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Is it really 1 in 1000 sea turtle hatchlings that survive to adulthood?

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Offspring survival is a central component in understanding the life-history of species. With sea turtles, estimates of hatchling survival to adulthood can be traced back to theoretical considerations made over 50 years ago and before key parameters needed in the hatchling survival calculation had been quantified. Here, using up-to-date figures for adult survival rates and hence adult longevity and lifetime reproductive output, we show that the survival rate of hatchlings to adulthood will generally lie between 1 in 400 and 1 in 2000. We show that this survival rate probably varies across populations and species in line with variations in adult survival rates, remigration intervals and clutch frequency and will likely be impacted by factors such as local management, resource availability and bycatch pressures. Popular articles that tend to quote this survival rate as 1 in 1000 are broadly comparable with our estimates, although the survival rate likely varies appreciably across populations. We identify the key parameters that need to be measured for this value to be determined accurately for individual populations around the world. This approach of using values for adult reproductive output to estimate offspring survival rates to adulthood likely has broad utility across reptiles and other taxa.

1. Introduction

The probability of survival of offspring to adulthood is a fundamental component of the life-history of species and variations in this probability will impact the conservation of endangered species [1]. Sea turtles have long been a group of

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conservation concern due to historic declines, which are often linked to anthropogenic impacts such as harvesting and bycatch [2], although conservation efforts in recent decades have led to increased abundance in many populations [3]. Popular news articles often report that around 1 in 1000 to 1 in 10 000 sea turtle hatchlings survive to adulthood (e.g. [4]). Although widely reported, the scientific basis for this figure is often not clear. Yet this figure is of interest because it helps define how conservation efforts to protect eggs and hatchlings might benefit populations by increasing the number of breeding adults. For example, what might be the benefit of protecting eggs by moving them to hatcheries, in terms of likely future benefits to adult recruitment?

An approach to estimate the survival of hatchlings to adults in sea turtles was elegantly articulated over 50 years ago [5]. They proposed that from information on adult survival, the lifetime reproductive output of adult females can be estimated and, if population size is stable, then the number of hatchlings that need to survive to replace their parents can be estimated. However, at that time, there were no reliable estimates for adult survival, which precluded Hirth & Shaffer [5] from moving beyond their theoretical considerations. In the intervening 50 years, many studies have tried to estimate adult survival rates using mark–recapture techniques (e.g. [6]). In the first instances these mark–recapture studies used external numbered flipper tags to identify individual turtles (e.g. [7]). More recently, passive integrated transponder (PIT) tags that are injected subcutaneously are used alongside traditional flipper tagging since PIT tags are thought to be more durable [8,9]. Despite the widespread use of these tagging methods, problems remain with their use in survival estimates. A recent analysis concluded that tag loss remains a problem regardless of the type of tags used [10]. When a turtle loses its tags, two problems arise, namely, the turtle associated with the lost tags is assumed to have died or emigrated to elsewhere since the tags are never seen again, and when the turtle is resighted on nesting beaches, it might be incorrectly identified as a first-time nester (termed a neophyte). In other words, mark–recapture with some types of numbered identification tags may lead to underestimates of adult survival rate. Further, Pfaller *et al.* [10] showed that adult survival estimates vary with tag type, with tag loss of titanium tags being the least likely and hence generating the highest annual adult survival estimates. More recently mark–recapture estimates based on long-term photo identification have become available, an alternative approach which has potential to identify individuals with high accuracy [11].

Given the availability of estimates of adult survival rates and the recent information on which of these estimates are most reliable, it is timely to revisit the more than 50-year-old question: 'What is the survival rate of sea turtle hatchlings to adulthood?'. Here we set out to answer this question using the best available information.

2. Theoretical framework

We searched the literature for information on adult survival rates for sea turtles and other factors that drive lifetime reproductive output. Then, developing the logic previously outlined over 50 years ago [5], we estimated the lifetime reproductive output of females under different scenarios and calculated the survival rates of hatchlings to adulthood that would be needed to maintain stable populations. The mean lifetime reproductive output of turtles was calculated using values from the literature for adult survival rates. From these annual survival rates, the probability of an adult surviving for n years can be calculated (figure 1). Although it is known that sea turtles can survive for 50+ years [12], the probability of a turtle having an adult lifespan of decades is exceptionally low given known adult survival rates. We assumed that the maximum reproductive lifespan of adults was 60 years in our computations. However, as the calculated proportion surviving for >20 years as adults is so small, this assumption of a maximum reproductive lifespan of adults of 60 years, rather than say 70 years, does not impact our key conclusions. For example, with an annual survival rate of 0.89, the probabilities of a female having a reproductive lifespan of 60 or 70 years are tiny, being 0.0009 and 0.0003, respectively. Calculations were performed in Minitab v. 8.3 Extended.

In the simplest case, for population abundance to be stable, requires an adult female turtle to produce two offspring surviving to adulthood: one male and one female. From this axiom, proposed by Hirth & Shaffer [5], the hatchling survival required for a stable population can be assessed by calculating the mean lifetime reproductive output of mature females. For example, if the annual adult survival is known, then the proportion of individuals living as adults for 1, 2, 3, etc. years can be estimated. If the annual survival is known and a turtle breeds every 2 years, the probability that it is

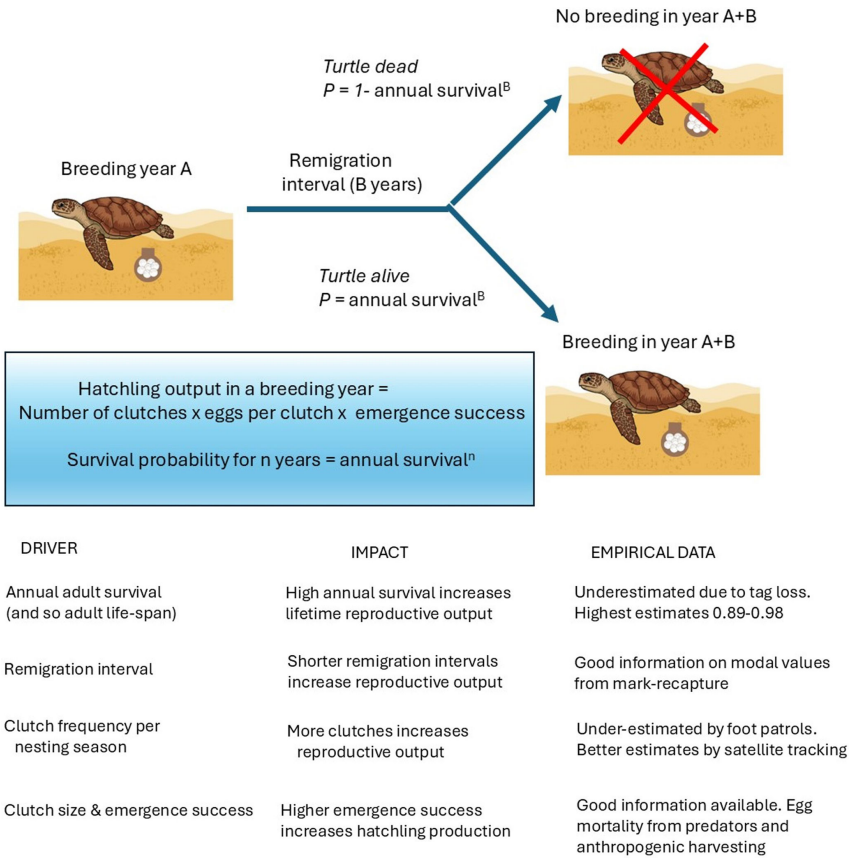

Figure 1. A schematic of the drivers of the reproductive output of adult female sea turtles and a summary of key drivers of adult female sea turtle lifetime reproductive output that underpin calculations of survival rates of hatchlings to adulthood. The range of annual adult survival estimates (0.89–0.98) comes from the literature [10,11]. If for example, the remigration interval (termed B in the schematic) was 2 years, and a turtle bred in 2026, then it would be expected to breed again in 2026 + 2 years = 2028, but at that time it could be dead (and so no breeding occurs) or alive, as represented in the alternatives on the right-hand side of the schematic.

still alive after 2 years to breed again is: p = annual survival^2. Likewise, the probability of being alive after 3 years is: p = annual survival^3.

From these proportions of adults surviving for different numbers of years, the proportion dying in each year can then be estimated and hence the mean longevity calculated. If (i) the interval between breeding seasons (termed remigration interval), (ii) the mean number of clutches per nesting season and (iii) the mean clutch size are known, then the mean lifetime reproductive output (total eggs produced) of adult females in a population can be calculated. With information on the percentage of eggs surviving to emerge as hatchlings from the nest (termed emergence success), the proportion of hatchlings surviving to adulthood can then be calculated in order to produce one adult male and one adult female for a population where adult abundance is stable and the hatchling sex ratio is balanced (figure 1). We then conducted sensitivity analyses by altering various parameters in the model, in line with parameter estimates reported in the literature. In this way, we set out not to simulate every possible scenario, but rather to give an indication of whether the survival rate of hatchlings to adulthood is likely to vary appreciably or not. Using literature values, in our model we varied the annual adult survival rate from 0.89 to 0.9482, the mean number of clutches per season from 2 to 6, the remigration interval (interval between successive breeding seasons) from 2 to 5 years and the adult sex ratio from 50% to 90% female.

3. Case example

The easiest place to start the parametrization of this theoretical framework is with populations where the abundance is stable, hatchling sex ratios are balanced and there is good information on reproductive output. An example of where adult female survival rate is well documented is for

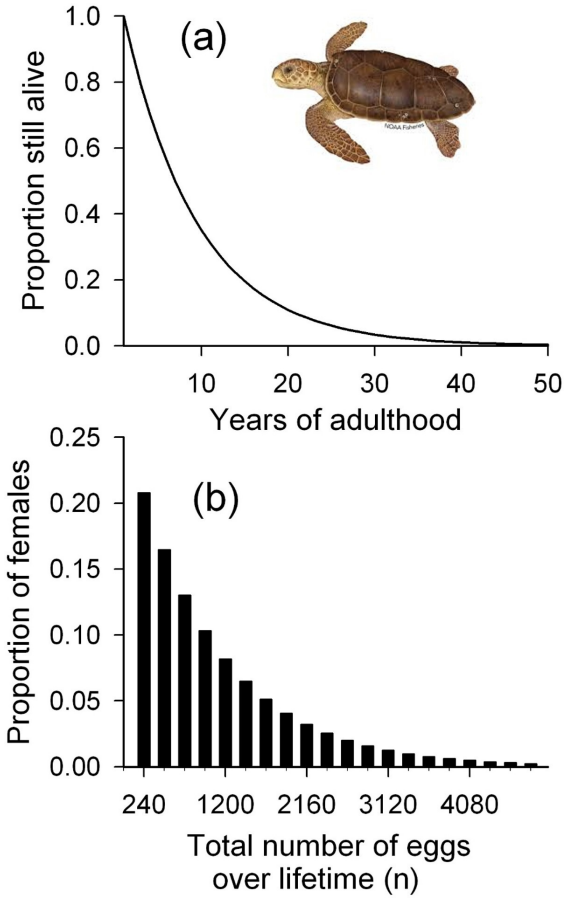

Figure 2. For loggerhead turtles in Greece, where mean annual adult female survival has been measured by photo identification at 0.89, graphs show (a) the proportion of females surviving for different lengths of time as adults and (b) the proportion of adult females that lay different number of eggs in their lives, assuming that the interval between breeding seasons is 2 years, 2 clutches are laid per breeding season and the mean clutch size is 120 eggs (see text for supporting references for these values). The mean and median number of eggs produced by a female in her lifetime can be calculated from the values in (b). The number of bars plotted is simply a reflection of the width of the bins. For example, the first bar includes more than just the turtles that die after one breeding season. In the model, the assumed maximum reproductive lifespan of adults was 60 years.

loggerhead turtles (*Caretta caretta*) nesting in Zakynthos, Greece. This is one of the largest loggerhead turtle rookeries in the Mediterranean [13]. The survival rate of adult females has been estimated from long-term mark–recapture studies based on photo identification as 0.89 (95% confidence interval 0.87–0.90) , i.e. if a female is alive at time t, then the probability she is alive at time $t + 1$ year is 0.89 [11]. From this value, we can estimate the proportion of turtles surviving different lengths of time once they are adults. For example, the probability of a female surviving for 2 years is 0.89^2, for 3 years is 0.89^3, etc. So there is, for example, a small probability that a female might survive as an adult for 15 years (i.e. 0.89^{15}, which equals 0.174), with this probability being supported by empirical observations [11] (figure 2a).

Loggerhead turtles nesting in Greece typically nest every 2 years (i.e. the modal remigration is 2 years) [11], the reported mean clutch size is 120 eggs [14], and the estimated mean clutch frequency in the Mediterranean in each year that an individual nests is 2 clutches per season [15]. So we can estimate the number of clutches laid by nesting females over their lifetimes. For example, of all females reaching adulthood, 0.11 (i.e. 1–0.89) are expected to breed in only 1 year before they die and so they will lay a mean of 2 clutches and 240 eggs, while a female surviving for 15 years as an adult (the probability of this occurring is 0.174) will be expected to breed in 7 seasons and lay 14 clutches and 1680 eggs. So some females will lay relatively few eggs before they die while others will live for longer as adults and lay more eggs. Across this range of adult lifespans we calculated both the mean and median number of eggs laid. Under this scenario, the mean number of eggs produced by a female in her lifetime is calculated as 1147 eggs, while the median number is 720 eggs (figure 2b), i.e. many turtles lay relatively few eggs while a few that survive for longer produce far more. The emergence

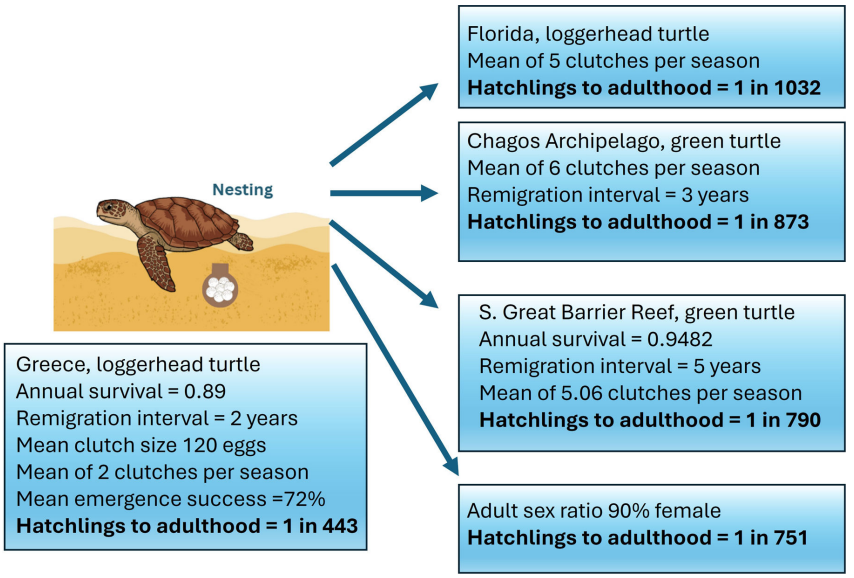

Figure 3. Examples of the sensitivity analysis to show how the estimate for the survival of hatchlings to adulthood will vary with life-history parameters that impact a female's lifetime reproductive output. From the starting point of parametrization of the model for loggerhead turtles in Greece, certain parameters in the model were varied in line with those measured for other species and populations. In each of these cases, the parameter that was changed is indicated. The aim was not to simulate every single possible combination of life-history parameters, but simply to show the range of hatchling survival estimates under some different scenarios.

success in Greece has been measured at 72% [16], so 1147 eggs will translate to 826 hatchlings (i.e. 0.72 × 1147). For two of these hatchlings to survive to adulthood to produce one adult female and one adult male, a survival of hatchlings to adulthood of 1 in 413 is necessary. With this model, we do not partition when the mortality occurs between hatching and adulthood, but rather simply the integrated mortality between these times.

4. Variation in adult survival rates, remigration intervals, clutch frequency and sex ratios

It might be expected that there are differences in adult survival rates between species and populations. For example, using titanium tags, from four studies with flatback turtles in Australia, a mean annual adult survival rate of 0.94 was estimated [10]. By contrast, annual adult survival rates for olive ridleys nesting in Mexico were estimated to be 0.48 using monel tags [10]. Furthermore, higher clutch frequencies have been estimated by satellite-tracking turtles, rather than relying on the incomplete coverage of foot patrols [17]. For example, for loggerhead turtles nesting in Florida and green turtles nesting in the Chagos Archipelago, modes of five and six clutches per season have been reported, respectively [17]. From flipper tagging, remigration intervals are well characterized across regions and populations, with remigration intervals of 2 to 4 years frequently being reported [18,19].

Reparametrizing the calculations for Greece, but assuming a mean of 5 clutches per season (i.e. the modal value reported for Florida), a survival rate to adulthood of 1 in 1032 hatchlings is generated. Assuming a mean of 6 clutches per season (i.e. the modal value for green turtles in the Chagos Archipelago) and a remigration interval of 3 years (i.e. the modal value for green turtles in the Indian Ocean), produces a survival rate of hatchlings to adults of 1 in 873. Substituting an annual adult survival value of 0.94 in the calculations for Greece, produces a survival rate of hatchlings to adults of 1 in 661. Another example using values for the southern Great Barrier Reef green turtles of annual adult survival of 0.9482 [20], a mean of 5.06 clutches per female per nesting season [21] and a remigration interval of 5 years [22] produces a survival rate of hatchlings to adults of 1 in 790.

For many sites around the world, skewed hatchling sex ratios have been estimated due to the combination of high incubation temperatures and temperature-dependent sex determination. For example, often hatchling sex ratios are around 90% female [23]. In this case, in a population when abundance is stable, each female needs to produce one hatchling that survives to be an adult female and 1 in 9 females needs to produce a hatchling surviving to be an adult male (i.e. a mean production

per female of 0.11 hatchlings surviving to be adult males). So for example, consider a population of 100 adults with 90% females, i.e. 90 adult females and 10 adult males. Together over their lifetimes those 90 females would then produce another 90 adult females and 10 adult males, keeping both the population and the sex ratio stable. So in this case, on average, each adult female produces 1.11 hatchlings surviving to adulthood. Reparametrizing the model for Greece with this value gives an estimated hatchling survival to adulthood of 1 in 751. Likewise, the same logic could be used to modify the hatchling survival estimate if there is a male bias in the adult population, which, although rare, might nonetheless occur. But again the survival rate of hatchlings to adulthood would remain within the same order of magnitude. We can combine some of the values that will produce the lowest hatchling survival from the above calculations, assuming an annual adult survival of 0.94, 6 clutches per season and a remigration interval of 2 years. This parametrization produces a mean of 5507 eggs produced over the lifetime of an adult female and hence 3965 hatchlings and so a survival to adulthood of hatchlings of 1 in 1983.

5. Discussion

Understanding how many hatchlings survive to adulthood is crucial for understanding sea turtle population dynamics. Our calculations based on empirical data for adult survival rates suggest the proportion of eggs surviving to adulthood for one well studied site is around 1 in 400. At sites where mature females produce more eggs during their lifetime this proportion might be as low as around 1 in 2000. Hence, we conclude that the popular reports of around 1 in 1000 hatchlings surviving to adulthood are broadly supported by empirical data.

The population trajectories of different species and populations of sea turtles around the world are highly variable with some stable populations, some increasing in size and some decreasing [24]. It might be expected that different survival rates of hatchlings to adulthood might contribute to these different population trajectories, but establishing this link has not yet been possible. Alternatively, it might be that the survival rate of adults might be a key driver of population trajectories, with for example, mortality of adult leatherbacks in fisheries bycatch thought to be a major contributor to their population declines in several parts of the world [2]. Identifying the life-history stages where high mortality is driving downward trajectories in nesting numbers, would clearly help triage key areas for conservation efforts.

The adult survival rate is clearly a huge driver in calculations of hatchling-to-adult survival rates. Put simply, if adults live for a shorter length of time, i.e. their reproductive lifespan is shorter, then a greater proportion of hatchlings need to survive to adulthood for population abundance to remain unchanged. We acknowledge that estimates of adult survival rates are often not robust. Others caution that survival rates are heavily impacted by methodological artefacts, with, for example, tags being lost leading to underestimates of adult survival [10]. In addition, even when tags are retained, mark–recapture studies may still underestimate annual survival because individuals may emigrate out of the study area. Emigration may happen from nesting beaches, since adults may nest on more than one beach (e.g. [17,25]) and also on foraging grounds, since individuals may relocate to new foraging grounds if conditions deteriorate [26]. Adult survival rate artefacts from tag loss are likely to be reduced in the mark–recapture study of loggerhead turtles breeding in Greece, since photo identification was used, which has been shown to have long-term reproducibility [11]. Further these estimates in Greece were derived from in-water studies in the area offshore from nesting beaches, so that any small changes in nesting beach fidelity (e.g. over the scales of a few 10 s of km) would likely have been unimportant. However, even in this example, larger scale breakdowns in nesting beach fidelity would have led to underestimates of adult survival.

In our sensitivity analysis, the highest annual adult survival we used was even higher than that measured in Greece (0.95 versus 0.89, respectively), suggesting that we were minimizing the underestimation of hatchling-to-adult survival rates. Moving forward, improvements to tagging methodology to increase tag retention will help improve survival estimates. For example, double (or indeed triple) tagging individuals and regular maintenance of the tags in the successive sightings will improve long-term identification of individuals [27]. Furthermore, estimation of tag loss (e.g. [28]) can be included in survival rate calculations. Recording 'tag scars', a sign of previous tagging, from each turtle will avoid wrongly identifying a turtle, which was previously tagged but the tag went lost, as a neophyte. Additionally, satellite tracking individuals, which is now reliable and fairly routine, will allow the extent of emigration from mark–recapture sites to be measured [29]. Long-term studies might

establish if egg production (e.g. clutch size, clutch frequency and remigration interval) of adult females continues at a constant level throughout their adult life or whether females start to show reproductive senescence at some point. If there is reproductive senescence so that the reproductive output of females declines in their adult lives, then the mean number of eggs produced by adults over their lives will be less than in our calculations and so the survival rate of hatchlings to adulthood will be higher than our estimates. However, there are few studies on reproductive senescence in turtles [30]. Future studies might also establish if there are sex-specific differences in hatchling survival rates to adulthood and how this rate varies across species and populations and over time (e.g. due to varying levels of threats [2], density-dependent processes or habitat suitability).

We have shown how variations in numerous factors such as adult survival rates, remigration intervals, clutch frequency per nesting season and emergence success influence mean adult reproductive output and hence the calculation of survival rate of hatchlings to adults. Improvements in the estimates for these parameters will allow refinements to be made for calculations of the proportion of hatchling surviving to adulthood. While information on modal remigration intervals and emergence success is widespread (e.g. [31]), there is still uncertainty over the mean number of clutches females lay per nesting season in many nesting beaches. This uncertainty stems from the fact that foot patrols, which are the typical way of observing nesting events, produce incomplete datasets if nesting females are not observed or identified every time they nest [17]. In this regard, satellite tracking has shown great utility for identifying nesting events and estimating clutch frequencies [17,32]. Our results also highlight how the median number of eggs laid over their adult lives by females may be much less than the mean number (i.e. a few adults that live for longer) contribute hugely to the mean number of eggs laid by females overall. This finding further highlights the key role of adult survival in driving the hatchling-adulthood survival estimate and how relatively few very long-lived females may be crucial to maintaining populations.

The factors that drive lifetime reproductive output of females likely vary across populations and species, and hence, it is likely that there is real variation in hatchling-to-adult survival rates across populations. For example, increased predator abundance or light pollution adjacent to nesting beaches is likely to increase hatchling mortality at some sites [33,34]. Hatchling fitness, and hence survival, may vary with incubation conditions [35]. Variation in annual adult survival rates are probably linked to different threats for different population and species. We have assumed that population size is stable. In many cases, nesting numbers around the world are either increasing or decreasing (e.g. [3]). Hatchling survival to adulthood may be insufficient to maintain population size where abundance is declining [36]. Where the adult survival rate is low (e.g. due to high levels of threats), then much higher survival rates of hatchlings to adulthood would be needed to maintain a stable adult population size but might be unattainable. For example, mortality of adult leatherback turtles is thought to be very high in some regions, due to fisheries bycatch [2] driving declines in abundance [24]. In the most extreme case, it might be that adults only breed in one season before dying. If this were the case for leatherbacks and their mean clutch size was 69 eggs per clutch and they lay 6 clutches per season [37] and the emergence success is 49% [38], then a female would only produce a mean of 203 hatchlings in her reproductive lifetime and so the survival of those hatchlings to adulthood would need to be 1 in 102 for population stability. It might be that such high rates of hatchling survival to adulthood are not possible, which is why leatherback populations with high adult mortality are in decline.

Conservation interventions can be an effective route to increasing adult survival rates. For example, conservation actions to reduce the harvesting of nesting loggerhead turtles in Cape Verde (Atlantic) have been implicated in the massive increase in nesting numbers that have probably made this site now the largest loggerhead turtle rookery in the world with many tens of thousands of nests each year [39,40]. In addition, other factors such as improved foraging conditions might drive population increases.

Where and when mortality occurs as hatchlings grow to adults is poorly known and requires further research effort. Presumably the risk of predation decreases as hatchlings grow to become juveniles and certainly hatchlings may be widely consumed by a range of birds and fish (e.g. [33]). Yet juveniles remain at risk both from predators, such as sharks, as well as anthropogenic mortality, such as through pollution or bycatch [2]. Furthermore, assembling key demographic parameters including clutch size, clutch frequency, hatching success and annual adult survival for of all seven marine turtle species might help improve the estimate of hatchling survival to adulthood across regions and species. It is important to stress that developing turtles face a large number of anthropogenic threats, such as pollution, climate warming and fisheries bycatch [2]. Future increases in the mortality might lead to decreases in the survival rate of hatchlings to adulthood and so contribute to losses of recruitment

and/or sea turtle declines in abundance. Hence, it is important to mitigate threats as much as possible [2] so that the survival rate of hatchlings to adulthood does not decline. Clutch size generally increases with body size in sea turtles, i.e. larger individuals lay bigger clutches and since adult turtles continue to grow, albeit slowly, older turtles will generally be bigger and so might be expected to lay more eggs per clutch than younger adults (e.g. [41]) if there is no reproductive senescence. In the future, our calculations might be improved by taking into account changing reproductive output with turtle age, but this improvement would not be easy to parametrize accurately with current knowledge.

In summary, while there is still uncertainty regarding the values for some life-history traits (e.g. annual adult survival rates), the popular reporting that around 1 in 1000 sea turtle hatchlings survives to adulthood is broadly comparable with our calculations based on the available empirical evidence. The approach of calculating mean adult reproductive output in order to shed light on offspring survival rates to adulthood probably has broad utility across reptiles and other taxa.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data are provided in the original papers cited in the manuscript.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. G.C.H.: conceptualization, formal analysis, funding acquisition, investigation, project administration, resources, visualization, writing—original draft; J.-O.L.: investigation, methodology, writing—review and editing; T.S.: conceptualization, investigation, methodology, resources, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Seminoff JA *et al*. 2015 Status review of the green turtle (*Chelonia mydas*) under the endangered species act. NOAA technical memorandum NMFS;NOAA-TM-NMFS-SWFSC, 539. See https://repository.library.noaa.gov/view/noaa/4922.
2. Fuentes M *et al*. 2023 Key issues in assessing threats to sea turtles: knowledge gaps and future directions. *Endang. Species. Res.* **52**, 303–341. (doi:10.3354/esr01278)
3. Mazaris AD, Schofield G, Gkazinou C, Almpanidou V, Hays GC. 2017 Global sea turtle conservation successes. *Sci. Adv.* **3**, e1600730. (doi:10.1126/sciadv.1600730)
4. National Ocean Service 2026 Sea turtles. See https://oceanservice.noaa.gov/news/june15/sea-turtles.html.
5. Hirth HF, Schaffer WM. 1974 Survival rate of the green turtle, *Chelonia mydas*, necessary to maintain stable populations. *Copeia* **1974**, 544. (doi:10.2307/1442553)
6. Casale P, Mazaris AD, Freggi D, Basso R, Argano R. 2007 Survival probabilities of loggerhead sea turtles (*Caretta caretta*) estimated from capture-mark-recapture data in the Mediterranean Sea. *Sci. Mar.* **71**, 365–372. (doi:10.3989/scimar)
7. Mortimer JA, Carr A. 1987 Reproduction and migrations of the Ascension Island green turtle (*Chelonia mydas*). *Copeia* **1987**, 103. (doi:10.2307/1446043)
8. Omeyer LCM, Casale P, Fuller WJ, Godley BJ, Holmes KE, Snape RTE, Broderick AC. 2019 The importance of passive integrated transponder (PIT) tags for measuring life-history traits of sea turtles. *Biol. Conserv.* **240**, 108248. (doi:10.1016/j.biocon.2019.108248)
9. Wyneken JE, Epperly SP, Higgins B, McMichael ER, Merigo CO, Flanagan JP. 2010 PIT tag migration in sea turtle flippers. *Herpetol. Rev.* **41**, 448–454.
10. Pfaller JB, Chaloupka M, Bolten AB, Bjorndal KA. 2018 Phylogeny, biogeography and methodology: a meta-analytic perspective on heterogeneity in adult marine turtle survival rates. *Sci. Rep.* **8**, 5852. (doi:10.1038/s41598-018-24262-w)
11. Schofield G, Klaassen M, Papafitsoros K, Lilley MKS, Katselidis KA, Hays GC. 2020 Long-term photo-id and satellite tracking reveal sex-biased survival linked to movements in an endangered species. *Ecology* **101**, e03027. (doi:10.1002/ecy.3027)
12. Mayne B, Tucker AD, Berry O, Jarman S. 2020 Lifespan estimation in marine turtles using genomic promoter CpG density. *PLoS One* **15**, e0236888. (doi:10.1371/journal.pone.0236888)
13. Margaritoulis D, Lourenço G, Riggall TE, Rees AF. 2022 Thirty-eight years of loggerhead turtle nesting in Laganas Bay, Zakynthos, Greece: a review. *Chel. Conserv. Biol* **21**, 143–157. (doi:10.2744/CCB-1531.1)
14. Hays GC, Speakman JR. 1991 Reproductive investment and optimum clutch size of loggerhead sea turtles (Caretta caretta). *J. Anim. Ecol.* **60**, 455. (doi:10.2307/5290)

15. Broderick AC, Glen F, Godley BJ, Hays GC. 2003 Variation in reproductive output of marine turtles. *J. Exp. Mar. Biol. Ecol.* **288**, 95–109. (doi:10.1016/S0022-0981(03)00003-0)
16. Hays GC, Speakman JR, Hayes JP. 1992 The pattern of emergence by loggerhead turtle (*Caretta caretta*) hatchlings on Cephalonia, Greece. *Herpetologica* **48**, 396–401.
17. Esteban N, Mortimer JA, Hays GC. 2017 How numbers of nesting sea turtles can be overestimated by nearly a factor of two. *Proc. R. Soc. B* **284**, 20162581. (doi:10.1098/rspb.2016.2581)
18. Hays GC. 2000 The implications of variable remigration intervals for the assessment of population size in marine turtles. *J. Theor. Biol.* **206**, 221–227. (doi:10.1006/jtbi.2000.2116)
19. Martins S, Cardona L, Abella E, Silva E, Loureiro NS, Roast M, Marco A. 2022 Effect of body size on the long-term reproductive output of eastern Atlantic loggerhead turtles *Caretta caretta*. *Endang. Species. Res.* **48**, 175–189. (doi:10.3354/esr01198)
20. Chaloupka M, Limpus C. 2005 Estimates of sex- and age-class-specific survival probabilities for a southern Great Barrier Reef green sea turtle population. *Mar. Biol.* **146**, 1251–1261. (doi:10.1007/s00227-004-1512-6)
21. Limpus CJ. 2009 *A biological review of australian marine turtles, vol. 2: green turtle* Chelonia mydas. Queensland, Australia: Queensland Environmental Protection Agency.
22. Limpus CJ, Eggler P, Miller JD. 1994 Long interval remigration in eastern Australia Chelonia (eds BA Schroeder, BE Witherington). In *Proceedings of the thirteenth annual workshop on sea turtle biology and conservation*, pp. 85–88. Miami, FL: National Oceanic Atmos. Admin.
23. Hays GC, Mazaris AD, Schofield G. 2014 Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Front. Mar. Sci.* **1**, 43. (doi:10.3389/fmars.2014.00043)
24. Hays GC, Schofield G, Papazekou M, Chatzimentor A, Katsanevakis S, Mazaris AD. 2024 A pulse check for trends in sea turtle numbers across the globe. *iScience* **27**, 109071. (doi:10.1016/j.isci.2024.109071)
25. Hart KM, Lamont MM, Sartain AR, Fujisaki I, Stephens BS. 2013 Movements and habitat-use of loggerhead sea turtles in the northern Gulf of Mexico during the reproductive period. *PLoS One* **8**, e66921. (doi:10.1371/journal.pone.0066921)
26. Shimada T, Limpus CJ, Hamann M, Bell I, Esteban N, Groom R, Hays GC. 2020 Fidelity to foraging sites after long migrations. *J. Anim. Ecol.* **89**, 1008–1016. (doi:10.1111/1365-2656.13157)
27. Fossette S *et al*. 2023 Reducing the impact of tagging on flatback turtles using double passive integrated transponder tags. *Chel. Conserv. Biol* **22**, 241–248. (doi:10.2744/CCB-1582.1)
28. Limpus CJ. 1992 Estimation of tag loss in marine turtle research. *Wildl. Res.* **19**, 457–469. (doi:10.1071/WR9920457)
29. Shimada T, Duarte CM, Al-Suwailem AM, Tanabe LK, Meekan MG. 2021 Satellite tracking reveals nesting patterns, site fidelity, and potential impacts of warming on major green turtle rookeries in the Red Sea. *Front. Mar. Sci.* **8**, 633814. (doi:10.3389/fmars.2021.633814)
30. Warner DA, Miller DAW, Bronikowski AM, Janzen FJ. 2016 Decades of field data reveal that turtles senesce in the wild. *Proc. Natl Acad. Sci. USA* **113**, 6502–6507. (doi:10.1073/pnas.1600035113)
31. Booth DT, Staines MN, Reina RD. 2022 Sand characteristics do not influence hatching success of nests at the world's largest green turtle rookery. *Aust. J. Zool.* **69**, 113–124. (doi:10.1071/ZO21050)
32. Tucker AD. 2010 Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: Implications for stock estimation. *J. Exp. Mar. Biol. Ecol.* **383**, 48–55. (doi:10.1016/j.jembe.2009.11.009)
33. Wilson P, Thums M, Pattiaratchi C, Whiting S, Pendoley K, Ferreira LC, Meekan M. 2019 High predation of marine turtle hatchlings near a coastal jetty. *Biol. Conserv.* **236**, 571–579. (doi:10.1016/j.biocon.2019.04.015)
34. Shimada T, Limpus CJ, FitzSimmons NN, Ferguson J, Limpus D, Spinks RK. 2023 Sky glow disrupts the orientation of Australian flatback turtles *Natator depressus* on nesting beaches. *Reg. Environ. Change* **23**, 20. (doi:10.1007/s10113-022-02014-x)
35. Booth DT. 2006 Influence of incubation temperature on hatchling phenotype in reptiles. *Physiol. Biochem. Zool.* **79**, 274–281. (doi:10.1086/499988)
36. Frazer NB. 1986 Survival from egg to adulthood in a declining population of loggerhead turtles, *Caretta caretta*. *Herpetologica* **42**, 47–55.
37. Tucker AD, Frazer NB. 1991 Variation in leatherback turtles, *Dermochelys coriacea*, at Culebra National Wildlife Refuge, Puerto Rico. *Herpetologica* **47**, 115–124.
38. Perrault JR, Miller DL, Eads E, Johnson C, Merrill A, Thompson LJ, Wyneken J. 2012 Maternal health status correlates with nest success of leatherback sea turtles (*Dermochelys coriacea*) from Florida. *PLoS One* **7**, e31841. (doi:10.1371/journal.pone.0031841)
39. Hays GC, Taxonera A, Renom B, Fairweather K, Lopes A, Cozens J, Laloë JO. 2022 Changes in mean body size in an expanding population of a threatened species. *Proc. R. Soc. B* **289**, 20220696. (doi:10.1098/rspb.2022.0696)
40. Laloë JO, Cozens J, Renom B, Taxonera A, Hays GC. 2020 Conservation importance of previously undescribed abundance trends: increase in loggerhead turtle numbers nesting on an Atlantic island. *Oryx* **54**, 315–322. (doi:10.1017/S0030605318001497)
41. Hays GC, Laloë JO, Seminoff JA. 2025 Status, trends and conservation of global sea turtle populations. *Nat. Rev. Biodivers.* **1**, 119–133. (doi:10.1038/s44358-024-00011-y)