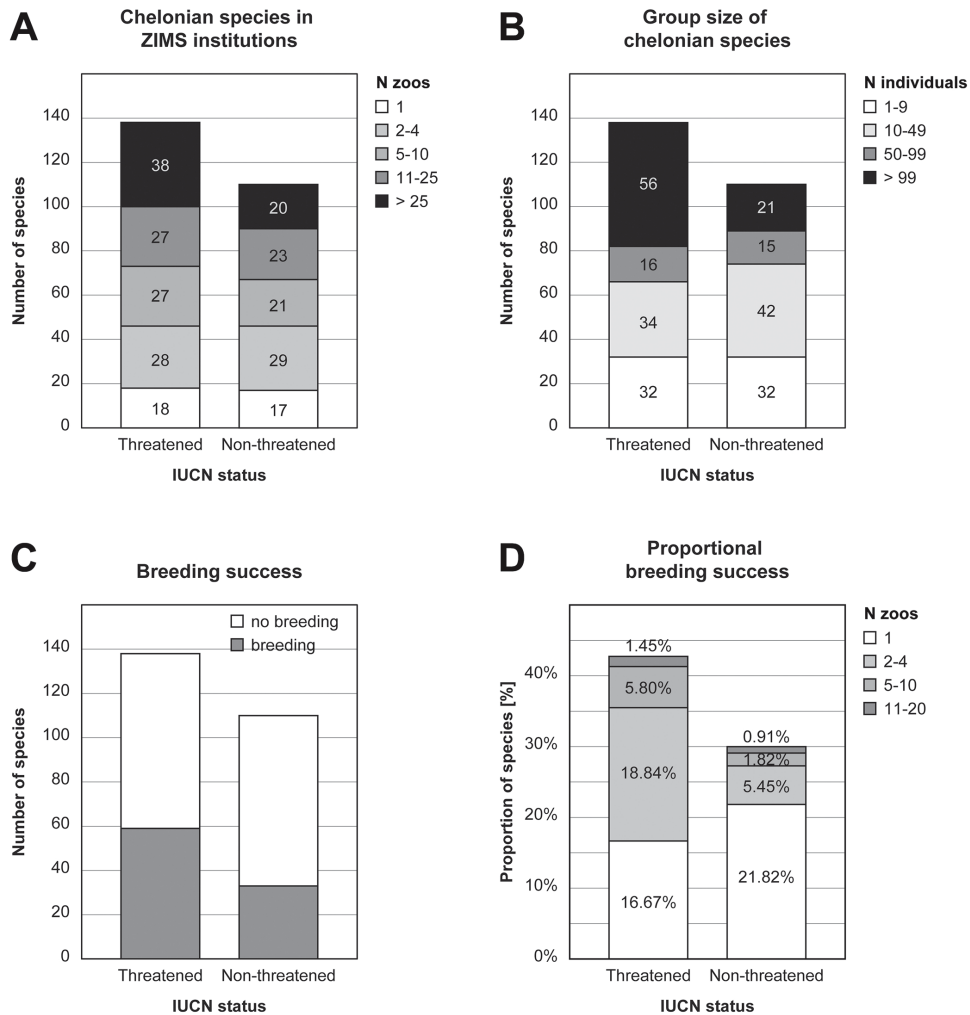


Figure 1. (A) Classification of turtle species according to the number of ZIMS institutions. The different shades of grey indicate whether the species were kept in one zoo (white), 2–4 (light grey), 5–10 (medium grey), 11–25 (dark grey) or > 25 zoos (black). (B) Group sizes of turtle species in zoos. The grey shades indicate how many individuals of a species are kept in zoos (white: 1–9 individuals, light grey: 10–49 individuals, dark grey: 50–99 individuals, and black: > 99 individuals). (C) Breeding in zoos. In grey: species that have bred in the last 12 months; in white: species for which no breeding has been reported. (D) Percentage of breeding in zoos. The different shades of grey show whether a species was bred in one (white), 2–4 (light grey), 5–10 (dark grey) or 11 to 20 zoos (black).

institutions keeping turtles, more than half of all kept turtle species (140 species, 56.45%) are kept in ten zoos or less (Fig. 1A). Some of them are Critically Endangered like e.g., *Cuora picturata* (five zoos), *Cuora zhoui* (six zoos; Fig. 4A), *Cuora aurocapitata* (six zoos) or *Heosemys depressa* (eight zoos). Overall, the distribution across ZIMS institutions between threatened and not threatened species is relatively similar and statistically not significantly different ($p = 0.465$). Overall, species kept in more than 25 zoos proportionally make up the largest group. Five threatened and six not threatened species are kept in far more than 25 (even > 100) zoos. Of the threatened turtles, *Testudo graeca* (132 zoos), *Macrochelys temminckii* (135 zoos), *Testudo horsfieldii* (145 zoos), *Astrochelys radiata* (173 zoos), *Malacochersus tornieri* (153 zoos) and *Centrochelys sulcata* (370 zoos) are distributed across the most ZIMS institutions. Of the not threatened turtles, *Emys orbicularis* (108 zoos), *Trachemys*

scripta (110 zoos), *Chelydra serpentina* (135 zoos), *Testudo hermanni* (164 zoos), *Stigmochelys pardalis* (212 zoos) and *Chelonoidis carbonarius* (275 zoos) are kept in most ZIMS institutions.

Of the 46 threatened turtle species kept in 1–4 zoos, 25 species are kept exclusively as individuals or in same-sex groups (see Supplementary document S1). Also, 15 not threatened species are kept only as individuals (eight species) or in same-sex groups or as single individuals distributed among several zoos (seven species)

For most ZIMS regions, there is a tendency to keep more threatened than not threatened species (Fig. 2A). In Oceanian zoos, the number of threatened and not threatened species is equal. Only South American zoos keep more not threatened (35 species, 68.63%) than threatened species (16 species, 31.37%), thus South American zoos differ significantly ($*p = 0.02$) from all other regions.

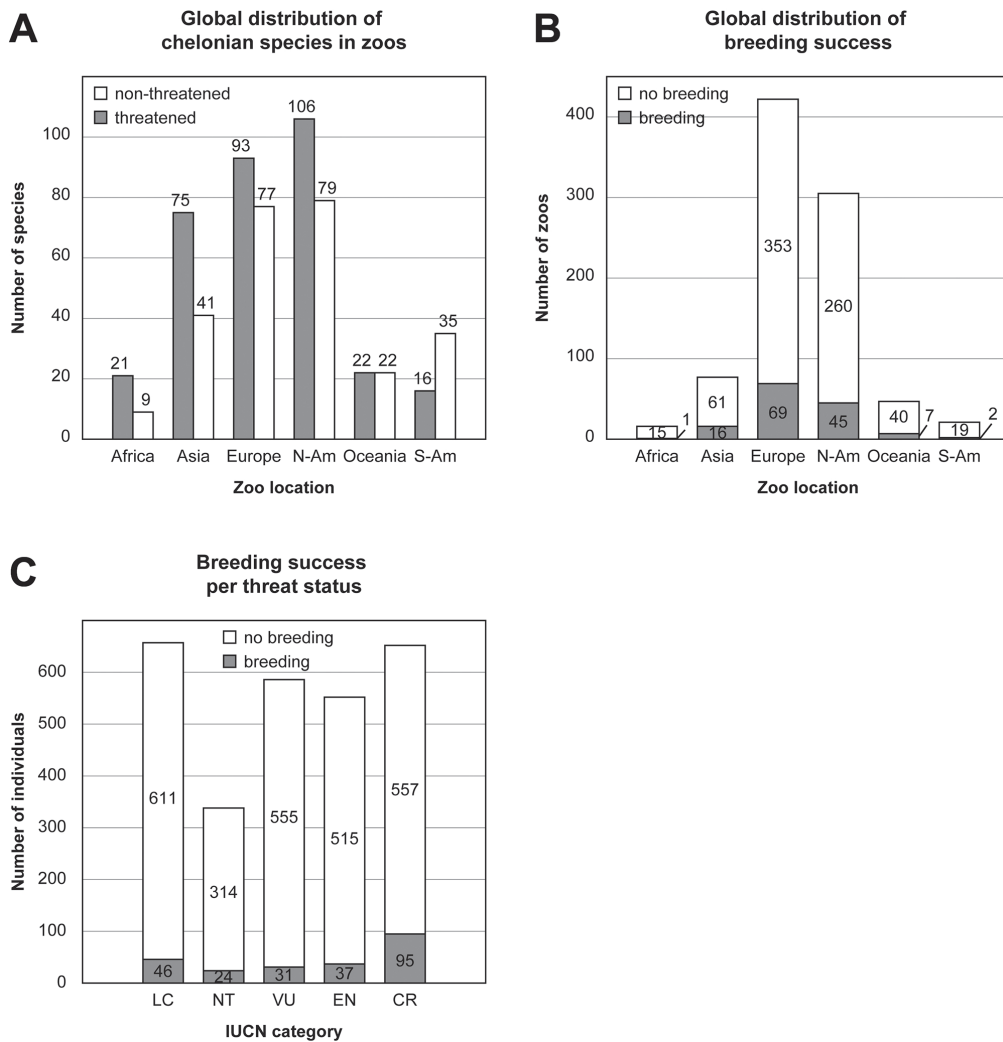


Figure 2. (A) Ratio of threatened (grey) and not threatened turtle species (black) kept in zoos according to the ZIMS regions they are kept (Africa, Asia, Europe, North America, Oceania and South America). (B) Global distribution of breeding in zoos according to the ZIMS regions of the zoos (Africa, Asia, Europe, North America, Oceania and South America) and the number of zoos that were able to successfully breed at least one turtle species within the last 12 months. (C) Breeding by IUCN Red List status.

Breeding

More than one third (92 species, 37.1%) of the 248 species (excluding unclassifiable species) kept in ZIMS institutions were bred within the last 12 months, while for almost two thirds (156 species, 62.9%) no breeding was reported during this time (Fig. 1C+D). Considering all kept species, breeding was achieved for 59 threatened (23.79%) and 33 not threatened species (13.31%). No significant difference ($p = 0.176$) was found in the ratio of breeding between threatened and not threatened species. The 59 threatened species with breeding represent 42.75% of all threatened species in zoos.

A total of 2,785 husbandry groups (= group of individuals of the same species that is kept together at one institution) are kept in zoos [LC: 657; NT: 338; VU: 586; EN: 522; CR: 652]. However, only 233 groups (8.37%) bred within the last 12 months (Fig. 2C). In relation to the other threat status categories, VU and CR differ significantly ($*p < 0.01$) from the other categories concerning breeding.

A total of 140 zoos (15.77%) bred at least one of the species kept (see Fig. 2B). Thereby, the ZIMS regions did not differ significantly from each other in their ratio of institutions with breeding ($p = 0.618$). If the focus is turned to the number of species with breeding and their threat status, no significant difference ($p = 0.181$) was found in the ratio of breeding of threatened and not threatened species among ZIMS regions (see Fig. 3). When comparing the breeding of the different ZIMS regions, the number of juveniles was divided according to their respective threat categories. A significant difference ($*p < 0.001$) was found for all categories (see Fig. 3).

In North American zoos, 570 juveniles of threatened turtles were bred, followed by Asia (280) and Europe (257). Considering not threatened species, 255 juveniles were bred by European zoos, followed by North America (42) and Asia (34) with some distance. Oceanian zoos bred primarily individuals of CR species (124), while other threat categories were underrepresented (Fig. 3). Overall, a tendency to breed CR juveniles was also evident in Asia (107), Europe (154) and North America (259). African and South American zoos both had low breeding numbers in threatened as well as not threatened species (7 and 3 individuals in total; Fig. 3).

Discussion

In general, the percentage of threatened species kept by zoological institutions is considerably higher among the turtles than in other groups such as amphibians (JACKEN et al. 2020), or other non avian reptiles such as monitor lizards (ZIEGLER et al. 2016) and skinks (WAHLE et al. 2021). Among the “reptiles”, turtles are a well-known and largely positively perceived species group for zoo visitors (NEVES et al. 2022) and thus can serve as flagship species for conservation. Several campaigns for turtle conservation have been run by zoos and zoo related associations during the past years, such as the “Shellshock Tortoise and Turtle Campaign” by the European Association of Zoos and Aquaria (<https://www.eaza.net/assets/Uploads/Campaign-factsheets/shellshock0610.pdf>), or the “Zoo Animal of the Year” campaign for Asian box turtles (*Cuora* spp.) by the Zoological Society for the Conservation of Species and Populations (ZGAP, <https://zootier-des-jahres.de/>).

Global breeding success per IUCN category

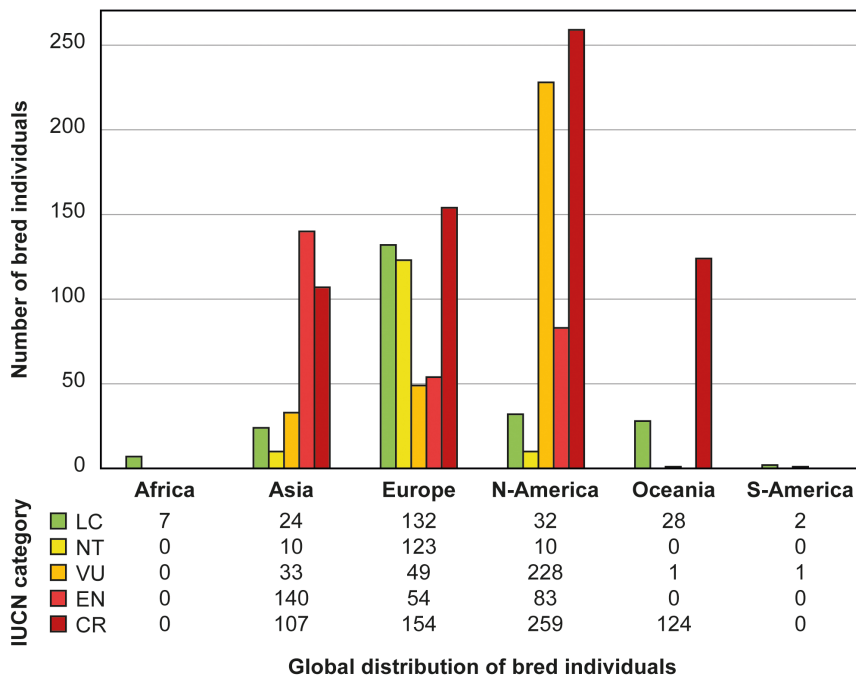


Figure 3. Number of juveniles bred at the respective ZIMS regions divided according to the respective IUCN Red List status.

Concerning the geographic regions, North America, Europe and Asia are the most species-rich ZIMS regions. These regions are all particularly economically strong and the regions with the most ZIMS institutions. Therefore, it might be that there has also been a stronger investment in a species conservation orientation. Interestingly, particularly Europe is the ZIMS region with the lowest native turtle species richness (15 species).

However, zoos still keep many species that are not threatened. Reasons might be that many zoos prefer species that are hardy, easy to handle, and less-demanding in husbandry as ambassadors for use in outreach and education through public contact. Rare or sensitive species may not be appropriate for such programs. Even zoos in areas of turtle diversity generally also display not threatened native species. These species are most likely to be both encountered by visitors and impacted by their actions. By seeing and learning about local species, visitors will hopefully gain a better appreciation for the species living in their own “backyards”, where they can make the greatest difference. Additionally, some zoos may house (and breed) species that are nationally or regionally threatened for local conservation efforts. As just one example, *Apalone spinifer* (globally LC but regionally threatened with only one viable

population in Quebec, Canada) by Zoo de Granby in Canada: <https://zoodegranby.com/en/conservation-and-research/in-the-wild/softshell-turtle>. Furthermore, the overrepresentation of not threatened turtle species may also be due to the longevity of turtles (D’ORTONA & McROBERT 2018). It is possible that many of the not threatened species entered zoo stocks when species conservation was less of a priority (ZIMMERMANN 2010), or that the IUCN Red List category has changed since individuals were obtained (e.g., *Testudo hermanni* which is now listed as Near Threatened, was listed as Vulnerable until 1994; IUCN 2022). But the opposite is also possible as *Indotestudo elongata* (Fig. 4B) was recognized as DD until 1996, as VU in 1996, as EN in 2000 and as CR in 2019. So, some individuals entered the zoos as not threatened species. However, almost half of the captive population is kept in one conservation breeding facility (Angkor Centre for Conservation of Biodiversity, Cambodia) in one of the countries of origin and this species has become a priority species for this and some more holders as a reaction of uplisting on IUCN Red List.

We only analysed on species-level, but some zoo populations might belong to more threatened subspecies (e.g., the subspecies *Testudo h. hermanni* is listed as Endangered, in contrast to *Testudo hermanni* being Near Threatened).

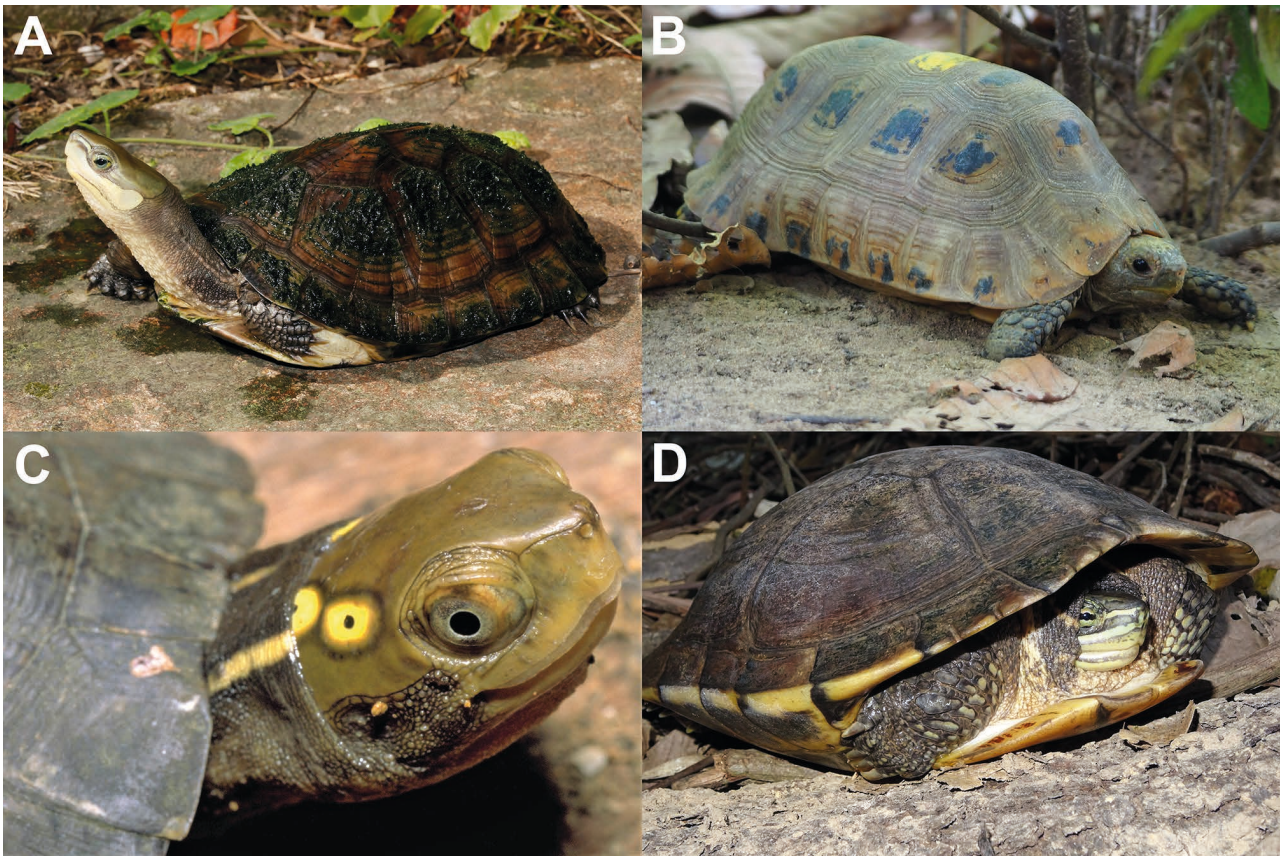


Figure 4. Critically Endangered turtle species: (A) *Cuora zhoui* kept at IZS (Germany; photo: PW), (B) *Indotestudo elongata* kept at ACCB (Cambodia; photo: PW), (C) *Sacalia quadriocellata* from Ha Tinh (Vietnam; photo: TZ) and (D) *Mauremys annamensis* from Melinh Station (Vietnam; photo: TZ).

Additionally, it might be that the databases of some zoos are not up-to-date, some individuals might be misidentified or species are listed under outdated or incorrect names, i.e., if a formerly widely distributed species has been split into several threatened species (i.e., *Pelodiscus sinensis* complex, FARKAS et al. 2019, GONG et al. 2021).

Some threatened species are only kept as single individuals in zoos, while others are over-represented (> 500 individuals). This may be due to the fact that some species are difficult to obtain and, in some cases, to keep, and many zoos prioritise keeping visitor-attractive and easier-to-keep species in their conservation efforts. A particularly visually appealing and readily available species is, for example, the Indian star tortoise (*Geochelone elegans*), which according to ZIMS, is over-represented in zoos worldwide with 738 individuals. Therefore, EAZA, represented by the TAG and the EEP, decided to phase out *G. elegans* in EAZA region in the long term in favour of the Critically Endangered Burmese star tortoise (*Geochelone platynota*).

On the other hand, zoos also have a responsibility in helping authorities taking over confiscated animals, and *Geochelone elegans* is one of the most heavily traded turtle species (VAMBERGER et al. 2019) and the most seized turtle species of the world and thus was recently uplisted from CITES appendix II to appendix I. Another explanation for the over-representation of some species, i.e., *Testudo* spp., *Trachemys scripta*, *Stigmochelys pardalis* etc., might be that these species are easily available in the pet trade and due to the longevity and size of some species, they are often released or offered by overstrained private keepers and finally end as rescued animals not only in sanctuaries and rescue stations but also still in zoos, where they block capacities.

Zoos could not only give more space and expertise to threatened species but also further fulfil their society-building function (ZEGEYE 2017). Here, targeted planning is required for the staffing of zoo facilities with species and, of course, increased networking among zoos, but ideally also between zoos, authorities, nature conservation organisations and private keepers. This is the only way to prevent some threatened species from being over-represented, while others still do not benefit from ex situ protection. The initial focus here should be on highly threatened and micro-endemic species, for which reserve populations should be established – ideally in cooperation with organisations and governments in the country of origin – and distributed across several global facilities as far as possible (ZIEGLER 2015, GONG et al. 2017).

However, especially the extremely rare species are still underrepresented in zoos. The genus *Cuora* is one of the most threatened genera as four of the 13 species are in the top ten and nine in the top 50 most threatened turtle species of the world. *Cuora aurocapitata*, no. nine of the ten most threatened turtles and probably extinct in the wild, is represented by 152 individuals in breeding programs of six institutions. The majority is held by Bronx Zoo with 26 individuals and Allwetterzoo's International Centre for the Conservation of Turtles (IZS; Fig. 5F) with 120 individuals of which 92 are on loan to private keepers.

HORNE et al. (2022) recommended an intensive management of the captive populations, including an exchange of individuals between institutions worldwide, to maintain genetic diversity. This is similar to the situation with *Cuora zhoui* (Fig. 4A), no. 6 of the ten most threatened turtles and again probably extinct in the wild. It is represented by 108 individuals (which is about two third of the global population) kept at six institutions. The majority again is housed in one institution as the IZS holds 22 individuals. However, 67 individuals in this institution are on loan to private keepers. This not only underlines the importance of private keepers, but also the need for more zoos involved in breeding the most Critically Endangered turtles (Fig. 5). Here, the build up and extension of existing conservation breeding networks is crucial.

This is already reflected within the zoo community by the EAZA Regional Collection Plan for Chelonians (GOETZ et al. 2019) focusing on species listed as Critically Endangered and Endangered, mostly from Asia, which are already kept in EAZA institutions. According to the Regional Collection Plan, besides their function as assurance populations, several turtle species can serve as important ambassadors to inform the visitors about the threats and to acquire funds for in situ projects, as well as to gain further knowledge about the successful keeping and breeding of the species.

As a result of the Collection Plan, an increasing number of EAZA ex situ programmes (EEP) for threatened turtle species are built up, e.g. for *Cuora* spp., *Mauremys* spp., *Geochelone elegans* and *G. platynota* as well as *Batagur* spp. and *Indotestudo elongata*. The challenge for many newly created studbooks is genetic uncertainty within the zoo populations that are often kept for decades (especially those held in high numbers which are known to represent a species complex like e.g., *Cuora amboinensis*), both regarding geographical origin and relatedness of individuals. Thus, the first measure for building up a coordinated breeding program often has to be a genetic analysis to clarify which individuals can serve as founders or which ones should not reproduce. This is one of the reasons why studbook keepers recommend breeding stops, even for Critically Endangered species, to avoid inadvertently mixing up conservation units. Whereas the Regional Collection Plans of EAZA have a very strong conservation focus, even partially for species that are not even kept in zoos (i.e., *Speleomantes* ssp., *Lyciasalamandra* ssp.), the Species Survival Plans (SSPs; including regional collection planning and breeding plans) of the Association of Zoos and Aquariums (AZA) prioritize the sustainability of zoo populations rather than conservation status. Therefore, in some cases, the breeding of threatened species is now less intensively managed than non-threatened species.

Overall, the breeding is rather low compared to the frequency with which the species of a threat status category are kept. On the one hand, this could be due to the fact that a total of 40 species are kept exclusively as individuals or in same-sex groups (25 species are threatened) or as the result of an animal management with a low capacity for offspring. Another reason could be that almost half of the

individuals (42.88%) kept in zoos have not yet been sexed and many of the animals are kept in sexually indeterminate groups. Particularly for the threatened species, which are kept as individuals or in same-sex groups in one institution, zoos should use existing resources and advance networking with other institutions to exchange individuals to create breeding pairs or groups. Many turtle species have to be kept solitary even as juveniles and therefore, the space for keeping juveniles and subadults together with a breeding group of adult specimens is limited. Even those centres with larger backup areas like the Angkor Centre for Conservation of Biodiversity (ACCB) in Cambodia are limited in the case of larger species like *Heosemys* spp. (Figs 5A, E). Some zoos contract the space limitations by housing multiple species together. While this may increase carrying capacity, it is not without drawbacks (potential biosecurity/

disease/parasite issues, enclosure retrofitting to make areas equally suitable for multiple different species, possible negative interspecific interactions, etc.).

It must be mentioned that the here provided data comprise of the breeding during the last twelve months and are, therefore, only a short-term reflection. However, as the juvenile phase of many turtles can last for several decades, it could also be that many individuals kept in zoos have not yet reached adolescence and are therefore not yet able to reproduce (D'ORTONA & McROBERT 2018, STANFORD et al. 2020). Further constraints are that some species are difficult to reproduce in husbandry (STERRETT et al. 2015) and other species have breeding restrictions under stud-books. Besides extensive non-breeding recommendations for some EEP-species, limited demand for offspring among EAZA-institutions and restraints to transfer animals out of



Figure 5. (A) Breeding facilities for *Heosemys* spp. at ACCB (Cambodia; photo: PW); (B) breeding facilities for *Geochelone platynota* at Cologne Zoo (photo: AR); (C) release of genetically identified *Pelodiscus variegatus* into breeding facilities of the Melinh Station (Vietnam) for the establishment of a conservation breeding program (photo: CUONG T. PHAM/IEBR); (D) breeding facilities for *Indotestudo elongata* at ACCB (Cambodia; photo: PW); (E) breeding facilities for *Heosemys grandis* at Dau Tieng Station of Wildlife at Risk (WAR; Vietnam), shortly before their reintroduction (photo: TZ); (F) breeding facilities for semi-aquatic turtle species at IZS (Germany; photo: PW).

EAZA might be another crucial reason for decision makers to completely avoid breeding or drastically limit reproduction. In contrast to natural conditions, where extremely high egg and juvenile mortality occurs in turtles, i.e. due to a very low reproduction rate, nest and juvenile predation (STANFORD et al. 2020, GIBBONS 1987), a much higher number of young can be bred under ex situ conditions in most of the species.

There are several examples of species that have been saved from extinction and bred back to a healthy population size by captive breeding colonies. For example, a long-running captive breeding program has restored the population of the Española giant tortoise (*Chelonoidis niger hoodensis*) from 14 to over 2,000 individuals with meanwhile reproduction documented from released individuals in the wild (CAYOT 2021). However, especially due to the generation lengths of turtles, these breeding programmes take time. *Chelonoidis niger hoodensis* took over 40 years to breed a viable population. Similar successes would therefore require rapid action before more turtle species become extinct or habitats are irreparably destroyed (ZIEGLER 2015). Other successful examples are the zoo conservation breeding of the Burmese star tortoise (*Geochelone platynota*) (Fig. 5B), the Northern river terrapin (*Batagur baska*) and the Southern river terrapin (*Batagur affinis edwardmollii*), all Critically Endangered and formerly (almost) functionally extinct in the wild.

For *Geochelone platynota*, more than 16,000 juveniles hatched in assurance colonies in Myanmar for subsequent release, leading to a promising future for the species (PLATT & PLATT 2019). However, due to the political unstable circumstances in Myanmar, the current situation of the population is uncertain. Considering *B. baska*, due to international cooperation of Zoo Schönbrunn, Turtle Island, Turtle Survival Alliance (TSA) and two local stations (Bhawal National Park and Karamjal, Bangladesh) the turtle could breed back from the brink of extinction and more than 340 juveniles could be bred, from those some could be released into the wild (<https://www.zoovienna.at/natur-und-artenschutz/artenschutzprojekt-batagur-baska/>). Combined ex situ programs both in the country and internationally in zoos can help to save species even in case of disease outbreaks in the assurance colonies, natural catastrophes or political unrest (PLATT et al. 2016). *Batagur a. edwardmollii* was thought to be extinct in the wild but is successfully back from extinction in Cambodia as nests have been found in the wild. The eggs have been incubated, partly used for reintroduction but also to establish two ex situ populations at WCS's Koh Kong Reptile Conservation Centre and Allwetterzoo's Angkor Centre for Conservation of Biodiversity (ACCB). Both centres had the first F1 generation in 2022.

Recommendations

Regularly, the Turtle Conservation Coalition provides an updated report of "Turtles in Trouble: The World's

25+ most endangered tortoises and freshwater turtles – 2018". The herein mentioned 50 turtle species provide a solid basis for the most threatened ones, which should also be most urgently prioritised for ex situ breeding programmes in zoos, in combination with the regional collection plans among zoos. In addition, by applying the results of our ZIMS analysis, the 50 ranked turtle species [rank according to a report of the Turtle Conservation Coalition (2018)] were emphasized by using a colour code according to their representation in ZIMS institutions: Green: represented by > 99 sexed individuals and > 9 institutions; yellow: represented either by > 99 sexed individuals and < 10 institutions or represented by < 100 sexed individuals and > 9 institutions; and red: represented by < 100 sexed individuals and < 10 institutions (Supplementary document S2).

For red-emphasized species, we recommend the most urgent ex situ conservation actions, especially for those species, which are not represented in any zoo (i.e. *Cuora yunnanensis*, *Psammobates geometricus*, *Cyclanorbis elegans*, *Ranacephala hogeii*, *Chitra vandijki* and *Chersobius solus*), which are represented by single individuals or same-sex groups only (i.e. *Mesoclemmys dahli* and *Pelochelys cantorii*), and for those species, whose number of individuals is unknown (i.e. *Sternotherus depressus*, *Nilsosonia formosa* and *N. nigricans*). However, this is sometimes due to political regulations, as *Cuora yunnanensis* is only kept by one facility without distributing individuals, even though it is highly recommended to move animals to additional holdings by e.g., HORNE et al. (2022).

For some species, breeding programs within the range countries exist (e.g., for *Astrochelys yniphora* in the Ampijoroa Chelonian Captive Breeding Center in Madagascar, GOETZ 2019). A special case is the Yangtze giant softshell turtle (*Rafetus swinhoei*), which is probably the rarest turtle species in the world, with only two known remaining individuals left (Anonymous 2021, LEE et al. 2021). For this species, urgent intense field surveys (i.e. LE DUC et al. 2020, PHAM et al. 2022) are required to find, catch and transfer possible new individuals to zoos/breeding facilities. This exemplifies that it is crucial to act in due time before it is too late to build up supportive ex situ measures.

A proactive example is the Spotted softshell (*Pelodiscus variegatus*) which represents a threatened but not by the IUCN Red List evaluated species of the *P. sinensis* complex (FARKAS et al. 2019). Strong and fast international networking between scientists, zoos and local breeding stations achieved the establishment of a breeding program and the foundation of reserve populations, a few years after the new species was described, both at the Melinh Station for Biodiversity of the Institute of Ecology and Biological Resources, IEBR, Hanoi and – to minimize risk – at another location in North Vietnam, where the first successful offspring subsequently succeeded. These juveniles are now available for reintroduction and further distribution to stations and zoos to expand the conservation breeding network (see ZIEGLER et al. 2020; Fig. 5C).

Considering the 50 most threatened turtle species (Turtle Conservation Coalition 2018), the majority of those species are native to Asia (29 species), followed by Africa (ten species), North America (six species), South America (three species) and last Oceania (two species). Overall, the majority of the 50 most endangered turtle species are strongly underrepresented in zoos (red: 29 species, yellow: 11 species, green: 10 species), also led by Asian species (red: 18), followed by African, North and South American (each three) and last Oceanian (two) species. Interestingly, African species partially show a very good representation in zoos (green: five of ten species), which might be due to conservation efforts focussed on some Malagasy species (i.e., *Astrochelys radiata*, *Astrochelys yniphora*, *Pyxis planicauda*). Concerning *A. yniphora*, it must be considered that most individuals are kept at the Ampijoroa Chelonian Captive Breeding Center (Madagascar), a center established by Durrell Wildlife Conservation Trust specifically set up to breed and release this species in site (GOETZ 2019). All individuals kept outside of Madagascar derive from confiscations from the illegal pet trade and are kept in low numbers in 11 institutions. This zoo population is managed as a separate conservation unit for biosecurity reasons.

Unfortunately, South American and Oceanian species (three and two, all emphasized red), and partially North American species (red: three, yellow: two, green: one), are strongly underrepresented or even not listed in ZIMS. However, the underrepresentation of some species and regions might be due to that ZIMS predominantly covers zoos, whereas most local ex situ programmes and also some zoos are not registered. For example, since 1989 Perth Zoo (Australia) has had a breeding program for the Critically Endangered Western swamp tortoise (*Pseudemys dura umbrina*), where they bred 800 juveniles from which they released 600 specimens back into the wild (<https://perth-zoo.wa.gov.au/animal/western-swamp-tortoise>). However, considering the IUCN guidelines (MCGOWAN et al. 2017) to focus ex situ programmes on local species, the respective countries/regions that did not participate in conservation breeding programmes of their local turtle species yet, should urgently start to protect their threatened turtle species. However, increased networking with economically strong regions such as Europe, where for example none of the 50 most threatened turtles occurs, but which has capacities, technical know-how and financial support, might be beneficial and necessary for the survival of the most threatened turtle species. However, national or international restrictions/law regulations such as CITES can hamper the transfer of animals among institutions. To enhance this issue, a special CITES system should be developed for zoos and conservation organizations to have easier possibilities for an exchange of individuals of conservation programmes.

Furthermore, zoos must intensify cooperations with private zoos and private holders, if they can provide the species-specific requirements and if they fulfil the specific agreements as this increases space capacities and enhances the exchange of know-how and individuals.

Confiscations can be turned from something bad into something good, if individuals are not only rescued but also used for the buildup of conservation breeding programmes. For example, the Burmese star tortoises (*Geochelone platynota*) in the Cologne Zoo derive from confiscated animals from the illegal pet trade. This chance was used by Cologne Zoo to change their stock to focus more on threatened species and to create a breeding group for this Critically Endangered species (Fig. 5B), which finally led to the establishment of a European ex situ programme/EAZA ex situ programme (RAUHAUS et al. 2021). Allwetterzoos' Angkor Centre for Conservation of Biodiversity (ACCB) in Cambodia has used confiscated individuals of *Indotestudo elongata* from illegal trade on local markets to establish an ex situ population of more than 400 individuals (Figs 4A, 5D). These individuals are now used for a reintroduction in northern Cambodia, managed by ACCB and Rising Phoenix, a Cambodian NGO. This is similar to *Cuora amboinensis* where ACCB holds an ex situ population of several hundred individuals and already reintroduced subadult individuals on local golf courses.

Furthermore, recent examples of genetic screening of confiscated turtles from unknown provenance showed that they were either suitable for direct rewilding or could be used for the previous establishment of managed reserve populations suitable for later release into the wild to support diminished natural populations. Moreover, LE et al. (2020) used a phylogeographic approach for four-eyed turtles (*Sacalia quadriocellata*; Fig. 4C), which can be applied to rewild confiscated specimens or their offspring without the risk of genetic pollution or animals being released into climatically unsuitable areas. And last, recently more than 70 Vietnamese pond turtles (*Mauremys annamensis*; Fig. 4D), a species that is so rare that it has been considered either extinct or functionally extinct in the wild, were confiscated in Hanoi and to resolve whether they are purebred or of hybrid origin, for potential future restocking efforts, the Asian Turtle Program, Cologne Zoo, and Central Institute for Natural Resources and Environmental Studies of Vietnam National University, Hanoi are currently working to assess the origin of these animals using a molecular approach. The three organizations are also collaborating to locate potential areas for future release. It is hoped that these efforts will help to recover the wild population of this Critically Endangered species (Anonymous 2022). These recent examples show, how in the sense of the One Plan Approach to Conservation, international networking between scientists and local institutions can considerably support or even facilitate species conservation.

Acknowledgements

We want to thank MINH D. LE (Hanoi) for providing informative literature and MORRIS FLECKS (Bonn) for his technical support. Moreover, we are grateful to two anonymous reviewers for their critical comments which helped to improve the manuscript.

References

- Anonymous (2021): Discoveries: A new female of the rarest turtle. – *Oryx*, **55**: 323.
- Anonymous (2022): Critically Endangered turtles confiscated in Hanoi. – *Oryx*, **56**: 488.
- BYERS, O., C. LEES, J. WILCKEN & C. SCHWITZER (2013): The One Plan Approach: The philosophy and implementation of CBSG's approach to integrated species. – *WAZA magazine*, **14**: 2–5.
- CAYOT, L. J. (2021): Chapter 21 – Española Island: From near extinction to recovery. – pp. 435–450 in: GIBBS, J., L. CAYOT & W. T. AGUILERA (eds): Galapagos giant tortoises biodiversity of world: Conservation from genes to landscapes. – Academic Press.
- CHESSMAN, B. C. (2021): Introduced red foxes (*Vulpes vulpes*) driving Australian freshwater turtles to extinction? A critical evaluation of the evidence. – *Pacific Conservation Biology*, **28**: 462–471.
- COLLÉONY, A., S. CLAYTON, D. COUVET, M. SAINT JALME & A.-C. PRÉVOT (2017): Human preferences for species conservation: Animal charisma trumps endangered status. – *Biological Conservation*, **206**: 263–269.
- COX, N., B. E. YOUNG, P. BOWLES, M. FERNANDEZ, J. MARIN, G. RAPACCIUOLO, M. GIOVANNI BÖHM, T. M. BROOKS, S. B. HEDGES, C. HILTON-TAYLOR, M. HOFFMANN, R. K. B. JENKINS, M. F. TOGNETTI, G. J. ALEXANDER, A. ALLISON, N. B. ANANJEVA, M. AULIYA, L. J. AVILA, D. G. CHAPPLE, D. F. CISNEROS-HEREDIA, H. G. COGGER, G. R. COLLI, A. DE SILVA, C. C. EISEMBERG, J. ELS, A. G. FONG, T. D. GRANT, R. A. HITCHMOUGH, D. T. ISKANDAR, N. KIDERA, M. MARTINS, S. MEIRI, N. J. MITCHELL, S. MOLUR, C. C. DE NOGUEIRA, J. C. ORTIZ, J. PENNER, A. G. J. RHODIN, RIVAS, A. GILSON, M.-O. RÖDEL, U. ROLL, K. L. SANDERS, G. SANTOS-BARRERA, G. M. SHEA, S. L. SPAWLS, K. A. TOLLEY, J.-F. TRAPE, M. A. VIDAL, P. WAGNER, B. P. WALLACE & Y. XIE (2022): A global reptile assessment highlights shared conservation needs of tetrapods. – *Nature*, **605**: 285–290.
- ELBERS, J. P. & D. MOLL (2011): Ingestion by a freshwater turtle alters germination of bottomland hardwood seeds. – *Wetlands*, **31**: 757–761.
- FARKAS B, T. ZIEGLER, C. T. PHAM, A. V. ONG & U. FRITZ (2019): A new species of *Pelodiscus* from northeastern Indochina (Testudines: Trionychidae). – *ZooKeys*, **824**: 71–86.
- GIBBONS, J. W. (1987): Why do turtles live so long? In natural populations, as in captivity, turtles are among the most long-lived animals. – *BioScience*, **37**: 262–269.
- GLOWKA, L, F. BURHENNE-GUILMIN & H. SYNGE (1994): Ex-situ conservation. – pp. 39–51 in: GLOWKA, L., F. BURHENNE-GUILMIN & H. SYNGE (eds): A guide to the convention on biological diversity. – IUCN, Gland and Cambridge.
- GOETZ, M. (2019): EAZA Best practice guidelines for the ploughshare tortoise, *Astrochelys yniphora*. First edition. – European Associations of Zoos and Aquariums, Amsterdam, The Netherlands.
- GOETZ, M., D. PLAZA, W. VAN LINT, E. FIENIG & N. HAUSEN (2019): EAZA reptile taxon advisory group, Regional Collection Plan for Chelonia. First edition. – European Association of Zoos and Aquaria. Amsterdam, The Netherlands.
- GONG, S-P, A. T. CHOW, J. J. FONG & H.-T. SHI (2009): The chelonian trade in the largest pet market in China: scale, scope and impact on turtle conservation. – *Oryx*, **43**: 213–216.
- GONG, S-P, H. SHI, A. JIANG, J. FONG, D. GAILLARD & J. WANG (2017): Disappearance of endangered turtles within China's nature reserves. – *Current Biology*, **27**: 170–171.
- GONG, Y-A, L.-F. PENG, S. HUANG, Y.-F. LIN, R.-Y. HUANG, Y.-H. XU, D.-C. YANG & L.-W. NIE (2021): A new species of the genus *Pelodiscus* Fitzinger, 1835 (Testudines: Trionychidae) from Huangshan, Anhui, China. – *Zootaxa*, **5060**: 137–145.
- HAITAO, S., J. F. PARHAM, M. LAU & C. TIEN-HSI (2007): Farming endangered turtles to extinction in China. – *Conservation Biology*, **21**: 5–6.
- HAITAO, S., J. F. PARHAM, F. ZHIYONG, H. MEILING & Y. FENG (2008): Evidence for the massive scale of turtle farming in China. – *Oryx*, **42**: 147–150.
- HASTINGS, A. K., J. KRIGBAUM, D. W. STEADMAN & N. A. ALBURY (2014): Domination by reptiles in a terrestrial food web of the Bahamas prior to human occupation. – *Journal of Herpetology*, **48**: 380–388.
- HOLE, F. D. (1981): Effects of animals on soil. – *Geoderm*: 75–112.
- HORNE, B. D., A. D. WALDE & C. M. POOLE (2022): Setting priorities for the conservation of Asia's tortoises and freshwater turtles: A ten-year update. – *ASAP Reports*: **32**.
- IUCN (2022): The IUCN Red List of threatened species. – <https://www.iucnredlist.org/en>.
- JACKEN, A., D. RÖDDER & T. ZIEGLER (2020): Amphibians in zoos: a global approach on distribution patterns of threatened amphibians in zoological collections. – *International Zoo Yearbook*, **54**: 1–19.
- KINLAW, A. & M. GRASMUECK (2012): Evidence for and geomorphologic consequences of a reptilian ecosystem engineer: The burrowing cascade initiated by the Gopher Tortoise. – *Geomorphology*, **157–158**: 108–121.
- LE DUC, O., T. VAN PHAM, T. ZUKLIN, C. BORDES, B. LEPRINCE, C. DUCOTTERD, V. L. QUANG & L. LUISELLI (2020): A new locality of presence for the world's rarest turtle (*Rafetus swinhoei*) gives new hope for its survival. – *Journal for Nature Conservation*, **55**, 125833.
- LE, M. D., T. E. M. MCCORMACK, H. V. HOANG, H. T. DUONG, T. Q. NGUYEN, T. ZIEGLER, H. D. NGUYEN & H. T. NGO (2020): Threats from wildlife trade: The importance of genetic data in safeguarding the endangered four-eyed turtle (*Sacalia quadriocellata*). – *Nature Conservation*, **41**: 91–111.
- LEE M. D., T. E. M. MCCORMACK & T. T. NGUYEN (2021): A new hope for the world's rarest turtle. – *The Tortoise* **2021**: 26–27.
- LOVICH, J. E., J. R. ENNEN, M. AGHA & J. W. GIBBONS (2018): Where have All the turtles gone, and why does It matter? – *BioScience*, **68**: 771–781.
- MANDIMBIHASINA, A. R., L. G. WOOLAVER, L. E. CONCANNON, E. J. MILNER-GULLAND, R. E. LEWIS, A. M. TERRY, N. FILAZAHA, L. RABETAFIKA & R. P. YOUNG (2018): The illegal pet trade is driving Madagascar's ploughshare tortoise to extinction. – *Oryx*, **54**: 188–196.
- MCGOWAN, P. J., K. TRAYLOR-HOLZER & K. LEUS (2017): IUCN guidelines for determining when and how ex situ management should be used in species conservation. – *Conservation Letters*, **10**: 361–366.
- MOLL, D. & K. P. JANSEN (1995) Evidence for a role in seed dispersal by two tropical herbivorous turtles. – *Biotropica*, **27**: 121–127.

- MOSS, B. (2017): Marine reptiles, birds and mammals and nutrient transfers among the seas and the land: An appraisal of current knowledge. – *Journal of Experimental Marine Biology and Ecology*, **492**: 63–80.
- NEVES, J., J. C. GIGER, V. ALVES & J. ALMEIDA (2022): The social representations of zoo goes toward crocodiles and turtles: Structural analysis and implications for conservation. – *Social Sciences*, **11**: 571.
- PENALOZA, C. L., O. HERNANDEZ, R. ESPIN, L. B. CROWDER & G. R. BARRETO (2013): Harvest of endangered sideneck river turtles (*Podocnemis* spp.) in the Middle Orinoco, Venezuela. – *Copeia*, **2013**: 111–120.
- PHAM, T. V., O. LE DUC, C. BORDES, B. LEPRINCE, C. DUCOTTERD, T. ZUKLIN, V. LUU QUANG, D. HA DINH & L. LUISELLI (2022): Female wanted for the world's rarest turtle: prioritizing areas where *Rafetus swinhoei* may persist in the wild. – *Oryx*, **56**: 396–403.
- PLATT S. G., K. PLATT, L. L. KHAING, T. T. YU, S. H. AUNG, S. S. NEW, M. M. SOE, K. M. MYO, T. LWIN, W. K. KO, S. H. N. AUNG & T. R. RAINWATER (2017): Back from the brink: Ex-situ conservation and recovery of the critically endangered Burmese star tortoise (*Geochelone platynota*) in Myanmar. – *Herpetological Review*, **48**: 570–575.
- PLATT, S. G. & K. PLATT (2019): Turtle Survival Alliance and Wildlife Conservation Society work together to avert the extinction of turtles in Myanmar. – *Turtle Survival*, **2019**: 30–35.
- RAUHAUS, A., C. NIGGEMANN, J. NICOLAUDIUS & T. ZIEGLER (2021): Keeping and breeding of the Critically Endangered Burmese star tortoise *Geochelone platynota* in the Cologne Zoo, Germany. – *Sauria*, **43**: 13–26.
- RHODIN, A. G., J. B. IVERSON, R. BOUR, U. FRITZ, A. GEORGES, H. B. SHAFFER & P. P. VAN DIJK (2021): Turtles of the world: Annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status (9th Ed.) Turtle Taxonomy Working Group (TTWG). – Chelonian Research Foundation and Turtle Conservancy, Vermont.
- SPOONER, S. L., S. L. WALKER, S. DOWELL & A. MOSS (2023): The value of zoos for species and society: The need for a new model. – *Biological Conservation*, **279**: 109925.
- STANFORD, C. B., J. B. IVERSON, A. G. RHODIN, P. P. VAN DIJK, R. A. MITTERMEIER, G. KUCHLING, L. LUISELLI, S. HAITAO, S. SINGH, RHODIN, A. G., J. B. IVERSON, R. BOUR, U. FRITZ, A. GEORGES, H. B. SHAFFER, P. P. VAN DIJK & A. D. WALDE (2020): Turtles and tortoises are in trouble. – *Current Biology*, **30**: 721–725.
- STERRETT, S. C., A. J. KAESER, R. A. KATZ, L. L. SMITH, J. C. BROCK & J. C. MAERZ (2015): Spatial ecology of female Barbour's map turtles (*Graptemys barbouri*) in Ichawaynochaway Creek, Georgia. – *Copeia*, **103**: 263–271.
- THOMPSON, M. B. (1993): Hypothetical considerations of the biomass of chelid tortoises in the River Murray and the possible influences of predation by introduced foxes. – pp. 219–224 in: LUNNEY, D. & D. AYERS (eds): *Herpetology in Australia: A diverse discipline*. – Royal Zoological Society of New South Wales, Melbourne.
- THOMSON, R. C., P. Q. SPINKS & H. B. SHAFFER (2021): A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. – *PNAS*, **118**: 1–10.
- Turtle Conservation Coalition (2011): Turtles in trouble: The world's 25+ most endangered tortoises and freshwater turtles – 2011.
- Turtle Conservation Coalition (2018): Turtles in trouble: The world's 25+ most endangered tortoises and freshwater turtles – 2018.
- UETZ, P., P. FREED & J. HOŠECK (2022): The Reptile Database. – www.reptile-database.org, assessed 04/08/2022.
- VAMBERGER, M., C. SPITZWEG, A. DA SILVA, R. MASROOR, P. PRASCHAG & U. FRITZ (2019): Already too late? Massive trade in Indian star tortoises (*Geochelone elegans*) might have wiped out its phylogeographic differentiation. – *Amphibia-Reptilia*, **41**: 133–138.
- WAHLE, A., D. RÖDDER, D. G. CHAPPLE, S. MEIRI, A. RAUHAUS & T. ZIEGLER (2021): Skinks in zoos: A global approach on distribution patterns of threatened Scincidae in zoological institutions. – *Global Ecology and Conservation*, **30**: e01800.
- ZEGEYE, H. (2017): In situ and ex situ conservation: Complementary approaches for maintaining biodiversity. – *International Journal of Research in Environmental Studies*, **4**: 1–12.
- ZIEGLER, T. (2015): In situ and ex situ reptile projects of the Cologne Zoo: Implications for research and conservation of South East Asia's herpetodiversity. – *International Zoo Yearbook*, **49**: 8–21.
- ZIEGLER, T., A. RAUHAUS & I. GILL (2016): A preliminary review of monitor lizards in zoological gardens. – *Biawak*, **10**: 26–35.
- ZIEGLER, T., T. T. NGUYEN, A. V. ONG, C. T. PHAM & T. Q. NGUYEN (2020): In search of the spotted softshell turtle in Vietnam: An implementation of the One Plan Approach. – *WAZA News*, **2020**: 24–27.
- ZIEGLER, T., A. RAUHAUS & F. SCHMIDT (2017): Review of crocodiles in Zoological Gardens with a focus on Europe. – *Der Zoologische Garten*, **86**: 18–40.
- ZIMMERMANN, A. (2010): The role of zoos in contributing to in situ conservation. – pp. 281–287 in: KLEIMAN, D. G., K. V. THOMPSON & C. K. BAER (eds): *Wild mammals in captivity: Principles and techniques for zoo management*, Second Edition. – University of Chicago Press, Chicago.
- ZIMS (2022): Species 360 Zoological Information Software. – <http://www.species360.org/>, assessed 04/14/2022.
- ZTL (2022): Zootierliste. – <https://www.zootierliste.de/>, assessed 04/25/2022.

Supplementary data

The following data are available online:

Supplementary document S1. Threatened turtle species listed by superfamilies kept in ZIMS institutions.

Supplementary document S2. The 25+ (50) most endangered turtle species ranked by the Turtle Conservation Coalition (2018), their IUCN threat status, the ZIMS region where they are native to, the number of individuals in ZIMS institutions and the number of ZIMS institutions where they are kept.

Supplementary document S1. Threatened turtle species (n = 138) listed by superfamilies kept in ZIMS institutions; ↓ – decreasing, ↑ – increasing, ? – unknown. Number of individuals: M: male, F: female, U: undetermined. Species names with an asterisk resemble species that are kept only as single individual or in groups of the same sex per institution, so that breeding success can be excluded in the current constellation.

Superfamily Species	IUCN status	Pop. Trend	Number of individuals (M/F/U)	Number of institutions	Breeding success
Cheloidea					
<i>Acanthochelys pallidipectoris</i> *	EN	↓	2 (0/2/0)	1	0
<i>Chelodina mccordi</i>	CR	↓	405 (78/89/238)	50	58
<i>Elseya albagula</i>	EN	?	3 (1/1/1)	1	0
<i>Elseya branderhorsti</i>	VU	?	27 (5/11/11)	6	0
<i>Elusor macrurus</i>	EN	?	33 (13/7/13)	8	0
<i>Mesoclemmys dahli</i> *	CR	?	1 (1/0/0)	1	0
<i>Mesoclemmys zuliae</i> *	VU	?	1 (0/0/1)	1	0
<i>Myuchelys bellii</i> *	EN	?	2 (0/0/2)	1	0
<i>Myuchelys georgesi</i>	CR	?	185 (24/15/146)	3	60
<i>Pseudemysdura umbrina</i>	CR	?	289 (32/40/217)	3	63
Chelonioidae					
<i>Caretta caretta</i>	VU	↓	313 (19/29/265)	26	0
<i>Chelonia mydas</i>	EN	↓	956 (41/32/883)	40	0
<i>Dermochelys coriacea</i> *	VU	↓	2 (0/0/2)	1	0
<i>Eretmochelys imbricata</i>	CR	↓	54 (6/5/43)	11	0
<i>Lepidochelys kempii</i>	CR	↓	148 (9/12/127)	13	0
<i>Lepidochelys olivacea</i> *	VU	?	4 (0/1/3)	3	0
Chelydroidea					
<i>Dermatemys mawii</i>	CR	↓	6 (1/1/4)	5	0
<i>Kinosternon dunni</i>	VU	?	2 (1/0/1)	1	0
<i>Macrochelys temminckii</i>	VU	?	322 (101/73/148)	135	0
Pelomedusoidea					
<i>Erymnochelys madagascariensis</i>	CR	↓	42 (17/9/16)	12	0
<i>Peltocephalus dumerilianus</i> *	VU	?	10 (0/0/10)	5	0
<i>Pelusios broadleyi</i> *	EN	?	2 (2/0/0)	1	0
<i>Podocnemis erythrocephala</i>	VU	?	25 (13/7/5)	8	0
<i>Podocnemis expansa</i>	CR	?	230 (79/67/84)	36	0
<i>Podocnemis lewyana</i>	CR	?	43 (20/9/14)	2	0
<i>Podocnemis sextuberculata</i> *	VU	?	1 (0/0/1)	1	0
<i>Podocnemis unifilis</i>	VU	?	559 (215/97/247)	72	27
Testudinoidea					
<i>Actinemys marmorata</i>	VU	?	191 (42/23/126)	22	38
<i>Actinemys pallida</i>	VU	?	37 (25/10/2)	4	0
<i>Aldabrachelys gigantea</i>	VU	?	82 (30/28/24)	19	0
<i>Astrochelys radiata</i>	CR	↓	1.492 (479/455/558)	173	62
<i>Astrochelys yniphora</i>	CR	↓	714 (121/192/401)	12	0
<i>Centrochelys sulcata</i>	EN	↓	2.436 (697/523/1.216)	370	107
<i>Chelonoidis chilensis</i>	VU	?	182 (58/44/80)	16	0
<i>Chelonoidis denticulatus</i>	VU	?	452 (109/170/173)	105	19
<i>Chelonoidis niger</i>	VU	?	130 (48/51/31)	43	0
<i>Chersobius boulengeri</i> *	EN	↓	4 (0/1/3)	2	0
<i>Chersobius signatus</i>	EN	↓	8 (4/2/2)	3	1
<i>Clemmys guttata</i>	EN	↓	339 (100/124/115)	71	6
<i>Cuora amboinensis</i>	EN	↓	551 (77/91/383)	52	74

Superfamily Species	IUCN status	Pop. Trend	Number of individuals (M/F/U)	Number of institutions	Breeding success
<i>Cuora aurocapitata</i>	CR	?	65 (12/17/36)	5	11
<i>Cuora bourreti</i>	CR	↓	83 (14/20/49)	14	9
<i>Cuora cyclornata</i>	CR	?	29 (1/3/25)	4	0
<i>Cuora flavomarginata</i>	EN	?	135 (52/52/31)	33	0
<i>Cuora galbinifrons</i>	CR	↓	88 (20/36/32)	24	6
<i>Cuora mccordi</i>	CR	?	132 (25/34/73)	18	19
<i>Cuora mouhotii</i>	EN	↓	60 (14/20/26)	17	1
<i>Cuora pani</i>	CR	?	60 (13/13/34)	14	4
<i>Cuora picturata</i>	CR	↓	43 (8/7/28)	5	1
<i>Cuora trifasciata</i>	CR	↓	238 (41/59/138)	29	0
<i>Cuora zhoui</i>	CR	?	41 (2/16/23)	5	6
<i>Cyclemys atripons*</i>	EN	↓	4 (3/1/0)	2	0
<i>Cyclemys oldhamii</i>	EN	↓	20 (7/10/3)	5	0
<i>Cyclemys pulchristriata</i>	EN	↓	10 (2/4/4)	2	0
<i>Emydoidea blandingii</i>	EN	↓	317 (141/152/24)	28	60
<i>Geochelone elegans</i>	VU	↓	738 (257/263/218)	97	15
<i>Geochelone platynota</i>	CR	↑	270 (93/68/109)	35	63
<i>Geoclemys hamiltonii</i>	EN	↓	349 (74/151/124)	34	4
<i>Glyptemys insculpta</i>	EN	↓	222 (29/43/150)	37	7
<i>Glyptemys muhlenbergii</i>	CR	?	80 (14/10/56)	10	40
<i>Gopherus agassizii</i>	CR	↓	158 (66/49/43)	61	7
<i>Gopherus flavomarginatus</i>	CR	↓	37 (6/5/26)	4	8
<i>Gopherus morafkai</i>	VU	?	23 (8/4/11)	9	0
<i>Gopherus polyphemus</i>	VU	?	155 (50/42/63)	48	0
<i>Graptemys barbouri</i>	VU	↓	37 (6/17/14)	9	1
<i>Graptemys caglei*</i>	EN	↓	7 (2/1/4)	2	1
<i>Graptemys flavimaculata</i>	VU	↓	59 (23/21/15)	9	0
<i>Graptemys gibbonsi</i>	EN	↓	34 (4/1/29)	4	0
<i>Graptemys oculifera</i>	VU	?	7 (3/3/1)	3	0
<i>Graptemys pearlensis</i>	EN	↓	7 (2/5/0)	2	0
<i>Hardella thurjii</i>	EN	↓	14 (9/3/2)	5	0
<i>Heosemys annandalii</i>	CR	↓	228 (67/71/90)	22	5
<i>Heosemys depressa</i>	CR	↓	29 (8/12/9)	7	0
<i>Heosemys grandis</i>	CR	↓	418 (91/98/229)	37	39
<i>Heosemys spinosa</i>	EN	↓	160 (47/44/69)	36	4
<i>Indotestudo elongata</i>	CR	↓	910 (206/214/490)	53	81
<i>Indotestudo forstenii</i>	CR	↓	80 (34/32/14)	13	3
<i>Indotestudo travancorica</i>	VU	?	34 (4/14/16)	2	0
<i>Kinixys erosa</i>	EN	?	41 (10/18/13)	16	3
<i>Kinixys homeana</i>	CR	↓	126 (35/31/60)	25	10
<i>Kinixys lobatsiana*</i>	VU	↓	5 (0/1/4)	2	0
<i>Kinixys natalensis*</i>	VU	↓	6 (0/0/6)	3	0
<i>Kinixys nogueyi</i>	VU	?	22 (6/6/10)	9	7
<i>Kinixys spekii</i>	VU	?	15 (5/2/8)	7	0
<i>Kinixys zombensis*</i>	VU	?	1 (0/0/1)	1	0
<i>Leucocephalon yuwonoi</i>	CR	↓	91 (30/29/32)	13	3
<i>Malaclemys terrapin</i>	VU	↓	535 (36/193/306)	39	129
<i>Malacochersus tornieri</i>	CR	↓	669 (235/234/200)	153	17
<i>Mauremys annamensis</i>	CR	↓	221 (62/76/83)	41	6
<i>Mauremys mutica</i>	CR	↓	177 (20/12/145)	17	0

Superfamily Species	IUCN status	Pop. Trend	Number of individuals (M/F/U)	Number of institutions	Breeding success
<i>Mauremys nigricans</i>	EN	?	37 (7/9/21)	8	0
<i>Mauremys reevesii</i>	EN	?	174 (26/25/123)	46	0
<i>Mauremys sinensis</i>	CR	↓	313 (51/76/186)	45	0
<i>Melanochelys tricarinata</i>	EN	↓	135 (43/22/70)	7	4
<i>Morenia ocellata*</i>	EN	↓	1 (0/0/1)	1	0
<i>Notochelys platynota</i>	VU	↓	10 (6/3/1)	5	0
<i>Orlitia borneensis</i>	CR	↓	146 (50/57/39)	40	3
<i>Pangshura sylhetensis*</i>	CR	↓	1 (0/1/0)	1	0
<i>Pangshura tecta</i>	VU	↓	137 (5/6/126)	9	5
<i>Platysternon megacephalum</i>	CR	↓	48 (8/13/27)	13	15
<i>Sacalia bealei</i>	EN	?	36 (7/9/20)	6	1
<i>Sacalia quadriocellata</i>	CR	↓	72 (16/15/41)	12	3
<i>Siebenrockiella crassicolis</i>	EN	↓	120 (28/33/59)	24	1
<i>Siebenrockiella leytensis</i>	CR	↓	7 (4/3/0)	2	0
<i>Terrapene carolina</i>	VU	↓	363 (75/78/210)	86	39
<i>Terrapene coahuila</i>	EN	↓	66 (19/28/19)	17	1
<i>Terrapene mexicana</i>	VU	?	89 (21/37/31)	6	4
<i>Terrapene triunguis</i>	VU	?	194 (58/80/56)	85	3
<i>Terrapene yucatanana</i>	VU	?	12 (4/3/5)	3	2
<i>Trachemys callirostris</i>	VU	?	137 (15/56/66)	9	0
<i>Trachemys decorata*</i>	VU	?	7 (1/0/6)	3	0
<i>Trachemys gaigeae*</i>	VU	?	3 (0/3/0)	2	0
<i>Trachemys ornata*</i>	VU	↓	39 (0/6/33)	4	0
<i>Trachemys terrapen</i>	VU	?	15 (2/13/0)	1	0
<i>Manouria emys</i>	CR	↓	90 (7/18/65)	14	0
<i>Manouria impressa</i>	EN	↓	26 (7/13/6)	11	2
<i>Pyxis arachnoides</i>	CR	↓	76 (16/16/44)	18	7
<i>Pyxis planicauda</i>	CR	↓	135 (61/43/31)	21	5
<i>Testudo graeca</i>	VU	?	730 (146/162/422)	132	23
<i>Testudo horsfieldii</i>	VU	?	629 (140/178/311)	145	0
<i>Testudo kleinmanni</i>	CR	↓	504 (125/110/269)	70	19
<i>Batagur affinis</i>	CR	↓	222 (23/66/133)	9	0
<i>Batagur baska</i>	CR	↓	484 (36/51/397)	11	0
<i>Batagur borneoensis</i>	CR	↓	193 (55/36/102)	28	11
<i>Batagur kachuga</i>	CR	↓	192 (3/7/182)	3	0
<i>Batagur trivittata</i>	CR	↓	42 (9/12/21)	1	0
Trionychoidea					
<i>Amyda cartilaginea</i>	VU	?	33 (2/4/27)	10	0
<i>Carettochelys insculpta</i>	EN	↓	269 (122/42/105)	93	0
<i>Chitra chitra</i>	CR	↓	5 (2/3/0)	3	0
<i>Chitra indica</i>	EN	?	3 (1/2/0)	1	0
<i>Cycloderma aubryi</i>	VU	↓	4 (2/2/0)	1	0
<i>Nilssonina gangetica*</i>	EN	↓	3 (1/0/2)	3	0
<i>Nilssonina hurum*</i>	EN	↓	2 (1/1/0)	2	0
<i>Nilssonina leithii*</i>	CR	↓	1 (0/0/1)	1	0
<i>Pelochelys bibroni*</i>	VU	?	14 (0/0/14)	1	0
<i>Pelochelys cantorii*</i>	CR	↓	5 (1/0/4)	3	0
<i>Pelodiscus sinensis</i>	VU	↓	107 (23/19/65)	51	0
<i>Trionyx triunguis</i>	VU	↓	28 (6/3/19)	10	0

Supplementary document S2. The 25+ (50) most threatened turtle species ranked by the Turtle Conservation Coalition (2018), their IUCN threat status, the ZIMS region where they are native to, the number of individuals in ZIMS institutions and the number of ZIMS institutions where they are kept. Colour code: Green: represented by > 99 sexed individuals and > 9 institutions; yellow: represented either by > 99 sexed individuals and < 10 institutions or represented by < 100 sexed individuals and > 9 institutions; and red: represented by < 100 sexed individuals and < 10 institutions. An asterisk behind a species name represents a species that is only kept as single individual or in same-sex groups per institution.

Rank	Species	IUCN status	ZIMS region	Number of individuals	Number of institutions
1	<i>Rafetus swinhoei</i>	CR	Asia	0	0
2	<i>Astrochelys yniphora</i>	CR	Africa	714 (121/192/401)	12
3	<i>Cuora yunnanensis</i>	CR	Asia	0	0
4	<i>Batagur baska</i>	CR	Asia	484 (36/51/397)	11
5	<i>Batagur trivittata</i>	CR	Asia	42 (9/12/21)	1
6	<i>Cuora zhoui</i>	CR	Asia	41 (2/16/23)	5
7	<i>Cuora mccordi</i>	CR	Asia	88 (20/36/32)	24
8	<i>Psammobates geometricus</i>	CR	Africa	0	0
9	<i>Cuora aurocapitata</i>	CR	Asia	65 (12/17/36)	5
10	<i>Mesoclemmys dahli*</i>	CR	South America	1 (1/0/0)	1
11	<i>Cyclanorbis elegans</i>	CR	Africa	0	0
12	<i>Cuora trifasciata</i>	CR	Asia	238 (41/59/138)	29
13	<i>Geochelone platynota</i>	CR	Asia	270 (93/68/109)	35
14	<i>Chelodina mccordi</i>	CR	Asia	405 (78/89/238)	50
15	<i>Chitra chitra</i>	CR	Asia	5 (2/3/0)	3
16	<i>Myuchelys georgesi</i>	CR	Oceania	185 (24/15/146)	3
17	<i>Mauremys annamensis</i>	CR	Asia	221 (62/76/83)	41
18	<i>Dermatemys mawii</i>	CR	North America	6 (1/1/4)	5
19	<i>Erymnochelys madagascariensis</i>	CR	Africa	42 (17/9/16)	12
20	<i>Batagur affinis</i>	CR	Asia	222 (23/66/133)	9
21	<i>Batagur kachuga</i>	CR	Asia	192 (3/7/182)	3
22	<i>Leucocephalon yuwonoi</i>	CR	Asia	91 (30/29/32)	13
23	<i>Pseudemydura umbrina</i>	CR	Oceania	289 (32/40/217)	3
24	<i>Ranacephala hoguei</i>	CR	South America	0	0
25	<i>Siebenrockiella leytensis</i>	CR	Asia	7 (4/3/0)	2
26	<i>Podocnemis lewyana</i>	CR	South America	43 (20/9/14)	2
27	<i>Batagur borneoensis</i>	CR	Asia	193 (55/36/102)	28
28	<i>Sternotherus depressus</i>	CR	North America	NA (ZTL only)	NA (ZTL only)
29	<i>Cuora pani</i>	CR	Asia	60 (13/13/34)	14
30	<i>Testudo kleinmanni</i>	CR	Africa	504 (125/110/269)	70
31	<i>Heosemys depressa</i>	CR	Asia	29 (8/12/9)	7
32	<i>Cuora picturata</i>	CR	Asia	43 (8/7/28)	5
33	<i>Pyxis planicauda</i>	CR	Africa	135 (61/43/31)	21
34	<i>Chitra vandijki</i>	CR	Asia	0	0
35	<i>Mauremys nigricans</i>	EN	Asia	37 (7/9/21)	8
36	<i>Chitra indica</i>	EN	Asia	3 (1/2/0)	1
37	<i>Terrapene coahuila</i>	EN	North America	66 (19/28/19)	17
38	<i>Astrochelys radiata</i>	CR	Africa	1.492 (479/455/558)	173
39	<i>Cuora bourreti</i>	CR	Asia	83 (14/20/49)	14
40	<i>Cuora galbinifrons</i>	CR	Asia	88 (20/36/32)	24
41	<i>Pyxis arachnoides</i>	CR	Africa	76 (16/16/44)	18
42	<i>Gopherus flavomarginatus</i>	CR	North America	37 (6/5/26)	4
43	<i>Glyptemys muhlenbergii</i>	CR	North America	80 (14/10/56)	10
44	<i>Chersobius solus</i>	VU	Africa	0	0
45	<i>Nilssonina formosa</i>	CR	Asia	NA (ZTL only)	NA (ZTL only)
46	<i>Nilssonina nigricans</i>	CR	Asia	NA (ZTL only)	NA (ZTL only)
47	<i>Pelochelys cantorii*</i>	CR	Asia	5 (1/0/4)	3
48	<i>Malacochersus tornieri</i>	CR	Africa	669 (235/234/200)	153
49	<i>Gopherus agassizii</i>	CR	North America	158 (66/49/43)	61
50	<i>Cuora cyclornata</i>	CR	Asia	29 (1/3/25)	4