The illusion of stability in long-lived species: Poor early-life survival threatens the persistence of Giant Aldabra tortoise populations.

Abstract

Long-lived species share several life-history traits that make them susceptible to extinction debt: a concept referring to the delayed extinction of species due to their limited ability to adapt to environmental change. This threat may go unnoticed, since adult populations can persist for prolonged periods of time before underlying issues with recruitment lead to sudden declines. Using novel methods for assessing rates of hatching success and embryo survival in reptiles, we provide evidence of extremely low early-life survival across multiple populations of the long-lived Giant Aldabra tortoise in the Seychelles, which is highly suggestive of future declines in this species. We argue that a reassessment of the Giant Aldabra tortoise threat status incorporating this information would result in an uplisting from Vulnerable to Endangered. More broadly, we stress the importance of considering reproductive success and productivity when evaluating the threat status and conservation management of long-lived species.

Introduction

Long-lived species play critical roles in ecosystem stability and functionality, often serving as key players in food web structures (Kopf et al., 2024; Hazen et al., 2019) and undertaking fundamental roles in environmental nutrient cycling and ecosystem engineering (Albertson et al., 2024; Lovich et al., 2018). They can provide insights into the evolutionary and physiological basis of longevity and age-related disease (Omotoso et al., 2021; Quesada et al., 2019), and many hold significant cultural and economic value (Kopf et al., 2024).

However, long-lived species are more vulnerable to extinction than shorter-lived species, due to their limited ability to adapt quickly to environmental change (Albaladejo-Robles et al., 2023). They typically exhibit several life-history traits which make them less likely to recover following demographic perturbations (Briggs-Gonzalez et al., 2017), such as long generation times (Capdevila et al., 2022; Jackson et al., 2020), low reproductive output (Capdevila et al., 2022), late maturation, slow growth, and relatively low recruitment rate (McCann & Shuter, 1997). These traits also make long-lived species more likely to have a delayed response to environmental change and therefore more susceptible to extinction debt: a concept referring to the delayed extinction of species following perturbations such as habitat destruction (Liao et al., 2022; Haddou et al., 2022).

From a conservation perspective, understanding the population dynamics of long-lived species is crucial for informing estimations of population growth rates, future population sizes, and extinction risk (Kopf et al., 2024; Jackson et al., 2020; Briggs-Gonzalez et al., 2017). However, data on the life history traits of long-lived species is typically deficient due to the challenges of monitoring their populations over prolonged time periods (Edwards et al., 2019; Briggs-Gonzalez et al., 2017). While modelling approaches can be used to predict future population trajectories, a comprehensive understanding of species life-history and population demography is essential for informing such models (Benton et al., 2006). Population dynamics of long-lived species have traditionally been expected to be most sensitive to adult survival rate (Souchay et al. 2013), but there are many cases where factors such as fecundity or juvenile survival have been found to be more influential. A study on the long-lived (30-86 years; Wiese & Willis, 2004) and endangered Asian elephant (*Elephas maximus*), using data collected over 40 years, showed that variation in age-specific survival and reproduction significantly impacted population growth rates (Jackson et al., 2020). Similarly, while adult survival was shown to be the most important factor influencing population growth in a 36-year study of American crocodiles (*Crocodylus acutus*), juvenile and subadult survival rates also had a significant influence on population growth (Briggs-Gonzalez et al., 2017). In a >15-year study of the imperilled bog turtle (*Glyptemys muhlenbergii*), increased survival rates at egg and juvenile stages were shown to buffer adult mortality and emigration rates, and in some populations, overall population decline was induced by reduced survival at multiple life stages (including the egg and juvenile stage) (Knoerr et al., 2021). These findings demonstrate the complexity of population dynamics in long-lived species and the need for long-term data collection on factors such as population age structure, longevity, and juvenile survival, to inform conservation and management strategies.

Species categorisation on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species is arguably one of the most influential current drivers of conservation policy. The IUCN assesses species' threat status using the following five criteria: "i) Population size reduction (past, present and/or projected); ii) Geographic range size, and fragmentation, few locations, decline or fluctuations; iii) Small and declining population size and fragmentation, fluctuations, or few subpopulations; iv) Very small population or very restricted distribution; v) Quantitative analysis of extinction risk (e.g., Population Viability Analysis)" (IUCN, 2012). The accuracy of the IUCN's assessments relies on the quality of data available for each criterion, which is in turn dependent on

monitoring effort and understanding of key life history traits. For species with limited data, assessments can still be made via "inference, suspicion, and projection", provided assumptions are documented (IUCN Standards and Petitions Committee. 2024). Many IUCN Red List assessments are based on changes in population size, which is why risk assessments are often based on population census data (i.e., counts of mature individuals). However, even if census data is available for long-lived species, changes in reproductive output and population demography which may undermine long term population persistence can be easily masked due to the longevity of mature individuals.

It is known that long-lived species can maintain seemingly stable populations despite low recruitment, and this can eventually lead to sharp population declines. A >20 year (1970s-1990s) multi-population study of long-lived hellbender salamanders (*Cryptobranchus alleganiensis*), for example, showed an average population decline of about 77%, which started in the 1980s and was characterised by a sustained shift in age structure and density across all populations, with a disproportionate decline in young individuals and relative increase in larger, mature individuals over time (Wheeler et al., 2003). Proposed causes included lack of recruitment, reproductive failure, and/or low survival of eggs or young (Wheeler et al., 2003). Mark-recapture surveys corroborated the trend of rapid decline in hellbenders, with studied populations consisting nearly exclusively of large, older individuals with limited signs of reproduction (Burgmeier et al., 2011). In 2004, hellbenders were listed as 'Near Threatened' by the IUCN, but in 2022, guided by these and other studies (IUCN SSC Amphibian Specialist Group, 2022), the species was uplisted to 'Vulnerable' because of their estimated 30-50% decline over the past three generations. This demonstrates the importance of detailed demographic data for informing accurate threat status classification. More recently, the implementation of headstarting, where individuals are reared in captivity during the most vulnerable early life stages, before being released into the wild in an effort to increase survival and recruitment, has proved effective for rebuilding hellbender populations – specifically, the collection and captive rearing of wild eggs has resulted in up to seven times more individuals surviving to adulthood compared to natural reproduction and egg development (Kaunert et al., 2024).

The above examples collectively highlight the value of comprehensive, long-term demographic monitoring and the critical role that early life stage survival and recruitment has in sustainably maintaining populations of long-lived species. Inclusion of data on these life history traits can improve the accuracy of species' threat statuses, with important implications for the allocation of conservation and research funding as well as the design and implementation of recovery programs.

The Aldabra giant tortoise (*Aldabrachelys gigantea*), endemic to the Aldabra Atoll in the Seychelles (Çilingir et al., 2022), is a well-known example of an exceptionally long-lived species, with an estimated lifespan of 100+ years (Quesada et al., 2019). Aldabra tortoises are one of the most significant vertebrate biomass contributors in the world, with their heavy grazing having the capacity to alter landscapes and influence ecosystem health and function (Lovich et al., 2018; Coe et al.,1976). Recent extinctions of several large and giant tortoise species have led to dysfunctional island ecosystems, especially regarding seed dispersal and herbivory (Hansen et al., 2010). As one of only two remaining extant giant tortoise taxa, and the only extant species of giant tortoises in the Indian Ocean (Turtle Taxonomy Working Group, Rhodin et al., 2021; Kehlmaier et al., 2017), conservation practitioners are now attempting to use Aldabra tortoises to restore missing ecological functions on these islands (Hansen et al., 2010). In addition to their ecological importance, Aldabra tortoises also have significant economic and cultural value as both a tourist attraction and iconic symbol in local culture (Hansen et al., 2010; Hambler, 1994; Appendix I).

However, extinction debt may be a looming reality for the Aldabra tortoise due to an absence of detailed demographic data to inform its conservation status and management. The IUCN Red List

currently categorises Aldabra tortoises as 'Vulnerable' based on their restricted distribution, but this threat assessment was carried out almost three decades ago, data on population demography was not considered, and their assessment has been annotated as "Needs updating" by the IUCN (Tortoise & Freshwater Turtle Specialist Group. 1996).

Most of the current knowledge on the population ecology, dynamics and reproduction of the Aldabra tortoise comes from an intensive period of research carried out on the sub-populations on the Aldabra atoll of the Seychelles. A long-term monitoring programme and series of interrelated studies commenced in the early 1970s, revealing that Aldabra tortoise population dynamics are highly vulnerable to juvenile loss and poor recruitment (Gibson & Hamilton, 1984). However, since the 1990s, there has been no further consistent demographic monitoring, so detecting major shifts in population dynamics (especially in age structure) is challenging unless the adult population is severely impacted (Haverkamp et al., 2017; Bourn et al., 1999; Gibson & Hamilton, 1984), and data on the factors influencing productivity, early life survival, and recruitment are limited (Gibson & Hamilton, 1984; Swingland & Coe, 1979). Given that climate change has been suggested to have the greatest impact on juvenile survival in tortoises (Haverkamp et al., 2017), it is possible that the future persistence of this species is jeopardised by currently invisible processes. Furthermore, previous findings on Aldabra may not be applicable to populations on other Seychelles Islands that experience different environmental conditions (e.g., topography, vegetation, predation pressures).

Here, we share new insights into early-life survival of the Aldabra tortoise by assessing rates of fertility, early embryo survival, and hatching success, using novel methods across multiple populations in the Seychelles. We argue that low productivity could lead to functional decline in populations that currently appear stable based on adult census data. Information on reproductive success/productivity should therefore be considered not only in the much-needed reassessment of the Aldabra tortoise's IUCN Red List status, but in similar assessments of other long-lived species and the design of future monitoring programmes.

Materials and methods

We collected unhatched Aldabra tortoise eggs that showed no signs of development (i.e., undeveloped eggs) and determined their fertilisation status as described in Lavigne et al., (2024). Briefly, we used microscopy-based techniques to identify embryonic nuclei on the perivitelline membrane (PVM) of undeveloped eggs to confirm egg fertilisation. We considered eggs to be unfertilised if most of the PVM surrounding the yolk was retrieved but no embryonic nuclei and minimal/no sperm were found consistently across all PVM sections. If we couldn't retrieve sufficient PVM to confidently determine fertility status (i.e., to clearly identify embryonic nuclei), we classified eggs as inconclusive.

Due to the challenges of monitoring Aldabra tortoises and identifying active nests, our sampling approach differed between the 2022/2023 and 2023/2024 breeding seasons. In 2022/2023, we sampled 1-2 eggs that showed no signs of development, at random, per clutch, resulting in 18 undeveloped eggs being collected from 15 different wild clutches across 3 populations, supported by conservation partnerships with Seychelles Islands Foundation (Aldabra: 9.4237°S, 46.3433°E); North Island Company Limited (North Island: 4.3950°S, 55.2453°E); and Save Our Seas Foundation: D'Arros Research Centre (SOSF-DRC) (D'Arros Island: 5.4180°S, 53.2962°E). Since we found relatively few clutches in 2022/2023, we opted to collect as many undeveloped eggs as possible from clutches as they became available in 2023/2024, resulting in the collection and analysis of 48 eggs from 12 different clutches across 4 populations, supported again by SOSF-DRC, along with Nature Seychelles (Cousin Island: 4.3315°S, 55.6620°E); Cousine Island Company Ltd (Cousine Island: 4.3507° S, 55.6475°

E); and Island Conservation Society (Desroches Island: 5.6952° S, 53.6583° E). Partners identified as many tortoise nests as possible and recorded parent/clutch identity and lay dates where possible. At the end of incubation (~6-8 months), they excavated nests, collected unhatched egg samples, and recorded all egg fates. Hatching success was calculated as # hatched eggs / total clutch size.

Results

Hatching success varied considerably across Aldabra tortoise populations (Table 1) but was generally low. On average, 67% (16/24) of clutches suffered complete hatching failure, but success rates varied between islands, from 46% on Aldabra to 0% on Cousine, Desroches, and North Island. Across all locations, unhatched eggs were undeveloped, except for three Aldabra clutches that had visible embryo development in some eggs. Even those in those clutches that showed some degree of development/hatching success, a proportion of eggs remained undeveloped.

We determined the fertility status of 66 undeveloped eggs from 27 different clutches collected across the six different Seychelles islands. Fertilisation rates varied across populations: all conclusive samples from Aldabra, Cousin and Desroches were fertilised; most conclusive samples from Cousine and D'Arros were also fertilised; but we found no evidence of fertilisation in any conclusive samples from North Island (Figure 1). In most locations, hatching failure in Aldabra tortoises is predominantly driven by embryo mortality, with fertilisation failure presenting an issue for some populations.

Table 1. Clutch data from 24 different Aldabra tortoise clutches from six Seychelles island was used to calculate the number of clutches experiencing total clutch failure (i.e., 0% hatchings success) as well as their average, range and median hatching success.

	Number of clutches	Number of total clutch failures	Mean % Hatching success (all eggs)	% Hatching success range (per clutch, min–max)	Median % hatching success (all eggs)
Aldabra	7	2	46	0–91	44
Cousin	3	2	26	0–78	0
Cousine	3	3	0	0–0	0
D'Arros	4	2	11	0–36	3
Desroches	3	3	0	0–0	0
North Island	4	4	0	0–0	0
TOTAL	**24**	**16**	**19**	**0–91**	**0**

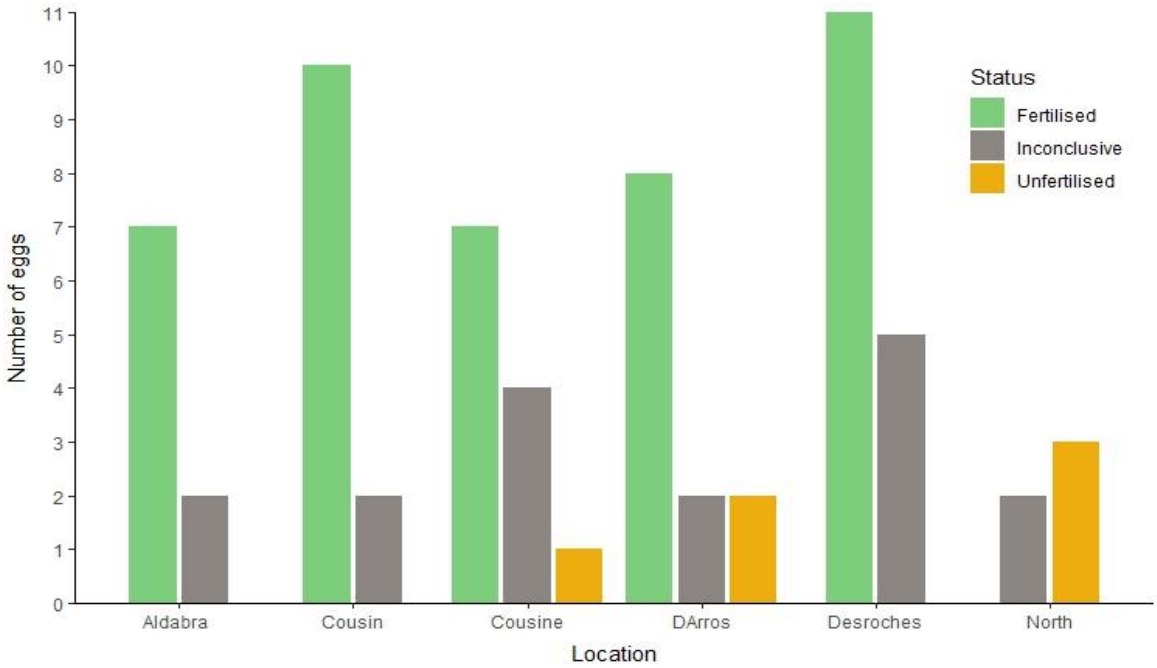

*Figure 1. Fertility statuses of undeveloped eggs produced by Aldabra Giant tortoises (*Aldabrachelys gigantea*, n = 66 eggs from 27 clutches) from six Island locations in the Republic of Seychelles. Eggs were deemed inconclusive if there was insufficient material for further analysis. Samples were collected from Aldabra and North Island during 2022/2023; Cousin, Desroches and Cousine from 2023/2024; and D'Arros samples were collected across both 2022/2023 and 2023/2024.*

Discussion

Functional declines in the populations of long-lived species, driven by low reproductive success and productivity, have the potential to be masked by apparently stable population sizes that persist due to long adult lifespans. Here, we report concerning evidence of low productivity across six Seychelles populations of the Giant Aldabra tortoise, a species whose average lifespan exceeds that of the humans who monitor them. Across all populations, over two thirds of identified clutches experienced complete hatching failure, with no offspring being produced. Even in clutches where some eggs hatched, embryo mortality was prevalent.

Capitalising upon recent methodological developments (Lavigne et al. 2024), our study is the first to accurately quantify fertilisation failure and early embryo death rates and compare these across tortoise populations. This novel approach reveals early embryo death to be a potentially significant barrier to tortoise productivity, with fertilisation failure also presenting an issue in specific populations, particularly on North Island, where we found no evidence of fertilisation in any clutches.

There is already evidence that productivity of Aldabra tortoises may be impacted by environmental change. For example, clutch size, egg weight and number of clutches per female, and rates of hatchling production and quality, all vary with rainfall, population density, and resource availability (Gibson & Hamilton, 1984; Swingland & Coe, 1979). Recent increases in drought frequency on Aldabra have also been posited to have a greater negative impact on juvenile survival/recruitment than adult survival (Haverkamp et al., 2017). Like other long-lived species with late maturation (Swingland & Coe, 1979) and slow generational turnover, Aldabra tortoises are unlikely to be able to adapt quickly to

environmental shifts (Albaladejo-Robles et al., 2023), yet the impact of this on population dynamics may go unnoticed for decades if only adults are monitored.

Although we sampled a relatively small number of eggs/clutches per population, low productivity was consistent across populations, with most clutches suffering low hatching rates and elevated levels of early embryo death. Our findings are also consistent with anecdotal reports from all participating conservation partners who report juvenile sightings to be uncommon or absent, regardless of whether terrestrial predators of hatchlings are present (personal communications). Together, these observations suggest that hatching outcomes may play a significant role in determining overall juvenile production, survival and recruitment rates in these populations. Indeed, it is suspected that the experimental translocation of Aldabra tortoises to Curieuse Island failed to establish a wild colony due to elevated loss of juveniles and poor recruitment (Hambler, 1994). While we found hatching success rates to be higher on Aldabra, where the world's largest tortoise population is found, around 30% of clutches still experienced complete failure. Overall, our findings suggest that for long-lived species, adult population census data may be insufficient for accurate threat assessment. When adults live for several decades, extinction risk that emerges from low productivity may be hidden for long periods of time, severely impacting our ability to understand the drivers of population decline and delaying appropriate conservation interventions. Indeed, in some populations, reduced survival at the egg and juvenile stage significantly contributed to overall population decline (Knoerr et al., 2021).

The existing IUCN risk assessment for Aldabra tortoises (VU D2) was based on a restricted Area of Occupancy (AOO), typically less than 20km^2, and a plausible threat that would drive the species to Critically Endangered or Extinct in a short timeframe (Tortoise and Freshwater Turtle Specialist Group, 1996). In the last 29 years since that assessment, this species' AOO has not expanded beyond the threshold for the Endangered category under Criterion B2. Given that climate change is the major pervasive threat to this species (Gerlach et al., 2013; Ihlow et al., 2012) the number of threat-based locations would be less than five. Our findings provide new information relating to the population status of the species, which given the low rates of hatching success, project future declines in numbers of mature adults. Applying the Guidelines for Using the IUCN Red List Categories and Criteria, this means that a reassessment of this species would justify an uplisting from Vulnerable to Endangered, with an assessment outcome of EN B2ab(v)c(v) (IUCN Standards and Petitions Committee. 2024).

Large, persistent declines and/or failures in reproductive success and recruitment have also been proposed as a potential future threat for Galapagos tortoises (Blake et al., 2024), the only other extant giant tortoise taxa. Like the Aldabra tortoise, Galapagos tortoises are long-lived (Blake et al., 2024) with cryptic early life-history stages. Their reproductive ecology (including hatching success, natal dispersal and recruitment rates) is poorly understood for similar technical and logistical reasons (Blake et al., 2024), but in recent years productivity and recruitment have been more intensively monitored. By measuring female condition, nest temperature, clutch characteristics, and survival, tracking individual movements using global positioning system telemetry and radiotelemetry, monitoring temperature and rainfall, and assessing primary productivity along elevation gradients, Blake et al. (2024) have begun to elucidate how environmental variability influences female productivity and juvenile recruitment. The novel insights from this nine-year study will support the development of conservation strategies that consider the tortoises' unique reproductive ecology as well as their slow life histories. Such strategies are crucial for maximizing the resilience of critically endangered Galapagos tortoises in the face of projected rapid and dramatic shifts in land use, climate and invasive species in the Galapagos Islands; all of which are very similar to what is expected in the Seychelles Islands.

In summary, many long-lived species with seemingly persistent adult populations and extended generation times may be at risk of experiencing an 'invisible' extinction debt fuelled by poor productivity. This may go unnoticed due to a lack of detailed monitoring of population demography (particularly age structure) and productivity output (e.g., hatching success and recruitment) over generations. This paucity in data may in part be due to species generation times exceeding those of the humans who study them, but it is also driven by technical and logistical challenges associated with investigating their cryptic life stages. Ultimately, we risk having no clear baseline information to refer to when assessing the threat status of long-lived species, and without this reference point, what we perceive as 'normal' will inevitably change over time (Papworth et al., 2009). By the time problems become apparent, for example in the form of sudden declines in adult populations, low juvenile numbers, and/or a collapsing ecosystem, it may be challenging not only to recover population sizes but maintain the key ecological roles that primarily adult individuals contribute (Kopf et al., 2024). In such a scenario, an already dwindling population of juveniles with low productivity will not only face anthropogenic threats (e.g., climate change, pollution, invasives, habitat loss) but a decline in habitat quality without sufficient adults to maintain it.

Our work demonstrates the need for finer scale monitoring of not just adult numbers, but the reproductive rates that underpin longer-term changes in population demography of long-lived species. We also require innovative approaches to facilitate this monitoring when early life history stages are cryptic. In the meantime, considering that "inference, suspicion, and projection" are recognised factors of assessment, the IUCN should consider the data presented here as part of a much-needed reassessment of the Aldabra tortoise's threat status, reflecting more accurately the potential threats they face and helping them receive the conservation and research attention they need.

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Appendix

*APPENDIX I. The Aldabra giant tortoise (*Aldabrachelys gigantea*) is observed as an important cultural symbol in the Republic of Seychelles as described or circled in red on the country's (Left) Official coat of arms (Image credit: Seychelles Government, 2015); (Middle) Seychelles ten Rupee coin, currently circulating since 2016 displaying the Aldabra giant tortoise at the front of the coin and the coat of arms at the back (Image credit: Central Bank of Seychelles, 2019); (Right) Seychelles 100 Rupee bank note, issued in 2013 and demonetised in 2017 (Image credit: Central Bank of Seychelles, 2019).*

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