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Ex situ population of *Aldabrachelys gigantea* (Reptilia: Testudines) in the European Association of Zoos and Aquaria and its perspectives: Hidden extinction and how to prevent it

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Abstract. For the needs of adequate management, we carried out an assessment of the *Aldabrachelys gigantea* (Schweigger, 1812) population in the institutions of the European Association of Zoos and Aquaria. This population was established a hundred years ago and is continuously growing. Today it is the largest *ex situ* population of all regional zoo associations. Currently it has 402 individuals, including animals aged over 100 years (up to 162 years). However, our study shows that this increase is depending on the import of individuals from outside sources. The longevity of this species and the relatively low mortality rate in the population makes this process very slow, so that it goes unnoticed. Our predictions show that without imports, this population would become extinct in the long term unless existing natality increases. If there is no change in the reproductive rate (and there is no import), within 20 year the population will drop from current 402 to approx 280 individuals. To maintain current population size 8–9 hatches/year are needed. However, the successful reproduction of *A. gigantea* in EAZA remains an exceptional event. Our analysis of the demographic and genetic status shows that it has enormous potential. If it was used, the population would have a very long-term perspective secured. Achieving this goal will mean significant improvements in husbandry practices, the issues of which we outline.

Key words. Conservation, demography, European *Ex situ* Programme, population assesment, studbook, zoo biology, giant tortoises, Aldabra.

INTRODUCTION

The Aldabra giant tortoise, *Aldabrachelys gigantea* (Schweigger, 1812) is, next to the Galapagos tortoise, *Chelonoidis niger* (Quoy et Gaimard, 1824), the largest representative of recent tortoises (Fig. 1). The largest individuals of the Aldabra giant tortoise reach a straight carapace length of 140 cm and a weight of around 300 kg (record 363 kg) (Pritchard 1979, White 2015). The current occurrence of giant tortoises exclusively on remote islands leads to the often stated view that their considerable body size is a product of insular gigantism (in accordance with Foster's rule). However, this contradicts the existence of a number of species of fossil giant tortoises on the continents. In the case of giant tortoises, rather than being a product of insular gigantism, the large body size is an advantageous adaptation for island colonization (overseas dispersal) (for details see Rehák 1997)

The intraspecific taxonomy and nomenclature of the Aldabra giant tortoise has been the subject of much controversy (Frazier 2006, 2009, 2010, Fritz & Havas 2007, Rhodin et al. 2021). According to the decision of the International Commission on Zoological Nomenclature (ICZN 2013), the correct species name is "*gigantea*". It is currently classified as a polytypic species with

Fig. 1. *Aldabrachelys gigantea* (Schweigger, 1812) – male (top) attempting to mate with female (bottom), Prague Zoo. Photo by PV.

four recognized subspecies (Rhodin et al. 2021): *Aldabrachelys gigantea gigantea* (Schweigger, 1812), *A. g. daudinii* (Duméril et Bibron, 1835) (extinct ca. 1850), *A. g. hololissa* (Günther, 1877) (extinct in the wild), and *A. g. arnoldi* (Bour, 1982) (extinct in the wild). The autochthonous occurrence of the nominotypical subspecies is on Aldabra atoll (terra typica of the species) north of Madagascar, the other subspecies are from the granitic Seychelles. Their classification is based on morphology (Gerlach 2011). However, genetic studies (Palkovacs et al. 2003, Balmer et al. 2011, Çilingir et al. 2022) show very low genetic intraspecific differentiation in *A. gigantea* and do not support the distinction of subspecies.

An important island area with the occurrence of giant tortoises are the islands east of Africa, where, until the arrival of man, many species of giant tortoises existed as a result of overseas dispersal (Arnold 1979, Austin et al. 2003, Kehlmaier et al. 2023). According to current ideas (Kehlmaier et al. 2023), there were two different independent basic colonizations of this island world in Western Indian Ocean. While the first of them (Eocene) led to the settlement of the Mascarenes by giant tortoises of the genus *Cylindraspis* Fitzinger, 1835, the second colonization led first (Upper Eocene/Oligocene) from the African continent to Madagascar, where a radiation occurred that resulted, among other, in the emergence of giant tortoises of the genus *Aldabrachelys* Loveridge et Williams, 1957. This was followed by the colonization by tortoises of this genus of the granitic Seychelles (Lower Pliocene) and from there, relatively recently (Upper Pliocene), repeatedly of Aldabra Atoll.

Giant tortoises were extremely successful on the colonized islands. Their individual island populations were very abundant. By intensive grazing and browsing, giant tortoises conditioned the existence of plant species highly specialised for the intense pressure (dwarf plant species adapted to grazing and unable to survive without grazing, in other plants defensive elements like spines, heterophylly, unpalatability) from tortoises and determined the character of island ecosystems (Bourne 1977, Coe et al. 1979, Swingland & Coe 1979). The arrival of humans in the tortoise island world was a disaster for giant tortoises. On almost all the islands, the giant tortoises were quickly exterminated, and with the extinction of key species, native ecosystems collapsed.

Giant tortoises of the Western Indian Ocean islands only survived in a single species (*Aldabrachelys gigantea*) on the remote Aldabra. Even there, at the end of the 19th century, the tortoises faced an imminent threat of extinction, which was averted literally at the last moment. Tortoise hunting was banned and their population gradually recovered. After a very dramatic conservation history (for details see Rehák 1997), Aldabra Atoll has been strictly protected since 1970s and is home to a large population of *A. gigantea* estimated at around 150,000 (Bourn 1977, Coe et al. 1979). Aldabra giant tortoises are extremely efficient grazers (the special snout morphology allows them to graze vegetation extremely close to the ground surface – Fig. 2) and browsers (due

Fig. 2. *Aldabrachelys gigantea* (Schweigger, 1812) – the distinctive head morphology is an adaptation for efficient grazing and intake of hard-to-reach water. Photo by PV.

to their extremely stretchable neck and the ability to lift the body high) and are of fundamental importance in the ecology of Aldabra. On Aldabra the biomass of *A. gigantea* reaches 58 t/km² and tortoises consume 12 million kg of plant matter per year (Coe et al. 1979, Swingland et Coe 1979, Lovich et al. 2018). Their high abundance has a key role in rejuvenating and maintaining the local unique ecosystem not only through grazing and browsing, but also tortoise movements.

Today, in adition to former deliberate introductions of the Aldabra giant tortoises as attractions or to create their insurance populations (e.g. Bird, Cousin, Curiese, and Fregate islands), there are several projects that use introduced *A. gigantea* as ecological engineers to help restore the original ecosystems (Hansen et al. 2010, Gerlach et al. 2013). They should replace extinct species in their complex role as key species of their ecosystems to reverse a devastating impact on the respective ecosystems caused by the extermination of native tortoise species. In an effort to rewild and restore island habitats and to achieve special goals (such as facilitating germination of seeds of endangered and disapearing plant species after passing through the digestive tract of tortoises), giant tortoises were intentionally introduced to some islands like Madagascar or Round Island (Andriantsaralaza et al. 2013, Falcon & Hansen 2018, Pedrono et al. 2020).

With their big size, the Aldabra giant tortoises are attractive animals of exceptional educational value in zoos and are traditionally extremely popular with visitors (Murphy 2016, Fig. 3). However, keeping them in human care also has a research dimension by enabling research activities

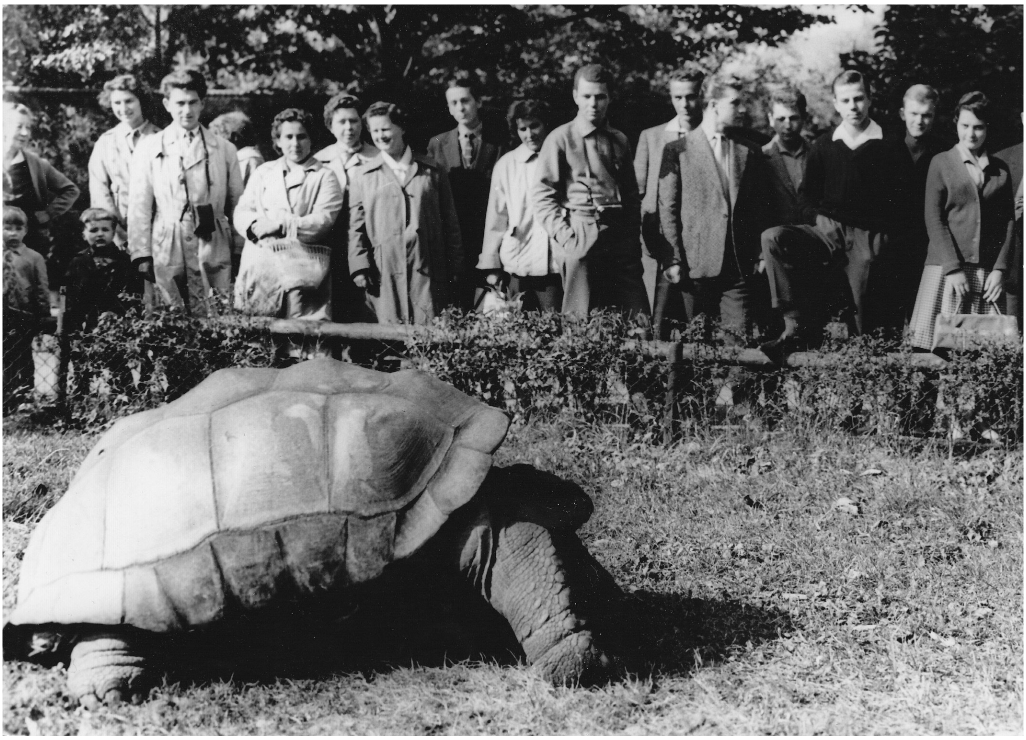

Fig. 3. Large tortoises have always been of great interest to visitors - the first Aldabra giant tortoise (male) came to Prague Zoo on 30 December 1948 and died on 28 July 1976. © Czech News Agency, Prague Zoo Archive.

that are difficult to carry out in the field and a potential for conservation as an insurance *ex situ* out range population. For example, we can imagine a threat to wild populations in the form of sea level rise or climate change (with a significant impact on the sex ratio in this oviparous species, where the sex of the individual is determined by incubation temperature). Due to the longevity of tortoises, genetically very valuable individuals, including carriers of genetic combinations that no longer occur in wild, can be kept in human care. According to the last IUCN Red List assesment, the wild population of *A. gigantea* is listed as Vulnerable (TFTSG 1996).

From the above it is obvious that due care should be given to management of *A. gigantea* in human care. Therefore, in line with the modern concept of the conservation strategy (the One Plan Approach to Conservation), the European Association of Zoos and Aquaria (EAZA), which maintains the largest *ex situ* population of any regional zoo association, at the suggestion of its Reptile Taxon Advisory Group (RTAG; chaired by Ivan Rehák), has adopted the highest level of management (EAZA Ex situ Programme – EEP) for *A. gigantea* (Goetz et al. 2019). This EEP (coordinated by Ivan Rehák) also maintains an EAZA studbook for *A. gigantea*.

In this paper, we present a demographic and genetic assessment of the current population status of *A. gigantea* in the EAZA, a prediction of its future development and corresponding management measures. In this context, we also outline best management practices for this biologically and culturally remarkable species.

The paper is dedicated to Professor Daniel Frynta (Charles University, Prague) on the occasion of his 60th birthday.

MATERIAL AND METHODS

Studbook

Input data for all analyses used are from the *A. gigantea* EAZA EEP studbook, kept by Ivan Rehák, assisted by Veronika Zahradníčková. Currently (23 May 2023) this studbook records 674 (208 males, 265 females, 201 sex unknown) specimens of *A. gigantea* from 100 institutions. Of these, 453 (139.172.142) specimens are alive and are located in 82 institutions. Of these, 402 (122.159.121) specimens from 64 EAZA zoos belong to the EAZA *ex situ* population managed under the *A. gigantea* EEP.

Each specimen in the studbook is assigned an identification number (Studbook ID) and a Global Accession Number (GAN). For each specimen in the studbook, we collect the following basic data based on reports from individual institutions: date of birth, location of birth, parents, sex, age, current and past locations and local identifications, transfers and transfer dates, and in the case of death of the specimen, the date of death. If possible, additional data (e.g. reproductive biological data, husbandry data, individual markings, causes of death, ownership, permits) are collected. Where exact data on dates of birth or dates of transfers are not known, they are given on the basis of a qualified estimate according to the available related information.

Studbook data were originally computerized by the Single Population Analysis and Record Keeping System (SPARKS) program, developed by the then International Species Information System (Scobie & Bingaman Lackey 2012), currently are processed by the Species360 Zoological Information Management System (ZIMS) – ZIMS for Studbooks (*Aldabrachelys gigantea*. Rehak, I.). Species360 Zoological Information Management System.

Population assessment and predictions

Population census, demographic analysis and genetic analysis were performed using the ZIMS for Studbooks (*Aldabrachelys gigantea*. Rehak, I., 16 and 23 May 2023). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org, and using the Software for Demographic and Genetic Analysis and Management of Pedigreed Populations (PMx; Balou et al. 2011, 2022, Lacy et al. 2012). Stochastic population projections were performed using the PMx (input data exported from ZIMS for Studbooks). Reproductive parameters were estimated using the ZIMS for Studbooks.

Definitions of terms and variables

Age distribution – shows an age pyramid figure and the number of animals in each age and sex class.

Census – shows census data (number, by sex, of births, deaths, imports, exports, captures and releases) over time.

Founder – an animal from a source (e.g., wild) population that actually produce offspring and has descendants in the living derived (e.g., captive) population and has no known relationship to any individuals in the derived population (except for its own descendants).

Founder Genome Equivalents (FGE) – the number of wild-caught individuals (founders) that would produce the same amount of gene diversity as is present in the living, descendant population.
Founders – a list of the animals at the top of the pedigree that have contributed genetically to the selected living population.
Gene diversity (GD) – the proportional gene diversity (as a proportion of the source population) is the probability that two alleles from the same locus sampled at random from the population are not identical by descent from a common ancestor. Gene diversity is calculated from allele frequencies, and is the heterozygosity expected in progeny produced by random mating, and if the population were in Hardy-Weinberg equilibrium.
Inbreeding Coefficient – probability that the two alleles at a genetic locus are identical by descent from an ancestor common to both parents. An individual's inbreeding coefficient is equal to the kinship coefficient of its parents.
Kinship Coefficient – the probability that at a given locus, an allele sampled from one individual is identical by descent to an allele sampled at random from that locus in a second individual.
Kinship Matrix – the pairwise coefficients of kinship (coancestry) for all animals.
Kinship Value (KV) – the weighted mean kinship of an individual, with the weights being the reproductive values of each of the kin. An individual with mostly old, nearly post-reproductive kin will have a low KV, while an individual with many young kin of breeding age will have a high KV.
Lambda (λ) – percent of population change per year. If lambda <1, Population is declining lambda =1, Population is stationary, lambda >1, Population is increasing.
Mean Inbreeding – mean inbreeding is the average of the inbreeding coefficients among the living individuals. The mean inbreeding coefficient of a population will be the proportional decrease in observed heterozygosity relative to the expected heterozygosity of the founder population.
Mean Kinship (MK) – the mean kinship coefficient between an individual and all individuals (including itself) in the living, captive-born population. The mean kinship of a population is equal to the proportional loss of gene diversity of the descendant (captive-born) population relative to the founders and is also the mean inbreeding coefficient of progeny produced by random mating.
% Pedigree known – percent of an individual's genome that is traceable to known group of founders. Thus, if an individual has an UNK sire, the % Known = 50.
Potential Founders – living individuals that have no living relatives in the population but have the potential to reproduce and contribute to the population.
Potential Gene Diversity – potential GD of the population if optimal reproduction of potential founders were to be achieved.
Projections – shows a deterministic or stochastic projection of the population. Deterministic projections are derived by applying fecundity and survival rates to the number of individuals in each age-sex class, and iterating across years. For stochastic projections, an individual-based simulation is run in which each individual survives with the probability determined by its age and sex, and number of offspring produced by each female is sampled from a Poisson distribution with the mean set to the age-specific fecundity, under the constraint that there must be sufficient adult males available for the breeding females. Deterministic projections are adequate for large populations (those with 1000s of individuals), but stochastic projections are more realistic for smaller population size, as skewed sex ratio and other chance events will typically depress and cause large variation in population growth. The stochastic projection graph in PMx shows the mean and 95 percentiles over all simulations.
Seasonality – presents births by month in a chart.

RESULTS

Census

The *ex situ* population of the Aldabra giant tortoise in Europe starts in 1923 with two individuals. It did not increase in size until the post-war years, when it grew by another 10 imported individuals between 1947 and 1955. The size of the population is continuously increasing from a long-term perspective, and at an accelerating pace in the last period: 1975 – approx. 50 individuals, 1985 – approx. 100 individuals, 1995 – approx. 150 individuals, 2005 – approx. 200 individuals, 2010 – approx. 250 individuals, 2015 – approx. 300 individuals, 2020 – almost 400 individuals (23 May 2023 – 402 individuals; Fig. 4). This is the largest *ex situ* population of all regional zoo associations (Table 1).

The representation of both sexes has been relatively balanced over the long term, but recently there has been a greater increase in females and also in individuals of unknown sex, so that the current (23 May 2023) population of *A. gigantea* in EAZA consists of 122 males, 159 females and 121 individuals of unknown sex (Fig. 5). Until the breakthrough year of 2009, the population

Table 1. Demographic and genetic data for *Aldabrachelys gigantea* (Schweigger, 1812) population in EAZA and in EAZA with the addition of the population of Stefan Merz, cooperating private breeder. Table compiled using ZIMS for Studbooks (*A.gigantea*. I. Rehak, 23 May 2023) data and PMx analyses. *Ex situ* population sizes in other regional zoo associations are shown for comparison (according to ZIMS Species holding report for *Aldabrachelys gigantea*). As of 23 May 2023

	EAZA	EAZA + Stefan Merz
population size	402 (122.159.121)	410 (124.164.122)
number of institutions	64	65
captive hatches/year 2018	9 (Taipei)	9 (Taipei)
captive hatches/year 2019	0	0
captive hatches/year 2020	0	0
captive hatches/year 2021	0	4 (Merz)
captive hatches/year 2022	13 (0.0.13) (Beauval)	27 (0.0.27) (Beauval, Merz)
captive hatches/ 1. 1 – 23. 5. 2023	1 (0.0.1) (Beauval)	2 (0.0.2) (Beauval, Merz)
captive deaths/year 2018	5 (2.3.0)	5 (2.3.0)
captive deaths/year 2019	10 (3.2.5)	10 (3.2.5)
captive deaths/year 2020	5 (1.2.2)	5 (1.2.2)
captive deaths/year 2021	6 (2.3.1)	6 (2.3.1)
captive deaths/year 2022	11 (4.6.1)	11 (4.6.1)
captive deaths/ 1. 1 – 23. 5. 2023	7 (2.4.1)	7 (2.4.1)
lambda (excluding 2023)	0.894	0.962
No.of hatches/y to maintain the pop.	8 to 9	8 to 9
founders	1	1
potential founders	62	62
% pedigree known	17.3%	16.9%
GD based on kinship matrix	0.461	0.461
GD potential	0.992	0.992
population mean kinship	0.538	0.538
founder genome equivalents (FGE)	0.93	0.93
potential FGE	63	63
mean inbreeding	0	0
population in other regions	Africa	47 (8.20.19) at 3 inst.
	Asia (excl. EAZA members)	112 (36.43.33) at 25 inst.
	Australia and Oceania	31 (9.11.11) at 7 inst.
	North America	270 (102.88.80) at 76 inst.
	South America	4 (2.2.0) at 1 institution

grew mainly due to imports of wild-born animals. Since then, the increase in the population has been driven mainly by animals born in human care (Fig. 6).

However, the results of demographic analyses shows that the growth of the *A. gigantea* population in EAZA is mainly due to imports of individuals (whether born in the wild or in captivity) from sources outside the EAZA. Reproduction of *A. gigantea* within EAZA institutions is minimal and natality is less than mortality (Table 1).

Projections

Although *A. gigantea* is very long-lived (see below) and the mortality rate in the EAZA population is not high, the prediction of its future according to the stochastic projection shows that if there is no change in the reproductive rate (and there is no import), within 20 year the population will drop from current 402 to ca. 280 individuals. The deterministic prediction shows a more moderate decline (to about 300 individuals; Fig. 7).

The deterministic approach can provide accurate results in case of sufficient data and large population. In our case, the data are insufficient (pedigree known 17.3% – see Table 1) and therefore

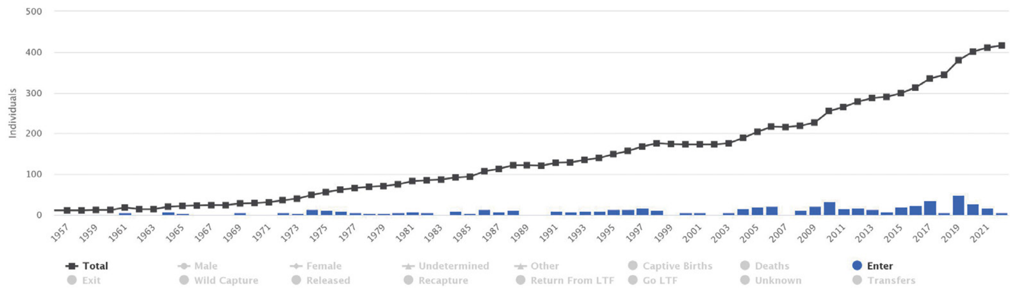

Fig. 4. *Aldabrachelys gigantea* (Schweigger, 1812) population development. Changes in population size (total) over the years (enter = addition to the population in the respective year). Graph constructed using ZIMS for Studbooks (*A. gigantea*, I. Rehak, 16 May 2023).

we consider the stochastic projection more reasonable. The stochastic projections approach takes in consideration stochastic elements (as variation in reproduction and survival of each individual) and uses multiple iterations (500 iterations by default) to calculate the result. The result reflects the range of variation around the mean using confidence intervals, and, therefore provides more realistic projection. Default birth ratio for stochastic projections is 0.50. To maintain current population size 8–9 hatches/year are needed (Table 1).

The alternative predictions (Figs. 8–9) show how each single institution with successful giant tortoise reproduction affects the future evolution of the entire population. The population in EAZA excluding the Asian member Taipei Zoo, where giant tortoise breeding has occurred (see Table 1) will drop from 373 to approx 240 individuals in 20 years according to stochastic projections,

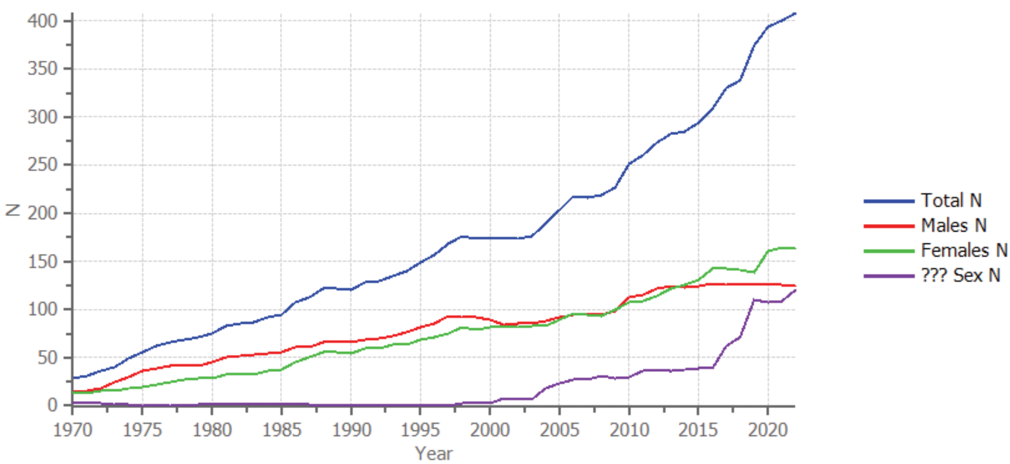

Fig. 5. *Aldabrachelys gigantea* (Schweigger, 1812) population development. Changes in population size over the years for the total population and separately for males, females and individuals of unknown sex. Graph constructed using PMx with data exported from ZIMS for Studbooks (*A. gigantea*, I. Rehak, 23 May 2023).

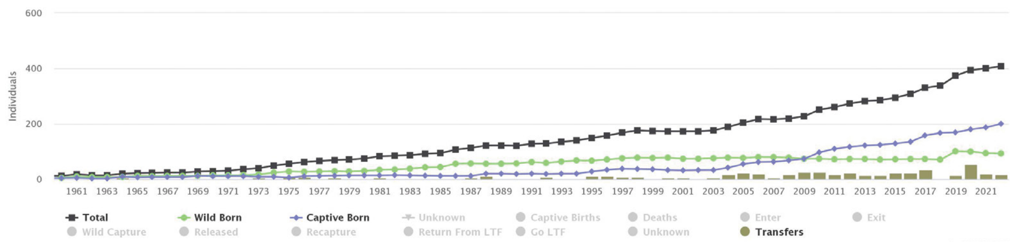

Fig. 6. *Aldabrachelys gigantea* (Schweigger, 1812) population development. Changes in population size over the years for the total population and separately for wild born and captive born individuals. males, females and individuals of unknown sex. Transfers indicate moves between locations. Graph constructed using ZIMS for Studbooks (*A. gigantea*, I. Rehak, 23 May 2023).

respective to ca. 270 according to deterministic projection, if no change of the reproductive rate will take place (and without imports). To maintain the population size at current level 9 hatches annualy are needed in this case. Conversely, with the eventual involvement of a cooperating private breeder (Stefan Merz) in the EEP, the population with current hatch rate and without imports would drop from current 410 to approx. 330 individuals in 20 years according to stochastic projections, respective to ca. 350 according to deterministic projection, The final part of the curve implies that the population might get balanced at this size. This is probably a reflection that at that time the youngs from the most recent successful breedings will be reproductively active and the population will reproduce in the rate, which will be sufficient to keep the population around 330 individuals. However, the data are not sufficient to expect this with certainty. To maintain the current population size, 8–9 hatches per year are needed.

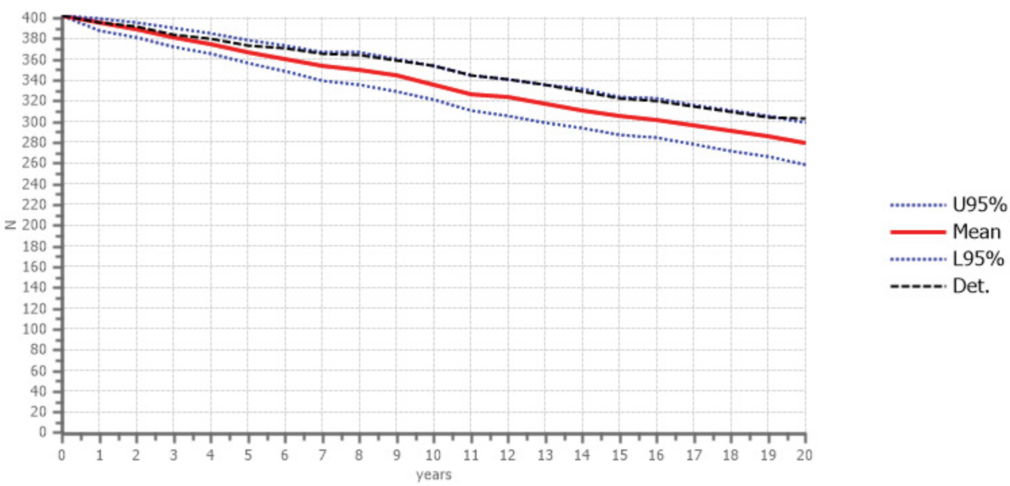

Fig. 7. Predicting the development of *Aldabrachelys gigantea* (Schweigger, 1812) population in EAZA. Stochastic projection in red (mean), its confidence intervals in blue, deterministic prediction in black. Graph constructed using PMx with data exported from ZIMS for Studbooks (*A. gigantea*, I. Rehak, 23 May 2023).

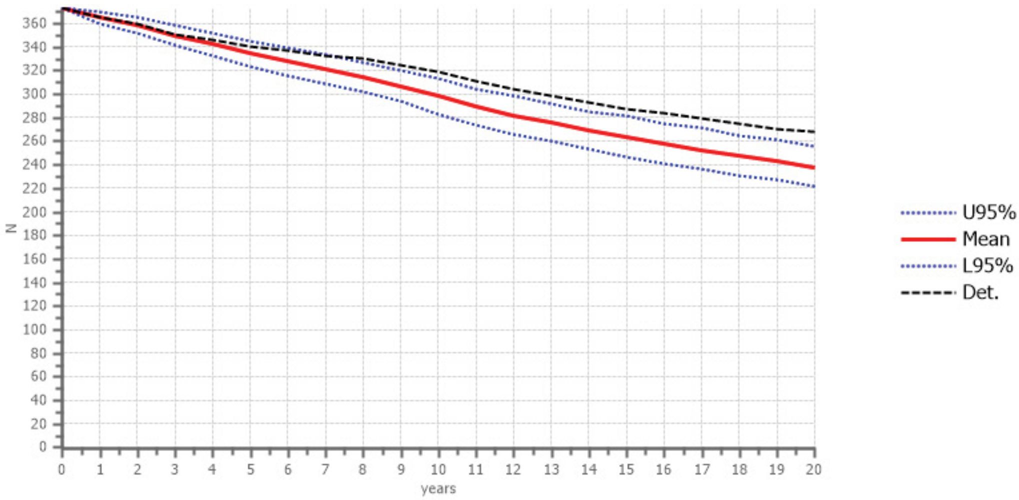

Fig. 8. Predicting the development of *Aldabrachelys gigantea* (Schweigger, 1812) population in EAZA (excluding Taipei). Stochastic projection in red (mean), its confidence intervals in blue, deterministic prediction in black. Graph constructed using PMx with data exported from ZIMS for Studbooks (*A. gigantea*, I. Rehak, 23 May 2023).

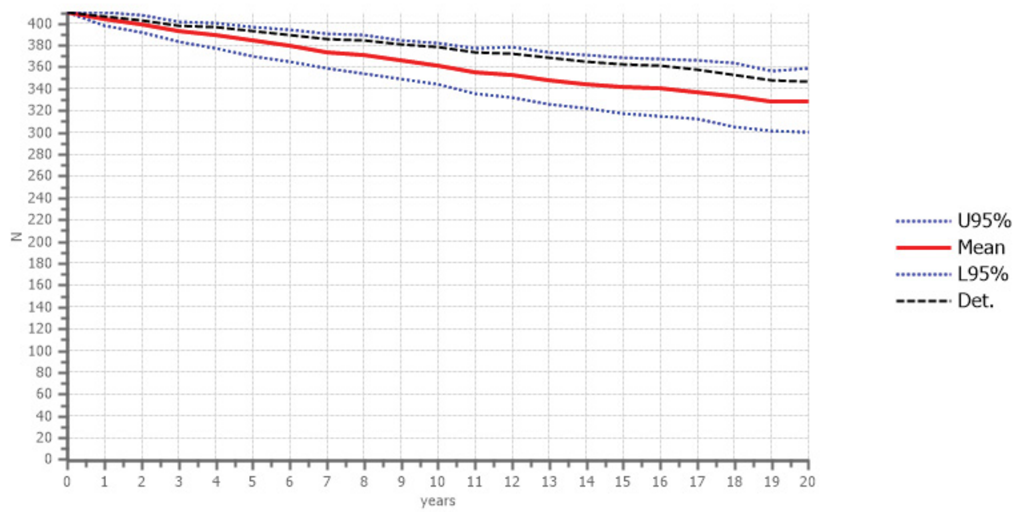

Fig. 9. Predicting the development of *Aldabrachelys gigantea* (Schweigger, 1812) population in EAZA (including S. Merz). Stochastic projection in red (mean), its confidence intervals in blue, deterministic prediction in black. Graph constructed using PMx with data exported from ZIMS for Studbooks (*A. gigantea*, I. Rehak, 23 May 2023).

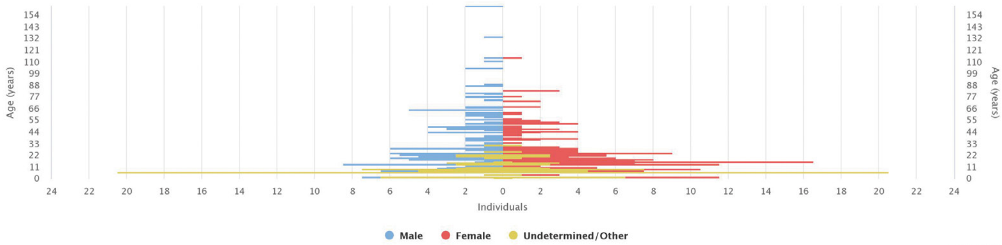

Fig. 10. Age structure of *Aldabrachelys gigantea* (Schweigger, 1812) population in EAZA). Graph constructed using ZIMS for Studbooks (*A. gigantea*, I. Rehak, 23 May 2023).

Age structure and longevity

The age structure (Fig. 10) is generally of a "high-tower pyramid" nature with a broad base consisting of juveniles in the under-15 category, followed by the large 15–25 year old category, and the remaining individuals in the higher age categories. Notably, there are eight individuals in the population over 100 years of age (ranging from 103 to 162). The sex ratio is fairly even (122 males, 159 females), with a slight female predominance particularly evident in the 15–25 years category. On the other hand, in the over 85 years category, with the exception of one female, there are only males. Reproductive animals are from the 15–25 years category. For 121 animals, mostly from the lower age categories, the sex is not yet known. The size and structure of the current *A. gigantea* population in EAZA population is adequate for a long-term perspective.

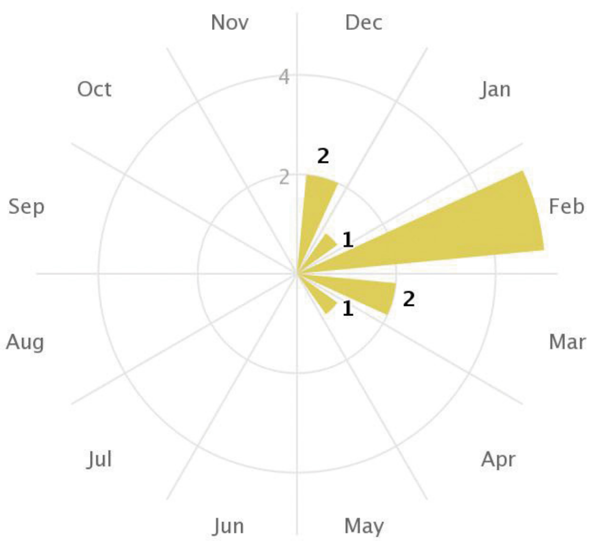

Fig. 11. Seasonality in hatching of *Aldabrachelys gigantea* (Schweigger, 1812) in EAZA (including S. Merz). Graph constructed using ZIMS for Studbooks (*A. gigantea*, I. Rehak, 16 May 2023).

Fig. 12. The first Aldabra giant tortoise in Prague Zoo (1948–1976). Photo by Richard Pavlovič, Prague Zoo Archive.

Reproduction

The successful reproduction of *A. gigantea* in EAZA institutions is still an exceptional event. Given the size and composition of the population, the current reproductive success rate is unacceptably low. Unless reproduction increases in this population, it will not be demographically sustainable. The first breeding within EAZA was reported by its Asian member, Taipei Zoo, in 2018. Nine hatchlings were born there, all of which are alive. The next breeding, and the only breeding in Europe to date, was achieved at Beauval Zoo, where a total of 14 young hatched (13 of which are alive) in 2022 and 2023. The first successful breeding in Europe was achieved at Stefan Merz's private breeding facility, Germany, in 2021; 19 offsprings were born there between 2021 and 2023 (see Table 1).

Hatching occurred mainly during the winter months (Fig. 11). The age of males at the time of breeding was 15.3–17.8 years, and females 17.2–31.5 years. There was a total of 11 clutches. The number of hatchlings from each clutch ranged from 1–11 (mean 4.2).

Genetic status

The population's pedigree of *A. gigantea* in EAZA is only 17.3% known. There are currently only one founder what is not enough to maintain a genetically sustainable population. However, there are an additional 62 potential founders. It is absolutely essential more of those potential founders to reproduce in order to help the population genetically and demographically. The current genetic parameters of the population (see Table 1) are quite adequate for its long-term independent perspective.

DISCUSSION

Census, projections and their reflection

The significant and persistent numerical increase in the population of *A. gigantea* in the EAZA is misleading when viewed superficially. Our more detailed demographic analysis and predictions of future trends show the existential dependence of this population on imports from external sources. This is unacceptable in the long term for reasons of the best husbandry practice, welfare, ethical,

Fig. 13. Riding large tortoises used to be a popular attraction, but such inadequate treatment is definitely one of the risk factors of Aldabra giant tortoise husbandry. © Prague Zoo Archive.

economic and scientific reasons. Without these imports, however, this population is doomed to extinction under current demographic conditions. The longevity of this species and the relatively low mortality rate in the population makes this process very slow, so that it goes unnoticed. However, an increase in natality is essential to guarantee the long-term prospects of the *A. gigantea* population in the EAZA. Under the current circumstances, to stabilise the population would be sufficient to realize 8–9 hatches per year.

With the current population size of 402 individuals, it is very worrying that this seemingly insignificant target has not yet been met in the long term. It is important to identify this problem.

The Aldabra giant tortoise has been kept in Europe continually since 1923, when two males were imported to Paris JP. While one (Kiki) died at the age of 127 years and his body is the pride of the Paris National Museum of Natural History, the other (Pericles) is still alive at the age of 111 years (MNHN 2023). As can be seen from the above age structure of the population of Aldabra giant tortoises in the EAZA, a not insignificant number of them live to a very old age, which might lead one to believe that they are kept in conditions that perfectly meet all their needs. But then why do they not breed? The answer may be that at least some are able to live to a ripe old age even in suboptimal conditions. It is therefore essential to analyse the conditions of their husbandry in human care and its adequacy. The methodology of Aldabra giant tortoise husbandry in Europe has undergone revolutionary changes during the history of their keeping. This can be illustrated well by the example of history of their husbandry development in Prague Zoo, where giant tortoises have been bred continuously since 30 December 1948 (Volf 1983, husbandry records and archival photographs of Prague Zoo). At that time, only five tortoises were kept in three zoos in Europe outside Prague (Fig. 12).

History of Aldabra giant tortoises at Prague Zoo

Until 1980, the husbandry must be judged from today's point of view as completely unsatisfactory, even though it was in accordance with the standards of the time. Although the tortoises were kept in spacious and sunny grassy enclosures during the summer, they had no access to heated areas, so that their body temperature had to drop to ambient levels, well below 20 °C, on cold days and nights. Nevertheless, they showed weight gains in the summer period. Conditions in winter were even worse. In records from the 1960s, when tortoises were kept from mid-October to early May in a house heated to 18–20 °C, we find an indication of a 9–16% reduction in the weight of an adult male giant tortoise kept at that time (Volf 1983). Even the feeding of the tortoises during this period cannot be described as satisfactory. From own experience (one of the co-authors, Petr Velenský, started his career at the zoo as a volunteer in the reptile department as early as 1975, and has been working continuously with giant tortoises since 1995) we can confirm the predominance of fruits and vegetables (especially carrots and apples) in the diet. According to the accounts of witnesses from the post-war years (Zdeněk Vágner, pers. comm. 1995), the feed also included buns soaked in milk and similar nutritionally rich items. Children's rides on tortoises, which were organized at that time (Fig. 13), can also be considered a significantly negative factor. It is not surprising that none of the 4 specimens (3.1) that the zoo acquired between 1948 and 1976 are alive today. Their lengths of life at the zoo were 0.5, 1, 27 and 43 years, respectively.

In 1982, the enclosure for giant tortoises in the lower part of the zoo (opposite the former Pachyderm House) was modernized and for the first time included a hutch with a heated floor. At that time, the tortoises moved to the Small and Rare Mammal House for the winter, where they occupied a quarters together with the sloths. This was heated to about 25 °C without a possibility for local basking. The tortoises' outdoor enclosure changed several times before 1995, and visitors could find them in the upper part of the zoo opposite the current Cassowaries, in the Penguin enclosure or in front of the current Sichuan House. However, the wooden hut with a heated floor was always moved with them. The initiative of the then curator of reptiles Simona Brantlová in the mid-1990s brought a fundamental breakthrough in the breeding conditions for Aldabra giant and elephant tortoises. With plans to build a new house dedicated to large tortoises, Simona Brantlová began to collect tortoises from zoos that had no such ambitions. Thus, in 1993 an adult male from Leipzig Zoo and in 1996, 3 males and 2 females from Dvůr Králové Zoo came to the zoo as a deposit (3 of these tortoises were returning in 2014). At the same time, the senior author (I.R.) managed to import two young females from a farm in Seychelles. In parallel with the acquisition of animals, the breeding conditions changed. In 1995, three years before the opening of the new house, there was a dramatic improvement in both summer and winter conditions. The tortoises spent the winter in a dedicated section of the Cat House visitor area (now the Reptile and Carnivore House), where they had radiant panels under which they could raise their body temperature above 30 °C. In summer, they already had access to their current enclosures with makeshift but spacious shelters heated to a similar temperature. The turtles' ration was also changed substantially in favour of hay and green fodder. The revolutionary change in the breeding of these animals was completed with the opening of the Giant Tortoise House in September 1998 (Fig. 14).

Since then, there have been continuous small improvements, especially in the lighting and heating of the house. In 2022, the inadequate swimming pool was rebuilt, specifically the significant enlargement and re-modelling of the steep banks. The internal area of the house, covered by a polycarbonate roof, is 200 m^2, and the area of the grassy summer enclosures, which are available to the tortoises from mid-May to the end of September, is 1000 m^2. The temperature in the house is maintained at 27–32 °C, but a wide strip along the back wall is heated by infrared radiators to 3–47 °C. The food ration consists of 90% high quality cut hay and grazing in summer (hay is

Fig. 14. Aldabra giant tortoise in the tortoise house at Prague Zoo. Photo by PV.

available all year round ad libitum), vegetables are greatly reduced, offered in very limited quantities twice a week romaine lettuce and Chinese cabbage. To compensate for possible problems with iodine deficiency we satiate the offered vegetables with seaweed extract (Algasol). The tortoises are very fond of tree leaves. In winter we irregularly offer them cut ficus branches from their enclosure, in summer they eat fallen leaves in the enclosure, especially from poplar trees. The described feeding ration has a very positive effect on the quality of the droppings. Summer and winter droppings are large, shaped cones full of fibre. The indoor and outdoor enclosures can be divided into two parts. We are currently using this arrangement to separate females and smaller animals from males and thus reduce the stress of the large males' inconsistent interest in these animals.

In 2023, we are keeping 15 giant tortoises. The group is based on a male that came from Leipzig Zoo in 1993, two females from Seychelles (1996) and two males and a female from Dvůr Králové Zoo (1996). This group was completed in 2009 with a juvenile male from Seychelles and in 2015 with two juveniles from Mauritius. In 2016, two juvenile males from Plzeň Zoo were deposited. In the spring of 2022 we received four adult males as part of the assistance of Heidelberg Zoo, where the tortoise house is being renovated. Despite these efforts to improve the breeding of giant tortoises, we have not yet been able to breed these tortoises in Prague.

Identification of best practice for reproduction of *Aldabrachelys gigantea* in human care

According to ZIMS (Taxon Report *Geochelone gigantea*; 23 May 2023), the first Aldabra giant tortoise hatchlings in zoos were born in USA at Six Flags Great Adventure in 1944 and then at Zurich Zoo in 1947 and 1948. In both cases, the figures are apparently confusing. The first contradicts the data of Collins (1984), who states that the first ever reproduction of giant tortoises in the entire Western Hemisphere was only in 1984 at the Jacksonville Zoo. The above data from Zurich was challenged by Fabian Schmidt (2023, ad verb). Confusion is also indicated by the fact that there are not registered any totoises that could be parents of those hatchlings in Zurich Zoo. Apparently, the first reproduction in the zoo was achieved in Taronga (Sydney, Australia) in the years 1976–1977. In the USA, in addition to the aforementioned Jacksonville Zoo, the Institute for Herpetological Research (California) also reported successful breeding (Stearns 1988). With the onset of this millennium, Tulsa Zoo became a prominent, and at the same time exceptional, breeder in the USA with regular breedings (approx. 70 bred hatchlings).

In general, however, Aldabra giant tortoises breed exceptionally in human care in temperate climates. In contrast, successful reproduction is quite common in breeding facilities in the Mascarenes, Seychelles and other islands in this region of the Indian Ocean, even in seemingly very primitive conditions (Rehák 1997). This suggests that mimicking the home life cycle of tortoises and its determinants may be essential. In Europe, systematic breeding successes have now been achieved by the German private breeder Stefan Merz. In accordance with his conclusions (Merz 2023), we believe that the basic conditions for inducing the reproductive cycle of turtles are as follows:

- Maintaining the body temperature of tortoises at a constant high level (28–32 °C) throughout the year. Ensuring this condition is not easy even in the winter enclosure, as it is necessary to maintain this temperature at floor level throughout the enclosure. This is even more difficult in summer when the tortoises are allowed out to graze. Not only do they need to have access to permanently heated indoor areas at this time, but it must be ensured that the tortoises do not get cold outside and spend every night indoors.
- Proper high-fibre nutrition, i.e. based on grass and hay. Properly fed turtles move easily on high upright legs. Improper energy-dense feeding results in heavily crawling, overweight turtles that are definitely out of reproduction. Seaweed or seaweed extract can play an important role in the diet.

– Ensuring an adequate lighting regime (especially in winter) with brightly lit light sources with a proportion of UV light (i.e. we cannot rely on natural greenhouse light in winter).
– Ensuring the psychological well-being of the tortoises kept. The fact that tortoises are highly sensitive creatures prone to stress is often underestimated, especially in zoos. Female tortoise can be stressed by the constant sexual interest of males, so we believe it may be beneficial to separate females from males for much of the year. Tortoises may also be inconvenienced by changing keepers and disrupting their daily routines. In zoos, they may also suffer from excessive visitor interest. In this respect, we consider the fact that the most stable breeding is currently carried out by private breeder to be significant.

Future management of *Aldabrachelys gigantea* in EAZA

The basic goal is not to allow the negative predictions off the EAZA population of *A. gigantea* to come true. The demographic and genetic status of the *Al. gigantea* population in the EAZA is still adequate for a starting of a perspective population. Despite possible objections that Aldabra giant tortoises are numerous and reproduce well in a number of facilities in the western Indian Ocean region from which we can supplement them, it is very important to realize this potential. At least because low reproductive success means that the present husbandry is not adequate for high-quality welfare and it is not acceptable for modern zoos. Moreover, it cannot be ruled out that in our large population there are individuals of extraordinary genetic value. In any case the population should be managed to guarantee minimal lost of its genetic diversity. Therefore, a more detailed assessment of the genetic composition of the population seems to be important for the near future. The wider implementation of best practice husbandry by EAZA member institutions is a crucial task.

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