Received: 1 July 2024 | Accepted: 22 April 2025

DOI: 10.1111/1365-2656.70093

BRITISH ECOLOGICAL SOCIETY Journal of Animal Ecology

RESEARCH ARTICLE

Does a lack of juveniles indicate a threat? Understanding body size distributions in a group of long-lived vertebrates

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Funding information
ARC Linkage; Arizona Game & Fish Department; Commonwealth Environmental Water Office; Department of Florida Fish and Wildlife; Felburn Foundation; Florida Department of Environmental Protection; Jane Fenwick Foundation; Kansas Department of Wildlife and Parks; National Science Foundation; New Mexico Department of Game and Fish; Office of Biological and Environmental Research; U.S. Department of Energy: Financial Assistant; Oklahoma Department of Wildlife Conservation; Texas Parks and Wildlife Department; Turtle Survival Alliance; United States Forest Service; University of New England Faculty of Science; Agriculture, Business and Law and the Commonwealth Environmental Water Office; Tiverton Agricultural Impact Fund; Winton Wetlands; Wodonga Council; Greening Australia; North East Water

Handling Editor: Xuan Liu

Abstract

1. Turtles are declining globally, and absences of juveniles during surveys are often interpreted as evidence of threats to early life stages. In Australia, for example, it is widely argued that a low number of juveniles is likely due to nest predation by introduced red foxes (*Vulpes vulpes*). However, small sample sizes within populations, low detectability of juveniles and turtles' long lifespans often confound the conclusion that a paucity of juveniles indicates a declining population. Because turtles have long reproductive lifespans, we might intuitively expect most turtle populations to be heavily weighted towards large individuals, but a 'typical' or 'healthy' size distribution for turtle populations has not been well established.
2. Therefore, we collated data on 41,021 freshwater turtles from 38 species and 428 populations located in parts of Australia both with and without introduced foxes, as well as populations in the United States of America, which naturally have raccoons (*Procyon lotor*), foxes and other nest predators. We examined population-level body size distributions to establish a baseline for 'typical' turtle populations and test whether populations that are exposed to introduced foxes have proportionately fewer juveniles compared to both AU populations that lack introduced foxes and USA populations that are naturally exposed to nest predators.
3. We found that most turtle populations in AU and the United States were heavily skewed towards adults and had few juveniles, regardless of the presence of foxes or other nest predators. There were, however, clear differences among population survey methods: those that target shallow areas (e.g. crawfish traps) tended

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to capture proportionately more juveniles, and small sample sizes (~<50) often produced inaccurate representations of size distributions. Additionally, we used a simulation to demonstrate that, given common turtle life history parameters, even stable populations should generally have low proportions of juveniles.

4. Based on our results, we encourage caution when interpreting turtle size distributions. A small number of juveniles does not inherently suggest that a population is declining due to high egg and/or juvenile mortality, and researchers should pay careful attention to the biases in their methods and strive to capture a minimum of 50–100 turtles before drawing inferences.

KEYWORDS
age, chelonian, conservation, declines, methods, sample size, turtles

1 | INTRODUCTION

For 220 million years, turtles have slowly ambled their way through history. Despite outliving mighty lineages such as the non-avian dinosaurs, turtles now face unprecedented threats, with precipitous declines in many species and nearly two thirds of extant species listed as threatened or endangered (Buhlmann et al., 2009; Lovich et al., 2018; Stanford et al., 2020). Habitat loss, overharvesting for food and pets, diseases, roads and introduced predators are all taking their toll on turtle populations (Chessman et al., 2020; Howell & Seigel, 2019; Stanford et al., 2020). There is a pressing need to gain a better understanding of threats to turtle populations so that further declines can be prevented and impacted populations can be restored.

Diagnosing declines in turtle populations is difficult because the historic data necessary to identify long-term trends are not available for many species. Indeed, given turtles' long lifespans and the enormous threats they have faced over the past century, it is often difficult to know if currently 'healthy' populations reflect historical abundances and demographics or simply represent shifting baselines over the course of a decline. In the absence of historic data, other metrics are needed. Turtle surveys have often concluded that populations are heavily shifted towards large adults with comparatively few juveniles, which has frequently been interpreted as evidence of ageing populations with little recruitment due to high nest and juvenile mortality (e.g. Browne & Hecnar, 2007; Chessman, 2011; Thompson, 1983). However, the question of what a 'healthy' or 'typical' body size distribution (or distributions) should look like has not been well addressed, making it difficult to interpret the size distributions of individual populations. Intuitively, we might predict that most turtle size distributions would naturally be skewed towards adults, with many eggs laid each year, followed by high nest mortality, high juvenile mortality that decreases each year until adulthood and low adult mortality (Bury, 1979; Iverson, 1991; Otten & Refsnider, 2024). For example, if a female matures at age 10, lives to age 40 and produces an average of 20 eggs a year, only two of the resulting 600 eggs need to survive to adulthood, on average, to maintain a stable population.

Wide-scale comparisons across many species can be a useful approach for providing baseline data on current-day turtle size distributions and the mechanisms influencing them, particularly if the suite of species includes variation in key threats to early life stages (e.g. nest predators). Turtles in Australia (AU) and the United States of America (USA) provide an excellent opportunity to apply this large-scale approach.

Australia is home to 25 native species of freshwater turtles, nearly half of which are considered threatened (Van Dyke et al., 2018). Much of the work in Australia has focussed on turtle populations in the Murray–Darling Basin (Bower et al., 2023), which have high rates of nest predation from invasive red foxes (*Vulpes vulpes*; introduced in the 1800s) and few juveniles compared to populations at Cooper Creek where *V. vulpes* are rare or absent (Thompson, 1983). It has been suggested that high rates of nest predation in the Murray–Darling Basin are causing the low number of juveniles (Thompson, 1983). Subsequent research has confirmed high levels of nest predation by foxes in the Murray–Darling Basin (Petrov et al., 2018; Spencer, 2002; Spencer et al., 2017), as well as comparatively higher numbers of juvenile turtles in Cooper Creek (McKnight et al., 2023). Further, the impact of nest predation on juvenile recruitment in the Murray–Darling Basin can be at least partially offset by releasing juveniles from protected nesting areas (Spencer et al., 2006). As a result, conservation measures have often included removing foxes by using poison baits or shooting them (Robley et al., 2016; Spencer & Thompson, 2005), protecting nests with fences, cages, or mesh covers (Campbell et al., 2020; Hughes et al., 2022; Streeting et al., 2023; Terry et al., 2023), and headstarting turtles in captivity (Spencer et al., 2017; Streeting et al., 2022).

While foxes certainly impact turtle nesting success and recruitment, the extent of their responsibility for declines in Australia's turtle populations has been questioned (Chessman, 2022). It is not known whether fox predation is added to predation by native predators (such as monitor lizards, bandicoots, echidnas and various birds) or has replaced native predators, resulting in no net change in nest destruction rates. Additionally, factors such as river regulation and threats to juveniles (e.g. predatory fish and degradation of water quality) also need to be considered (Campbell et al., 2020; Clark et al., 2009; Mathie & Franklin, 2006).

It is also noteworthy that in North America, predation rates on turtle nests from native predators (e.g. raccoons and foxes) are high, yet populations are able to persist (Chessman, 2022; Congdon et al., 1983, 1987). Geographic differences in native predation rates allow us to make broad comparisons between a region (USA) with abundant native nest predators (e.g. foxes and/or racoons), a region (southern AU) with abundant introduced nest predators (foxes) and a region (northern AU) without introduced foxes which is often presumed to have low nest predation rates (an assumption which requires testing).

Comparisons of studies, species and even long-term patterns within a site are complicated and often confounded. How should we interpret a study that documents a low number of juveniles? Does a dearth of juveniles indicate a declining population caused by increased mortality of nests and young turtles, a methodological artefact (Koper & Brooks, 1998; Mali et al., 2014; Ream & Ream, 1966; Tesche & Hodges, 2015), or is it typical for a turtle population? Perhaps populations with large numbers of juveniles (compared to adults) are aberrant and indicate high adult mortality from factors like recent overharvesting (*Dermatemys mawii*, for example; Ligon et al., 2019).

Determining whether low proportions of juveniles are indicative of high mortality rates at early life stages will help guide conservation plans and further our understanding of turtle ecology. To that end, we compiled a large dataset of turtle body sizes (41,021 individuals, 38 species, 203 sites and 428 populations) from across the United States of America (USA) and Australia (AU) to explore factors influencing the demographics of turtle populations cross-continentally. We were specifically interested in population-level patterns (e.g. the number of juveniles in a population relative to adults) rather than the factors affecting individual growth and body size within a population (Congdon et al., 2013, 2018; Congdon & van Loben Sels, 1993). Additionally, we constructed a simulation to examine how different life-history trait values influenced the relative abundance of juveniles in stable populations. Our goals were to (1) determine if there is a relative size distribution that represents a 'typical' turtle population and examine the life history factors influencing that distribution, (2) test the prediction that, due to their life history, most turtle populations would be heavily skewed towards adults, (3) use AU as a case study to test the proposal that a low proportion of juveniles is indicative of a decline caused by high egg and/or juvenile mortality, (4) test the effects of survey methods and aquatic habitat types on size distributions and the numbers of juveniles detected and (5) determine the sample size required for obtaining a reliable estimate of a population's size distribution.

2 | METHODS

2.1 | Simulating life history parameters

We wrote a simulation in R (v4.0.4; R Core Team, 2017) to examine the expected proportion of juveniles under different life history parameters (Supporting Information S1). The simulation takes the following parameters: eggs laid per female per year, egg survivorship, age at maturity, annual adult survivorship, maximum longevity and adult sex ratio. The model iteratively tests different rates of juvenile survivorship until it finds the survivorship rate that results in a stable population (i.e. a population that remains fixed at a given number of individuals) for a given set of parameters and returns the expected proportion of juveniles for that stable population. Turtles exhibit a Type III survivorship curve, with very low survivorship for hatchlings, with increasing, size-dependent survivorship as juveniles grow and high survivorship for adults (Iverson, 1991; Otten & Refsnider, 2024). To accurately reflect this age-specific increase in juvenile survivorship, the simulation increased the juvenile survivorship each year to the midpoint between the current juvenile survivorship and the adult survivorship (e.g. if adult survivorship was 0.900 and juvenile survivorship was 0.400 in year 1, then juvenile survivorship would increase to 0.650 in year 2, in year 3 it would increase to 0.775, etc.).

We ran this simulation on all combinations (15,625 total) of the following life history parameters: eggs laid per female per year = 5, 15, 25, 35, 45; egg survivorship = 0.05, 0.15, 0.25, 0.35, 0.45; age at maturity = 6, 9, 12, 15, 18; annual adult survivorship = 0.91, 0.93, 0.95, 0.97, 0.99; maximum age = 30, 45, 60, 75, 90; sex ratio (M:F) = 3:1, 2:1, 1:1, 1:2, 1:3. Note that for 383 of these combinations, no stable solution was possible, even with juvenile survivorship = 1. We chose these inputs to represent a large range of plausible turtle populations; however, the simulation is available as Supporting Information S1, and readers are encouraged to try additional inputs.

2.2 | Data collection and organization

We compiled a dataset by inviting researchers with empirically robust data on different species, locations, aquatic habitat types and capture methods to contribute datasets to this project (see Box 1: Terms and definitions; Supporting Information S2). If authors provided long-term, longitudinal data spanning multiple years, we only used the subset of consecutive years (usually ~3 years) containing the largest number of individuals. The decision on which years to use was based entirely on sample size, without first examining the size distributions. We attempted to gather relatively recent datasets, but we also included a few older sets to fill gaps in species or geographic coverage. On average (median), sampling efforts per population started in 2016 and ended in 2018 (full date range = 1996–2022). In nearly all cases, individual turtles were uniquely identified; therefore, only the size at the time of first capture was used in analyses (thus, the data points represent individuals, with one point per individual). Note that for models comparing methods, we used the size at first capture per method (thus, for those models, individuals could be included twice if they were captured by two methods). In total, we sampled 41,021 individuals, 38 species, 203 sites and 428 populations (Figure 1; Table 1).

BOX 1 Terms and definitions

- Country = Australia (AU) or the United States of America (USA)
- Country/fox category = Delineations within countries denoting whether foxes were often present in the general area. In AU, this category was crudely delineated as a single north/south split, with foxes generally absent (or at least rare) at the Cooper Creek sites and all sampled sites north of Rockhampton, and foxes generally present at sites south of those locations. This distinction was based on discussions among authors about observations in the areas of their sites and is in line with the fox density data presented by Stobo-Wilson et al. (2022). We used the following categories:
    - AU (foxes) = southern AU sites where foxes were likely present
    - AU (no foxes) = northern AU sites where foxes were absent or rare
    - USA = all sites in the United States (foxes and/or other mammalian predators were present throughout)
- Site = All sampling locations that were close enough together that a given species would be expected to regularly move among them (i.e. different sites represent different populations of a given species). Sites often included multiple sampling locations along a stretch of river as well as proximate land-locked bodies of water (e.g. farm ponds) that turtles migrate among. Sites often contained multiple species.
- Region = Broad geographical areas. Within species, there was often high variation in maximum body sizes among regions, with low variation within regions.
    - Within AU, regions were based on the Australian Bureau of Meteorology Topographic Drainage Divisions and River Regions (http://www.bom.gov.au/water/about/riverBasinAuxNav.shtml) with the exception of the Murray–Darling Basin, which we subdivided into Upper and Lower basins (see Figure 1)
    - Within the United States, sites were clumped into widely spaced clusters. Therefore, regions were generally defined as states. In two cases, several states were lumped together due to proximate sites on either side of state borders (Kansas, Oklahoma, and Texas, were lumped together as a region, and Arizona and New Mexico were lumped together; see Figure 1).
- Population = All individuals of a given species at a given site.
- Species = Throughout, we referred to species without the specification of subspecies (unless otherwise noted) and followed the official taxonomic list provided by the Australian Society of Herpetologists (2023) for AU taxonomy and the Turtle Taxonomy Working Group Checklist (Rhodin et al., 2021) for USA taxonomy.
- Capture method = Broad method of capture for a given turtle. In some cases, similar trap designs were combined into a single category.
    - Hand = Turtles captured by a means other than a trap or snorkelling (e.g. dip netting, captured crossing a road, grabbed while wading through a wetland, etc.).
    - Snorkelling = Using a mask and snorkel to free-dive for turtles (a.k.a., 'water goggling'; Marchand, 1945).
    - Crawfish traps = Small, fine-mesh traps designed for capturing bait such as crawfish and minnows, typically placed in very shallow water (e.g. collapsible spring traps such as those made by Promar® and Drasry®; Brown, 2023; Howell et al., 2016; McKnight et al., 2015).
    - Cathedral nets = Any form of tall net with openings near the bottom attached to a large 'snorkel' section to allow turtles to breathe. These traps were typically either upheld by floats or suspended from structures such as branches. 'Cathedral nets' included both traps that were simple crab pots attached to a vertical column of mesh (Kuchling, 2003) and more complicated traps that included a second vertical funnel and/or telescoping rings forming a vertical column.
    - Hoop nets = Traps with circular, square, or diamond-shaped mesh (typically 2.54 × 2.54 cm or smaller) supported by circular or D-shaped rings (typically 0.5–1 m diameter) containing one or two funnel-shaped horizontal openings (a.k.a. drum nets; Lagler, 1943; Legler, 1960). Hoop nets were placed horizontally in water that was typically shallow enough to provide access to air. We excluded all nets with a 'wing' or 'lead' from this category (see Fyke nets). Hoop nets generally included only one throat, but sometimes nets with two throats in a series were used. Hoop nets were generally, but not always, baited.
    - Fyke nets = Similar to hoop nets but contained at least one 'wing' or 'lead' (i.e. a large wall of vertical mesh [aquatic drift fence] that extended from the trap and guided animals into the mouth of the trap [Vogt, 1980]). Both traps with a single lead and traps with two leads oriented in a 'Y' were included as 'fyke nets' (sometimes two fykes were placed at opposite ends of leads). Fyke nets generally, but not always, included at least two throats in series. Fyke nets were generally (but not always) baited.
    - Crab pot = Low, flat traps with multiple openings leading into a single rectangular or cylindrical compartment. These were often fully submerged and checked regularly.

BOX 1 (Continued)

- Water body type = Broad categories used to group bodies of water by their habitat type. Due to the large number of sites used in this study (and the frequent presence of multiple proximate bodies of water), these categories are necessarily crude.
    - Rivers (perennial) = Flowing bodies of water that generally contained water year-round (contrast with Intermittent).
    - Intermittent = Seasonal creeks and rivers that frequently dried to disconnected water holes (e.g. many desert systems).
    - Floodplain wetlands = Lentic oxbows and other side channels directly connected to rivers at least seasonally. Sometimes vegetated.
    - Lakes and ponds = Lentic bodies of water that were disconnected from main rivers (with the exception of reservoirs formed by damming rivers), including farm ponds and heavily vegetated areas such as beaver ponds, swamps and marshes.

2.3 | Analysis—Overview

We primarily used two metrics to assess size distributions: straight line carapace length (CL) and the proportion of a population sample consisting of juveniles ('proportion of juveniles'). Comparing CL across species and populations is inherently challenging because species vary widely in size, and even within a species, there is often geographic variation. Further, different species exhibit differing levels of sexual dimorphism, and for genera such as *Graptemys* and *Apalone*, a small size distribution could indicate a large number of males, rather than a population dominated by juveniles. To account for size differences among species, regions and sexes, for each species within each region, we standardized (transformed) CL into a 'proportional CL' (relative to the largest individuals). We standardized by dividing the CL of each individual by the size of the *n*th quantile individual. Quantiles ranged from 96 to 99.5 and were selected based on sample size; large sample sizes often had outliers that would artificially skew the proportional distributions and, therefore, required the use of higher quantiles. We used simulations to calculate a regression between sample size and the appropriate quantile (see Supporting Information S3). Thus, all individuals were scored as ~0–1 (individuals above the *n*th quantile were slightly higher than 1). Transformations were performed separately for males and females, with juveniles included with the smaller sex (usually males). This transformation procedure, including examples showing why it is necessary and how it works, is extensively explained in Supporting Information S3. Additionally, population size distributions based on the original CL values are presented for each species in Supporting Information S4.

Proportional CLs were analysed using linear models (each individual was a data point). A power transformation was necessary to meet model assumptions, and for each model, we used the *transformTukey* function from the rcompanion package (v2.4.1; Mangiafico, 2021) to identify the best value ('lambda'; usually between 2 and 3) by which to raise the response variable (proportional CL).

In most turtle species, only males develop external sexual dimorphisms (e.g. enlarged tails). Therefore, we categorized all individuals smaller than the third smallest male (per species per region) as 'juveniles' and classified all other individuals as 'adults'. We acknowledge that this is a simplification, and the 'adult' category likely contained sub-adult males that have large tails but are not yet mature as well as immature females that mature several years after males mature. Ideally, these 'adult' and 'juvenile' categories would be based on the average age at maturity per population (see Georges et al., 2006). However, age data were not available for most populations; therefore, we used the simplification of assigning age categories based on size at the development of male secondary sexual dimorphisms to provide a point of comparison that was measurable per species per region. Additionally, this is the definition of 'juvenile' that is frequently used in the turtle literature, including in important papers on turtle declines and low numbers of juveniles (e.g. Campbell et al., 2020; Chessman, 2011). For statistical analyses, proportions of juveniles were assessed using binomial models (each individual was a data point scored as 0 [adult] or 1 [juvenile]).

Initial analyses suggested that small sample sizes often gave misleading results (i.e. when subsampling datasets, small samples often deviated strongly from the results consistently obtained by using larger samples; see results). Therefore, for all analyses (unless otherwise noted), we only used datasets (populations) with ≥50 captured individuals, resulting in a total of 36,806 individuals, 34 species, 108 sites and 157 populations (Table 1). Additional plots including all individuals (regardless of sample size) are available in Supporting Information S4.

We used R (v4.0.4; R Core Team, 2017) for all analyses, used the lme4 package (v1.1–26; Bates et al., 2015) for mixed effects models, assessed significance with the car package using a type II sums of squares (v3.0–1.0; Fox & Weisberg, 2011), checked model fits with the performance package (v0.8.0; Lüdecke et al., 2021), calculated fitted effects with the effects package (v4.2–0; Fox & Weisberg, 2011) and made plots using ggplot2 (v3.3.5; Wickham, 2016). For the sake of readability, we have presented limited details on the models and their outputs in the text, but additional information is available in Table 2, the figures, and Supporting Information S4. We have adopted the 'language of evidence' throughout and will use terms such as 'strong evidence' and 'little evidence' rather than relying strictly on $\alpha = 0.05$ as an arbitrary cut off (Muff et al., 2022); however, p values and other statistical outputs are presented in Table 2.

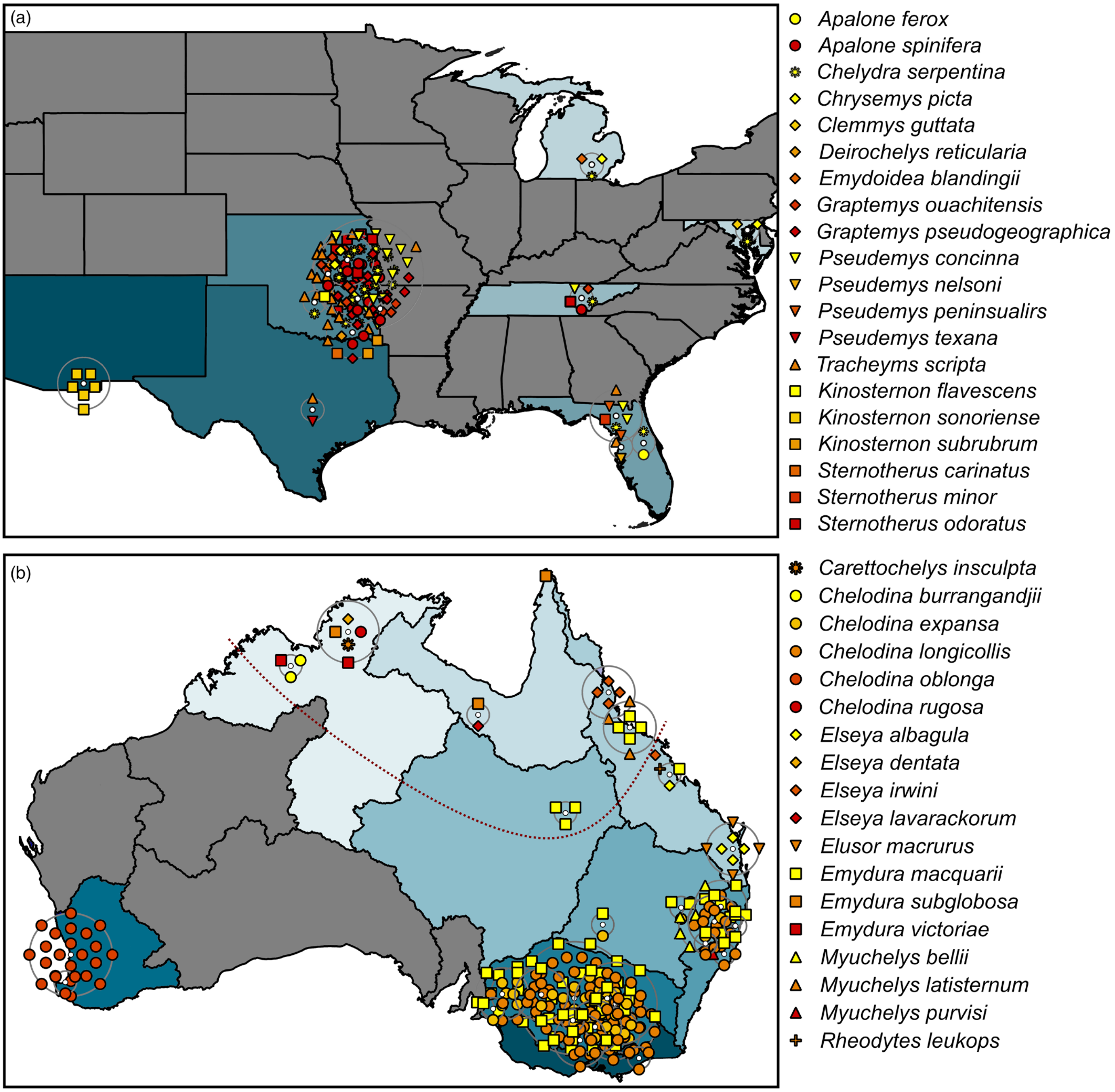

FIGURE 1 Map of species and locations sampled. Each 'region' used in statistical models is shown in a different shade of blue (regions we did not sample are shown in grey). In the United States of America (a), regions were based on states, with some states combined due to study sites on either side of the border, and in Australia (b) regions were defined based on river major drainage basins. The curved, dotted red line separates the sites that we included in the 'AU foxes' category (south) and 'AU no foxes' category (north). In many cases, multiple species were sampled at a site and/or multiple sites were in such close proximity that they would overlap on the map; these are lumped into concentric rings, with a small white dot in the centre and a thin grey line connecting the points on the outer ring. Enlarged subsections are presented in the Supporting Information S4: Figures S1–S4.

2.4 | Analysis—Effects of sample size

To examine the effects of sample size on inferences about population size distributions, we selected the five AU species (regardless of presence or absence of foxes) and the five USA species with the largest available datasets (populations). For each dataset, we then made 200 random samples at each interval between 10 and 200 individuals (e.g. 200 samples of 10 individuals, 200 samples of 11 individuals, etc.). Sampling was done with replacement (thus, the original population was treated as a size distribution). For each sample, we calculated the median and skew and plotted the results (Figure 2). Additionally, for hypothetical populations that consisted of 1%–10%, 15%, 20% and 25% juveniles, we calculated the probability of detecting zero juveniles in samples ranging from 10 to 200 individuals (Figure 3).

TABLE 1 Species sampled.

			All			Pops with $N \geq 50$		
Country/fox	Family	Species	*N* (CL)	*N* (age)	Pops	*N* (CL)	*N* (age)	Pops
AU (foxes)	Chelidae	*Chelodina expansa*	1039	1051	48	555	560	7
	Chelidae	*Chelodina longicollis*	4871	4887	98	4001	4014	26
	Chelidae	*Chelodina oblonga*	3395	3395	25	3161	3161	19
	Chelidae	*Elseya albagula*	337	338	4	259	260	2
	Chelidae	*Elusor macrurus*	359	359	4	359	359	4
	Chelidae	*Emydura macquarii*	3406	3435	67	2550	2578	19
	Chelidae	*Myuchelys bellii*	1921	1921	5	1842	1842	2
	Chelidae	*Myuchelys purvisi*	46	46	1	0	0	0
AU (no foxes)	Carettochelyidae	*Carettochelys insculpta*	341	341	1	341	341	1
	Chelidae	*Chelodina burrangandjii*	76	77	2	0	0	0
	Chelidae	*Chelodina rugosa*	71	74	1	71	74	1
	Chelidae	*Elseya albagula*	23	23	1	0	0	0
	Chelidae	*Elseya dentata*	115	116	1	115	116	1
	Chelidae	*Elseya irwini*	811	811	5	780	780	4
	Chelidae	*Elseya lavarackorum*	117	118	1	117	118	1
	Chelidae	*Emydura macquarii*	952	961	8	856	865	4
	Chelidae	*Emydura subglobosa*	177	183	3	97	97	1
	Chelidae	*Emydura victoriae*	216	224	2	216	224	2
	Chelidae	*Myuchelys latisternum*	291	291	3	225	225	1
	Chelidae	*Rheodytes leukops*	24	24	1	0	0	0
USA	Chelydridae	*Chelydra serpentina*	880	886	22	728	733	6
	Emydidae	*Chrysemys picta*	1359	1365	8	1347	1353	3
	Emydidae	*Clemmys guttata*	116	117	1	116	117	1
	Emydidae	*Deirochelys reticularia*	111	111	1	111	111	1
	Emydidae	*Emydoidea blandingii*	132	132	1	132	132	1
	Emydidae	*Graptemys ouachitensis*	1097	1101	14	860	864	4
	Emydidae	*Graptemys pseudogeographica*	484	485	12	391	392	2
	Emydidae	*Pseudemys concinna*	681	683	16	560	562	3
	Emydidae	*Pseudemys nelsoni*	41	41	1	0	0	0
	Emydidae	*Pseudemys peninsularis*	112	112	2	108	108	1
	Emydidae	*Pseudemys texana*	368	368	1	368	368	1
	Emydidae	*Trachemys scripta*	11,612	11,689	26	11,497	11,574	21
	Kinosternidae	*Kinosternon flavescens*	91	95	1	91	95	1
	Kinosternidae	*Kinosternon sonoriense*	996	996	6	996	996	6
	Kinosternidae	*Kinosternon subrubrum*	835	844	2	820	829	1
	Kinosternidae	*Sternotherus carinatus*	145	146	1	145	146	1
	Kinosternidae	*Sternotherus minor*	69	69	1	69	69	1
	Kinosternidae	*Sternotherus odoratus*	1613	1616	9	1535	1538	3
	Trionychidae	*Apalone ferox*	106	106	1	106	106	1
	Trionychidae	*Apalone spinifera*	1375	1384	21	1090	1099	4

Note: All = sample sizes based on all available data. 'Pops with $N \geq 0$' = sample sizes using only the subset of populations with data for ≥50 individuals. *N* (CL) = number of individuals sampled for carapace length. *N* (age) = number of individuals that could be assigned to juvenile or male/female. Pops = number of populations (sites) sampled per species.

2.5 | Analysis—Country/fox categories

We visualized the data by constructing density plots of proportional carapace length for populations and species within each country/fox category (Figure 4) and for the four species with the most data from AU (foxes) and the United States (Figure 5). See Box 1 for how areas with and without foxes were delineated.

We used mixed effects models and all available data (for populations with ≥50 data points) to provide broad comparisons of the United States, AU (foxes) and AU (no foxes). These models (linear for CL and binomial for proportions of juveniles) included the country/fox category as a fixed effect and species, water body type, capture method and site (nested in region) as random effects. We included water body type and capture method as random effects because the

TABLE 2 Sample sizes and model outputs for subsets used in pairwise comparisons.

Comparison	*N*	Species	Sites	Pops	CL mean (SD)	CL (*p*)	CL est. (95% CI)	Prop. J. mean (SD)	Prop. J. (*p*)	Prop. J. est. (95% CI)
AU (no foxes)	2818	9	11	16	0.72 (0.23)	0.934	–	0.25 (0.18)	0.098	–
AU (foxes)	12,727	7	63	79	0.77 (0.13)			0.11 (0.11)		
USA	20,801	19	34	62	0.72 (0.17)			0.11 (0.12)		
AU (no foxes)	700	4	5	7	0.76 (0.18)	0.324	−0.08 (−0.25–0.08)	0.17 (0.12)	0.141	−0.82 (−1.97–0.36)
AU (foxes)	7549	5	42	54	0.77 (0.12)			0.07 (0.09)		
USA	3797	11	3	14	0.70 (0.17)	0.167	−0.10 (−0.24–0.05)	0.11 (0.09)	0.696	0.31 (−1.21–2.03)
AU (foxes)	4478	7	45	57	0.76 (0.14)			0.14 (0.13)		
AU (no foxes)	1683	8	9	13	0.74 (0.21)	0.197	−0.16 (−0.41–0.07)	0.26 (0.16)	0.936	−0.05 (−1.55–1.39)
USA	1225	6	5	8	0.71 (0.22)			0.20 (0.19)		
Lake/pond	5898	3	17	18	0.67 (0.17)	**<0.001**	−0.14 (−0.21 – −0.08)	0.10 (0.10)	**0.002**	1.71 (−2.49 – −0.01)
River	5127	3	13	14	0.76 (0.15)			0.03 (0.04)		
Hand	127	3	2	3	0.65 (0.24)	**<0.001**	−0.09 (−0.13 – −0.04)	0.38 (0.18)	**<0.001**	1.12 (0.68–1.56)
Fyke	627				0.74 (0.16)			0.2 (0.06)		
Hand	537	3	5	6	0.55 (0.28)	**<0.001**	−0.12 (−0.15 – −0.08)	0.46 (0.15)	**<0.001**	0.90 (−0.61 – −1.20)
Hoop	372				0.71 (0.16)			0.22 (0.12)		
Crawfish	529	3	1	3	0.69 (0.2)	**0.007**	−0.03 (−0.06 – −0.01)	0.18 (0.16)	**<0.001**	0.73 (0.40–1.06)
Fyke	2445				0.69 (0.16)			0.09 (0.06)		
Crawfish	740	3	4	6	0.63 (0.21)	**<0.001**	−0.13 (−0.15 – −0.11)	0.2 (0.13)	**<0.001**	1.25 (0.99–1.51)
Hoop	3601				0.68 (0.17)			0.07 (0.05)		
Hoop	2164	11	3	12	0.7 (0.18)	0.288	0.01 (−0.01–0.02)	0.14 (0.13)	0.252	0.11 (−0.08–0.29)
Fyke	3666				0.7 (0.17)			0.14 (0.12)		
Fyke	1547	4	11	12	0.69 (0.2)	**<0.001**	−0.04 (−0.5 – −0.02)	0.13 (0.19)	**<0.001**	0.88 (0.63–1.12)
Cathedral	3987				0.79 (0.12)			0.07 (0.10)		
Snorkel	154	3	2	3	0.8 (0.19)	0.788	0.01 (−0.04–0.06)	0.22 (0.18)	0.081	0.54 (−0.07–1.15)
Cathedral										

Note: For the country/fox subsets: 'AU (no fox) vs. AU (foxes)' used cathedral nets, 'AU (foxes) vs. USA' used fyke nets, and 'AU (no foxes) vs. USA' used snorkelling. CL = proportional carapace length, Prop. J. = proportion of juveniles, est. = model estimate, 95% CI = 95% confidence interval around the model estimate. For each comparison of two groups, the group (location, water body type, or method) with the highest proportion of juveniles (in the fitted model estimates) is listed first, and the estimated effect sizes and CIs are shown for that group relative to the other (i.e. a negative CL est. and a positive Pro. J. est. means that the group on top had smaller mean body sizes and a higher proportions of juveniles). Note that original *p* values are shown, but patterns of significance do not change even if a sequential Bonferroni correction is applied liberally to all tests within each section. Statistically significant results are shown in bold.

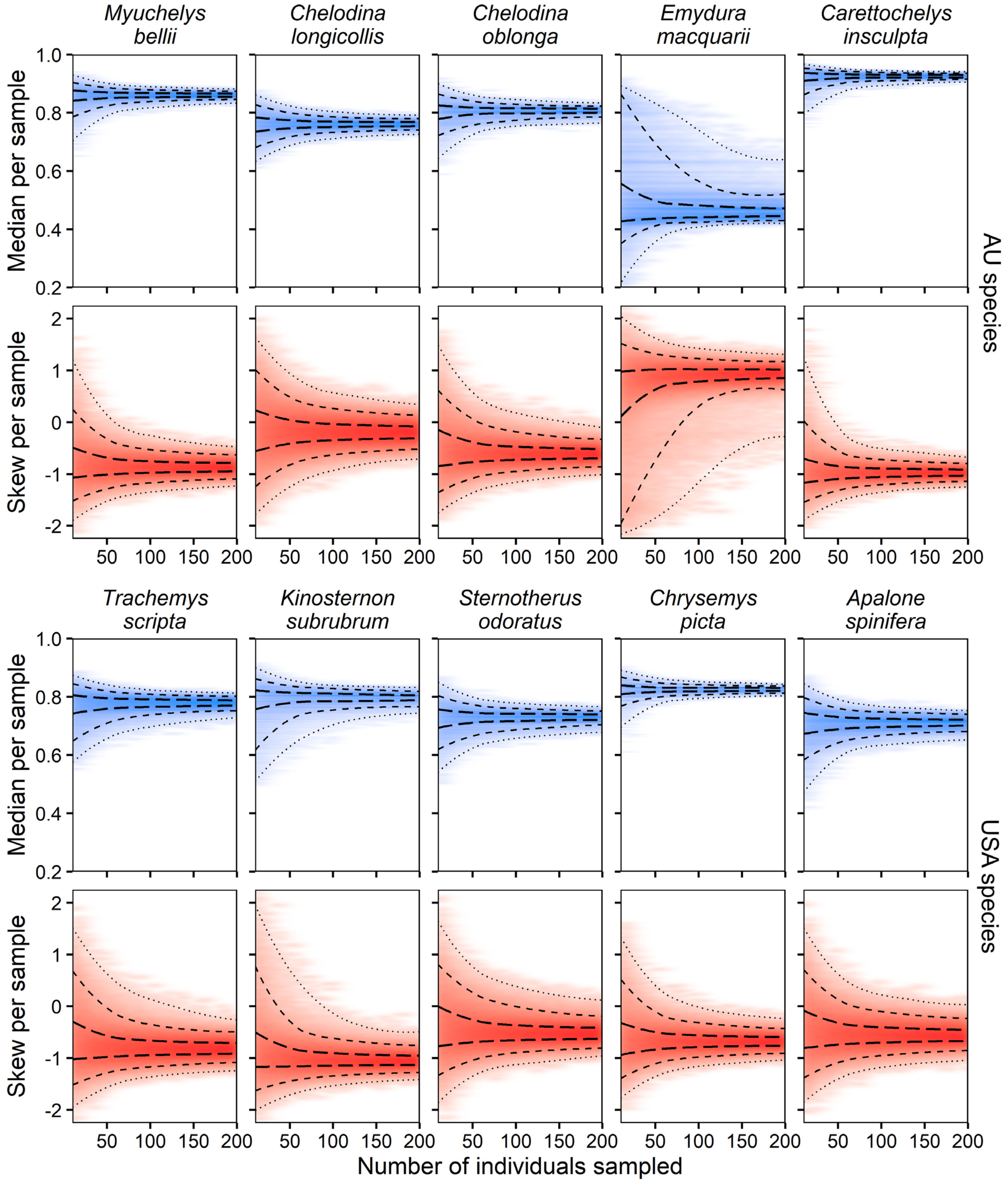

FIGURE 2 Results from randomly resampling the species (one population per species) with the largest sample sizes (for AU [regardless of fox status] and the USA). Each species was randomly sampled 200 times at each one-unit interval from 10 to 200 samples (e.g. 200 samples of 10, 200 samples of 11, etc.). Each point is a median (blue) or skew (red) from one of the random samples (i.e. random populations). Points were set with a transparency; thus, darker regions indicate a higher density of points. Lines represent smoothed general additive models (via geom_smooth()) for the interquartile range (25th and 75th quantile; long dashes), 2.5th and 97.5th quantile (short dashes) and minimum and maximum values (dotted lines) for the skews or medians of all random samples. Note that some points fall outside of the minimum and maximum lines, because they are smoothed regression lines, not boundary lines. The *Emydura macquarii* data shown here are from the Cooper Creek population (*E. m. emmotti*).

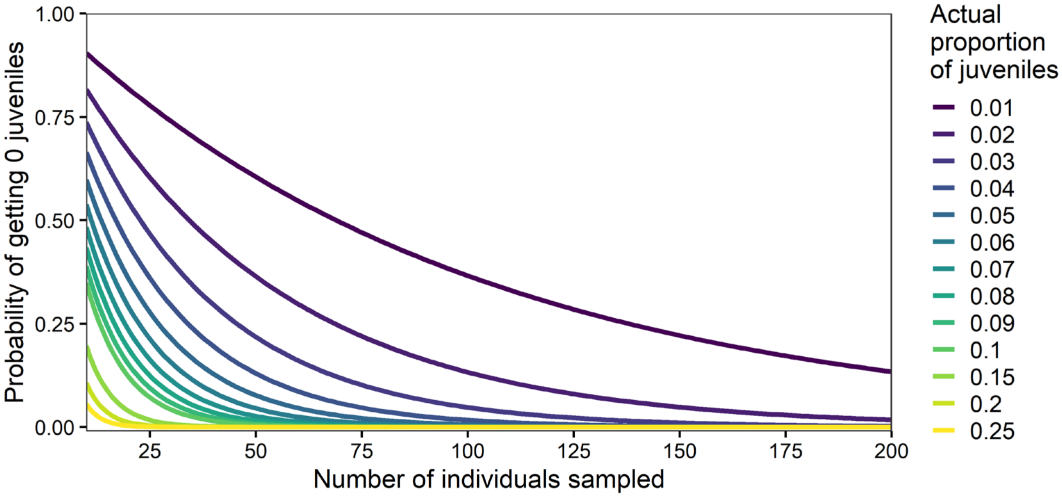

FIGURE 3 Curves showing the relationship between sampling effort and the probability of failing to detect any juveniles (false negative) for populations with proportions of juveniles ranging from 0.01 to 0.25. Note that this assumes equal catchability between adults and juveniles. In reality, juveniles probably have lower catchability, which will increase the probabilities of failing to detect them.

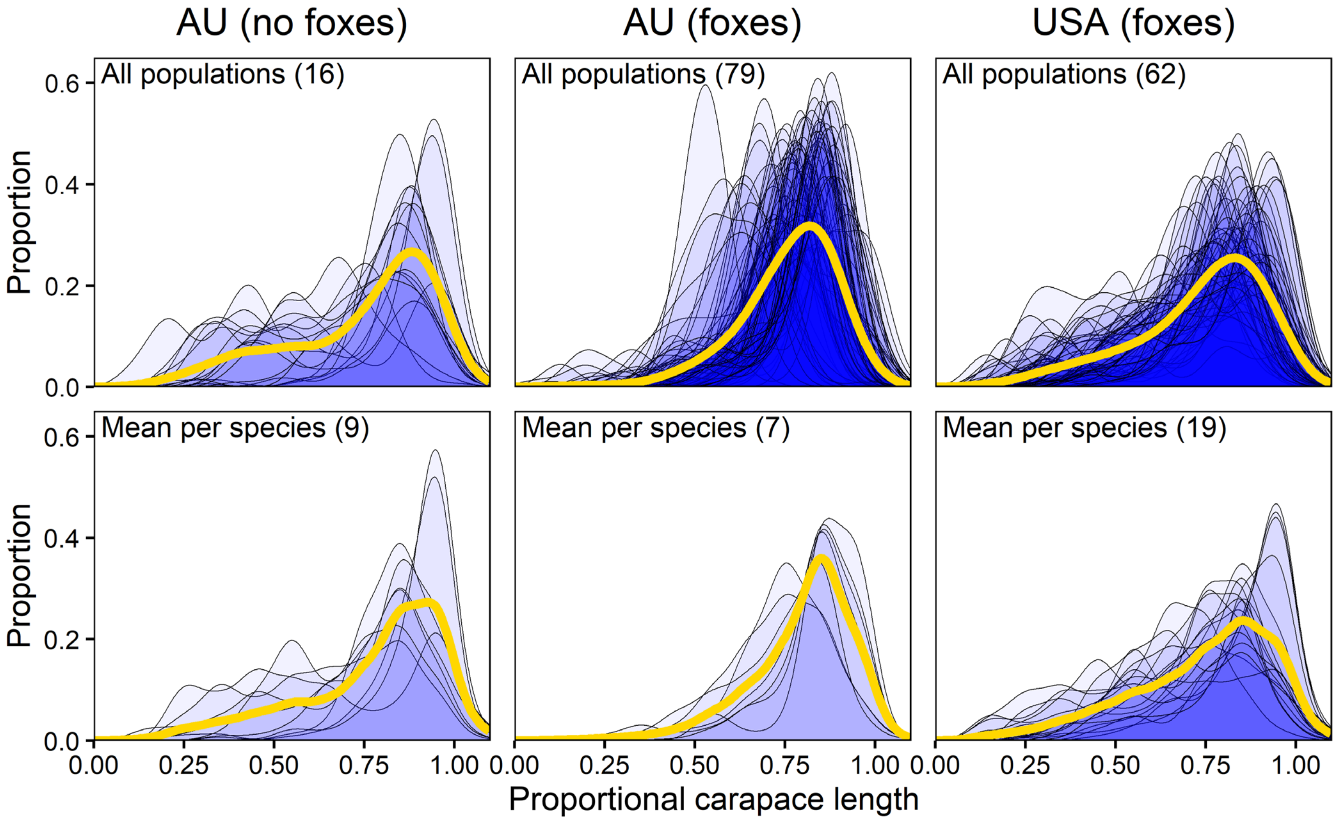

FIGURE 4 Density curves (smoothed histograms) showing the size distributions for all turtle populations where ≥50 individuals were sampled. The first row shows a curve per population (thin black lines), and the second row shows a curve per species (all populations averaged; thin black lines). In both cases, the thick yellow lines represent the mean of all thin black lines (mean of all populations or mean of species means). Numbers in parentheses show the sample sizes. All individuals were scaled based on the sizes of the largest individuals of that species in that region (proportional carapace length) to allow comparisons across species and populations. Data are presented for Australia (no foxes), Australia (with foxes), and the United States of America (with foxes).

spread of data across species, sites and countries was inconsistent enough that we were not justified in drawing any conclusions from those comparisons (e.g. crawfish nets were only used in the United States whereas cathedral nets were only used in AU). Therefore, we also ran similar models on a series of pairwise subsets (see sections below).

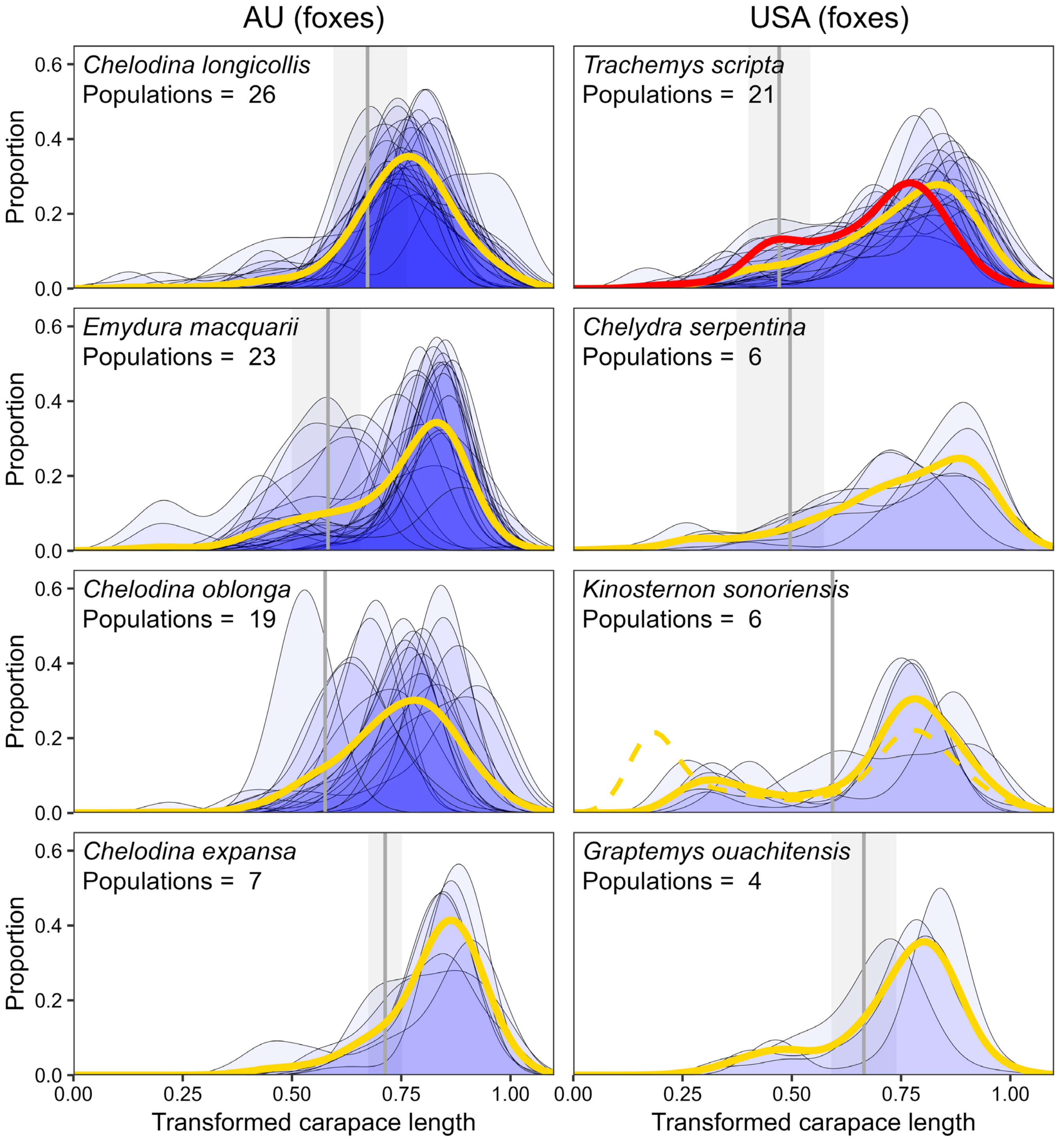

FIGURE 5 Density plots of turtle size distributions (displayed as proportions of individuals on the *y*-axis) for the four species in the United States of America (USA) and Australia (AU foxes) with the most populations with data for ≥50 individuals. Only populations with data for ≥50 individuals are shown. Each blue curve (with a thin black line) is a single population, and the solid yellow lines show the mean across all populations (calculated as the mean of the density curves per population to account for sample size differences). The shaded vertical grey bar indicates the ranges for the size below which turtles were considered juveniles (different values for different regions), and the dark vertical line shows the means of those values. For *T. scripta*, the red line shows the values for a population sampled by Cagle in 1941 in Illinois, USA (*N* = 1201; Cagle, 1950). This population was not included in the calculation of the mean line. For *K. sonoriense*, researchers were sometimes present as hatchlings were emerging, resulting in high numbers of hatchlings. The solid line and population curves show the data with the hatchlings excluded, and the dashed yellow line shows the mean with the hatchlings included. Density plots for all 38 species are available in Supporting Information S4.

To ensure that we had adequately compensated for methodological differences in our analyses of country/fox categories, we also ran the same models above on three methodological subsets: fyke nets (AU [with foxes] vs. USA), cathedral nets (AU [with foxes] vs. AU [no foxes]), snorkelling (AU [no foxes] vs. USA; Table 2). For each test, it was only possible to compare two country/fox categories at a time due to a lack of data from the third category. The models were constructed as before except that capture method was not included (because each model was run on a single method) and water body type was not included (because either all the data came from one water body type or including it resulted in a singular model fit).

2.6 | Analysis—Capture methods

We made pairwise comparisons among methods by subsetting to populations where two methods were used and each method captured ≥25 individuals (thus ≥50 total). We were forced to use this more relaxed threshold due to sample size limitations. We only performed pairwise comparisons for pairs of methods where at least three species (across sites) passed these filtering requirements. For each pair of methods, we used the same pair of models as before, but only species and site were included as random effects (there were insufficient data to fit additional random effects). We made the following pairwise comparisons: hands versus fyke nets, hands versus hoop nets, crawfish nets versus fyke nets, crawfish nets versus hoop nets, fyke nets versus hoop nets, fyke nets versus cathedral nets, snorkelling versus cathedral nets (see Table 2). Crab pots had insufficient sample sizes for comparisons. Finally, we examined trends in capture method usage among areas by looking at the number of sites at which each method was used.

2.7 | Analysis—Water body types

To examine the effects of water body types, we subset the data within each region to species where ≥50 individuals each were captured by the same method in at least two types of bodies of water (e.g. if a species had ≥50 individuals from fyke nets at a river and ≥50 individuals from fyke nets at a lake or pond within a region, it would be included). Only two water body types (rivers and lakes/ponds) and three species passed this filtering. We used the same pairs of models as before (CL and proportion of juveniles), but only species and site were included as random effects.

3 | RESULTS

3.1 | Effects of sample size

Randomly resampling our largest populations showed that small sample sizes often produced misleading representations of population size distributions (Figure 2), and samples of ~50–100 individuals were generally needed for reliable results. Further, small sample sizes often resulted in high probabilities of failing to document any juveniles even though some were present (i.e. they produced false negatives; Figure 3).

3.2 | Simulation results

In general, our simulations suggested that most turtle populations should consist predominantly of adults (Figure 6). While there was a large pulse of juveniles immediately after hatching, high mortality rates in the first year quickly reduced juvenile numbers, and when looking at turtles that were at least 1 year old, the proportion of juveniles was less than 0.5 in 88.1% of all life history parameter combinations. Further, instances of stable populations with high proportions of juveniles generally occurred on the extreme ends of turtle life history values, such as low adult survival and few eggs laid per year (resulting in very high juvenile survivorship to achieve a stable population), whereas more 'typical' turtles generally had low proportions of juveniles (Figure 6).

When comparing the effects of each parameter on the proportion of juveniles, maximum age and sex ratio had relatively small effects, while, unsurprisingly, age at maturity and adult survivorship had large effects, with juvenile proportions increasing as age at maturity increased and decreasing as adult survivorship increased (Figure 6). The number of eggs laid per year and the annual egg survivorship also had large effects. When looking at all juveniles (including hatchlings), the proportion of juveniles increased as either eggs laid per year or egg survivorship increased (as expected), but when looking only at turtles that survived the first year, the pattern reversed, with the proportion of juveniles decreasing as the number of eggs laid or egg survivorship increased. This pattern occurred because, to maintain a stable population, juvenile survivorship had to decrease to compensate for the increased annual reproductive output, resulting in the annual production of many hatchlings, followed by very high mortality rates that quickly reduced the juvenile population.

3.3 | General patterns of size distributions and country/fox categories

Most turtle populations were heavily skewed towards large adults regardless of species, country or the presence or absence of foxes (Figures 4 and 5). Populations generally had low proportions of juveniles, strongly negative skews (i.e. left-tailed) and high medians, indicating that they were predominantly comprised of large adults (Figures 5 and 7, Supporting Information S4: Figures S5–S80). A skew towards large individuals was present for nearly all species examined (see density plots in Supporting Information S4), except for a few species such as *Pseudemys concinna* (Supporting Information S4: Figure S34). When looking broadly at these data, without compensating for species, study sites or capture methods,

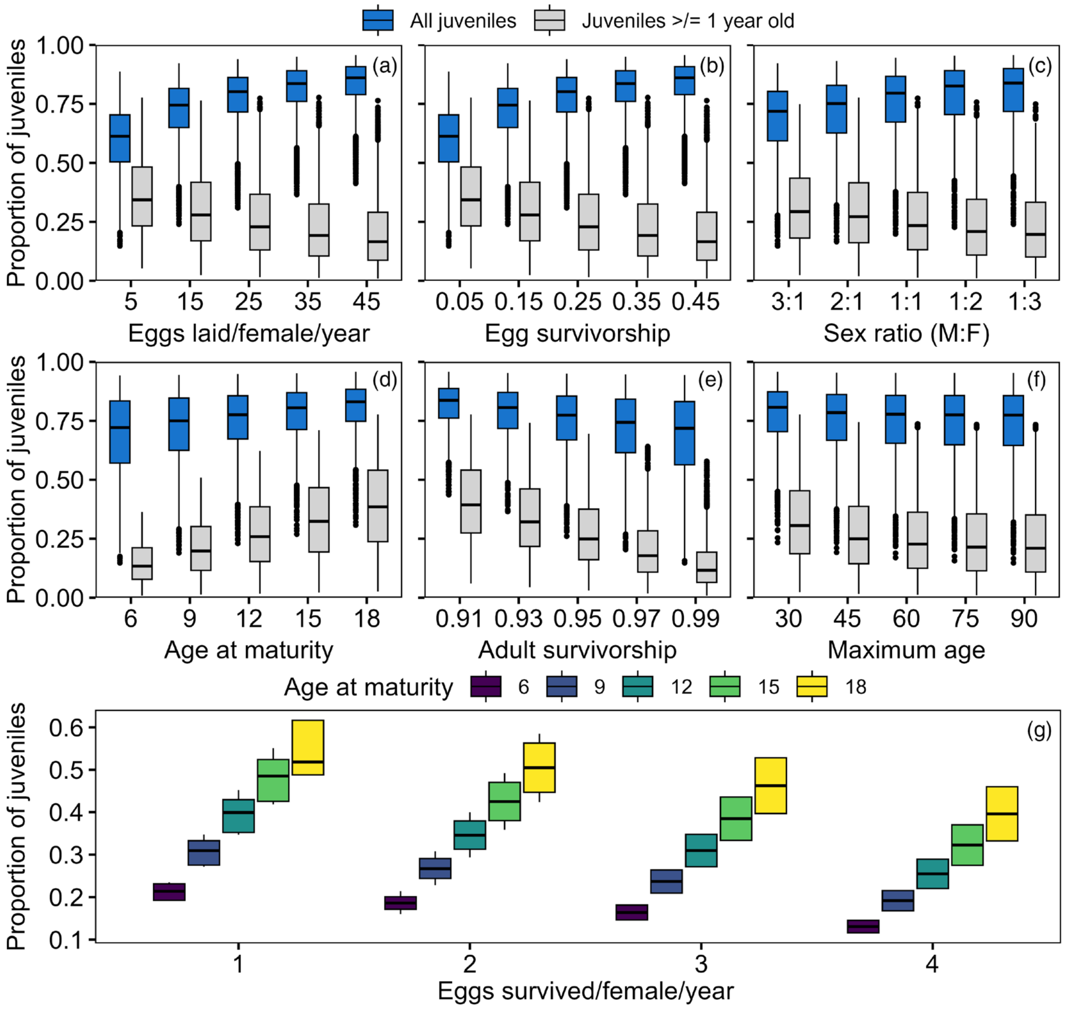

FIGURE 6 Simulation results testing the effects of different life history parameters on the proportion of juveniles in stable populations. There was generally a very high mortality rate in the first year after hatching, resulting in a pulse of juveniles when hatchlings were included (blue), followed by high mortality in the first year and low proportions of juveniles when excluding the hatchlings (grey). a-f = the results for all combinations of parameters, grouped by the values of a given parameter. f = the results subset to parameters for a 'typical' turtle population: Adult survivorship = 0.97, maximum age ≥45, sex ratio = 1:1. The eggs survived per female per year were calculated by multiplying the number of eggs laid per female per year by the egg survivorship.

there appeared to be a general trend for size distributions for turtles from AU (no foxes) and the United States to have thicker and longer left tails compared to size distributions for turtles from AU (foxes; Figures 4, 5 and 7). Likewise, AU populations (no foxes) appeared to have higher proportions of juveniles (mean = 0.25, SD = 0.18, range = 0–0.61) than AU (foxes; mean = 0.11, SD = 0.11, range = 0–0.50) or United States (mean = 0.11, SD = 0.12, range = 0–0.60; Figure 7). However, statistical analyses on the full dataset that accounted for confounding factors provided weak or no evidence to support those trends (Table 2). Likewise, analyses that were subset to specific methods (to ensure that the results were not influenced by methodological differences) did not find evidence of a difference between AU (no foxes) and the United States for snorkelling, or between AU (no foxes) and AU (foxes) for cathedral nets, or between AU (foxes) and the United States for fyke nets (Table 2).

3.4 | Capture methods

Pairwise comparisons of capture methods revealed multiple differences (Table 2; Figure 8). There was either very strong or strong evidence that both hand captures and crawfish nets captured smaller turtles and a higher proportion of juveniles than did fyke nets or hoop nets (hands and crawfish nets could not be directly compared). There was no evidence that fyke nets and hoop nets differed for either mean sizes of captures or proportions of juveniles, but there was very strong evidence that fyke nets captured smaller turtles and a higher proportion of juveniles than did cathedral nets. There was no evidence that snorkelling and cathedral nets captured different mean sizes of turtles, but there was weak evidence that snorkelling captured a higher proportion of juveniles (sample sizes for this test were limited). Based on which methods captured a higher proportion of juveniles, pairwise comparisons were combined into the following general hierarchy:

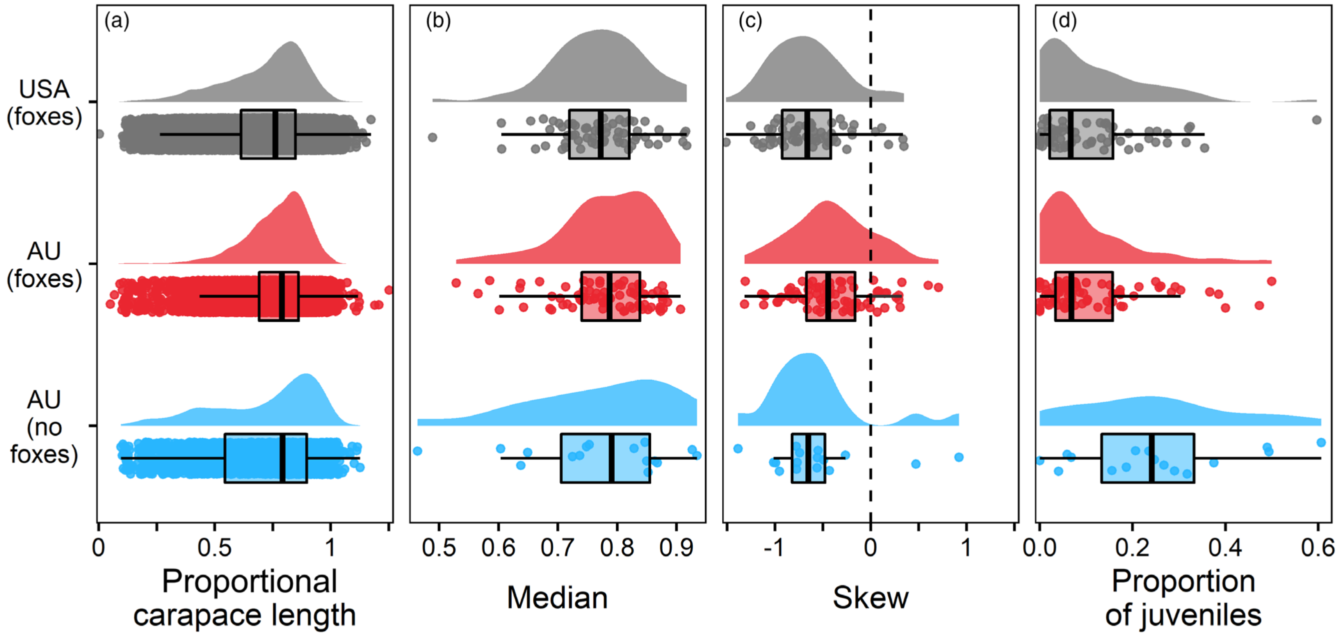

FIGURE 7 Size distribution data presented as half violin plots (density plots) and boxplots (calculated with the default formula in ggplot2; v3.3.6) with each data point overlayed on the boxplots. (a) All data combined across all populations (each point indicates the size of an individual; all individuals from all populations were included, regardless of species or sample size). (b) Median proportional carapace length per population. (c) Skew of proportional carapace lengths per population. (d) Proportion of each population that consists of juveniles. For (b–d), each point is the summary statistic of a population, and only populations with ≥50 sampled individuals are shown.

- Hands and crawfish nets > fyke and hoop nets
- Fyke nets = hoop nets
- Fyke nets > cathedral nets
- Snorkelling >? cathedral nets

There were large differences in the capture methods commonly used in different areas (Table 3). In AU (no foxes; i.e. the northern half of AU), snorkelling was the most common method, whereas it was never used in the southern half of the continent (AU with foxes) and was only used at five sites in the United States. Fyke nets were the most common method in AU (foxes) but were rarely used elsewhere. Cathedral nets were common in AU (used at roughly half the sites in both areas of AU) but were never used in the United States. Conversely, hoop nets were used at most sites (86.8%) in the United States but were only used at two sites in AU (foxes) and one site in AU (no foxes). In all three areas, roughly half of sites were surveyed with only one method (see details in Table 3).

3.5 | Water body types

There was very strong evidence that standing bodies of water that are not associated with main river channels (e.g. lakes, ponds, marshes, swamps) had turtle populations with smaller average proportional CLs and a higher proportion of juveniles compared to rivers (Figure 9). Rivers had larger turtles on average for all three species included, but the difference between water body types was greater for *Chelodina oblonga* and *Chelydra serpentina* than it was for *Trachemys scripta* (Figure 9).

4 | DISCUSSION

4.1 | What is a ‘typical’ turtle size distribution?

Our results were largely consistent with our prediction that turtle body size distributions will be skewed towards large individuals. Likewise, our simulation confirmed that for most stable turtle populations, adults should outnumber juveniles (with the exception of periods shortly after the nesting season when populations may briefly be flooded with hatchlings that rapidly experience high mortality rates). Further, we did not find evidence that areas in AU with foxes had unusually low proportions of juveniles when compared to either areas in AU without substantial fox predation or the United States (which has substantial nest predation from species such as raccoons and foxes). There are clearly many differences among these areas (such as climate and predators other than foxes), but our results were consistent across regions. Given turtles' long lifespans, high adult survival and high egg and juvenile mortality (Bury, 1979; Iverson, 1991; Otten & Refsnider, 2024), adult-dominated distributions are expected in stable populations, and for nearly all species we examined, most populations were skewed towards adults. Taken together, our results suggest that turtle populations typically have relatively few juveniles, and a lack of juveniles does not inherently indicate that a population is declining due to threats to early life

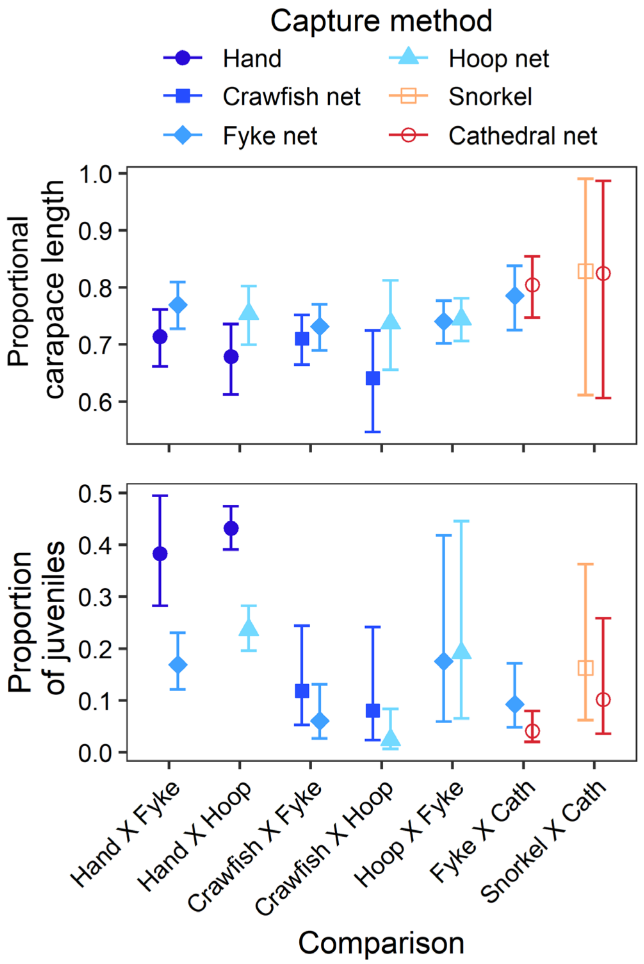

FIGURE 8 Fitted effects and confidence intervals from models making pairwise comparisons of methods (each comparison used only populations with at least 25 individuals captured by each of the two methods). See Table 2 and Supporting Information S4.

TABLE 3 Number of sites surveyed with each capture method, and the number methods used per site (based on all sites and species regardless of sample size). At a few sites, capture methods were not recorded.

	AU (no foxes)	AU (foxes)	USA
Hand	5	16	11
Crawfish net	0	0	9
Fyke net	4	109	5
Hoop net	1	2	33
Cathedral net	9	80	0
Snorkel	13	0	5
Crab pot	0	27	0
1 method	11	89	19
2 methods	7	22	14
3 methods	1	27	4
4 methods	1	5	1
Total sites	20	143	38

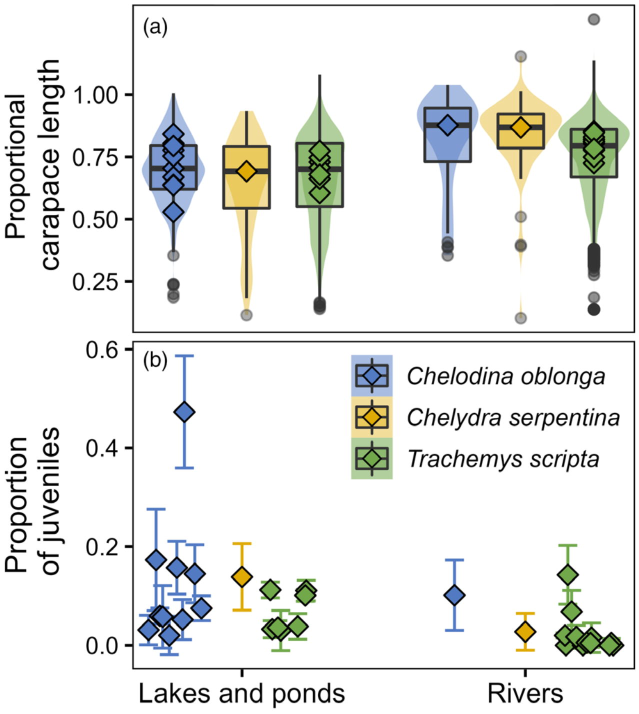

FIGURE 9 Size distributions from lentic bodies of water (lakes and ponds) compared to rivers for the three species where data from a single trap type per species (fyke nets for *C. oblonga*, and hoop nets *C. serpentina* and *T. scripta*) for ≥50 individuals were available from at least one site in each habitat category (within a region). (a) Proportional carapace length data presented as violin plots with overlayed boxplots for all populations combined. Diamonds show the median value of each population. Boxplots were calculated with the default formula in ggplot2 (v3.3.6) and all outliers are shown. (b) Proportions of each population that consisted of juveniles. Each diamond is a population, and the error bars are 95% confidence intervals.

stages. Therefore, we caution researchers not to over-interpret a lack of young turtles alone as evidence for declines in their populations. Certainly, factors like introduced nest predators can cause substantial problems for turtle populations, but long-term research using consistent methodologies and large sample sizes is necessary to detect a reduction in the proportion of juveniles over time, rather than simply a 'low' proportion at a given time.

Despite the general pattern of populations consisting primarily of large adults, there were exceptions that merit discussion. Data from Sonoran mud turtles (*Kinosternon sonoriense*) are informative. In some years, researchers were able to time their visits to the sites to coincide with or shortly follow hatchling emergence from nests, which resulted in a large number of small turtles being captured by hand and with dip nets on those visits, while that size class was largely absent in other visits. As a result, plotting all captures produces a bimodal pattern with peaks at both the low (young) and high (adult) ends of the graph, whereas excluding those bursts of hatchlings produces a trend that was skewed towards adults (Figure 3). This bimodal distribution suggests that juveniles experience a very high mortality shortly after entering the water. Our simulations produced a similar and corroborating result. In most simulated scenarios, there was a high proportion of juveniles immediately after hatching, followed by high mortality in the first year, resulting in low proportions of juveniles for all subsequent years (Figure 6).

It is also possible that turtles follow density-dependent population trajectories (Fordham et al., 2009; Spencer et al., 2006), and it has been suggested that following a die-off event or colonization of a site, turtles will experience a phase of population growth, during which the population is dominated by juveniles, before eventually maturing at a stable population size that is dominated by adults and has low recruitment and few juveniles (De Lathouder et al., 2009; Georges & Guarino, 2017; White, 2002; but see Keevil et al., 2018).

Finally, we should acknowledge that while we have provided size distributions from a large suite of species and sites, it is technically possible that most of these populations are severely degraded, and today's perception of a 'healthy' turtle population is actually an illusion created by shifting baselines. Even for common species, it is likely that populations have declined over the past century. For example, when Archie Carr wrote about USA turtle populations in 1952 (Carr, 1952), he described almost unfathomable turtle densities that are nowhere to be seen today (e.g. >40,000 kg of *Malaclemys terrapin* captured in a single year in Maryland). Likewise, a 1920 report (Clark & Southhall, 1920) noted that a single market in Chicago sold ~10,000 *Chelydra serpentina* per year. Similarly, in Australia, fishers engaged in turtle eradication at the turn of the 20th century (to protect Murray Cod spawn) reported killing over five thousand turtles in the Murray River in just a few months (Munn, 1902). Today, populations have declined to the point that capturing that number of individuals on a regular basis is almost unthinkable.

Nevertheless, while densities of many turtle species have declined over time, our simulations strongly suggest that a low proportion of juveniles should be expected even for stable populations. This result makes intuitive sense given turtles' long lifespans and low adult mortality. Indeed, a strong decrease in the proportion of juveniles as adult survival increases is clearly visible in our results (Figure 6e). Additionally, many of the major causes of turtle declines, such as overharvesting (particularly in the early 1900s) and road mortalities do not specifically affect juveniles and could cause general turtle declines without substantially altering size distributions. In other words, these declines would likely be detected via decreasing capture rates across multiple size classes, rather than specifically a lack of juveniles.

Appropriate historical comparisons of size distributions are difficult to obtain, but a few are available. For example, a population of 1201 *Trachemys scripta* that was sampled by hand in a drying ditch in 1941 (Cagle, 1950) produced a distribution that was slightly more shifted towards young turtles than the mean of our *T. scripta* individuals but was still well within the range of distributions we observed for that species (Figure 5). Cagle (1950) commented, 'Only five hatchlings were collected although the shores of the ditch provided excellent nesting sites and many predator-excavated nests were observed… Either the eggs and hatchlings were subject to intense predation or the young still remained in the nests'. Likewise, the proportions of juveniles Cagle (1942) reported for *T. scripta* (0.136), *Chrysemys picta* (0.350) and *Sternotherus odoratus* (0.221) were higher than our median but within the range of values we observed and are consistent with the results of our simulation (Figures 6 and 7; Cagle's data were from several populations combined; we reported values from his method 'B' for assigning juveniles, which was similar to ours).

4.2 | Methods, water body types, and sample sizes

Although a skew towards adults was present in most populations, there were multiple factors that influenced the results, and researchers should carefully consider them when planning and interpreting a study. In keeping with previous work (Tesche & Hodges, 2015), we found that most sites were surveyed using only a single method. The use of a single method could easily bias results, because each method has its own set of biases, and we echo previous researchers in encouraging the use of multiple capture techniques (McKnight et al., 2015; Ream & Ream, 1966; Tesche & Hodges, 2015). However, when possible, the suite of methods used should be consistent over time to allow for long-term analyses (Connell et al., 2018).

Importantly, we found a clear pattern among methods, with methods that target shallow areas tending to capture a higher proportion of juveniles. Like previous authors, we found that hand captures/dip nets (Bowers et al., 2022; Gulette et al., 2019; Ream & Ream, 1966; Tesche & Hodges, 2015) and small crawfish traps (Brown, 2023; Howell et al., 2016; McKnight et al., 2015) resulted in a high proportion of juveniles compared to fyke nets and hoop nets (which are typically used in deeper water: ~0.5–1 m). Further, cathedral nets, which are designed for even deeper water and are often suspended or floated in water that is >1.5 m, captured an even lower proportion of juveniles. There is evidence that for some species, young turtles prefer shallow areas with abundant structure and/or vegetation, often near banks (i.e. where dip nets and crawfish traps are often used; Micheli-Campbell et al., 2013; Santori et al., 2021; Spangler et al., 2021), whereas larger turtles prefer deeper water (where hoop, fyke and cathedral nets are used). A preference for shallow areas may explain the pattern we observed; however, other factors, such as mesh size (Ennen et al., 2021) and juvenile behaviour, should also be considered.

An additional complication arises from sample size biases. Our rarefaction results suggest that inferences about population demographics have a high probability of being incorrect below a sample size of ~50 individuals, and ideally, researchers should strive for sample sizes close to 100. Large sample sizes are particularly important for turtle research given the difficulty involved in capturing juveniles, and targeting a given number of individuals, rather than the number of captures, will increase the probability of detecting juveniles (i.e. in the course of capturing a given number of individuals [such as 50], adult individuals may be recaptured multiple times before any juveniles are captured). While these recommendations may seem intuitively obvious, we think they are important reminders in a field that frequently draws conclusions based on limited sample sizes.

Beyond the effects of capture methods, we also observed a difference in the size distributions of rivers/streams and enclosed ponds/lakes, with smaller turtles and more juveniles in the lentic bodies of water. Previous studies have documented that turtle growth rates and body sizes can vary among populations (Fehrenbach et al., 2016; Gibbons, 1967), but it is interesting that we observed the trend of small turtles in ponds and lakes across all three species we examined, even with the data restricted to the same capture method per species (although Germano & Bury, 2009 failed to find a difference in lentic and lotic systems for *Actinemys marmorata*). Perhaps lentic bodies of water provide better habitat for juveniles. This is a topic that future studies should examine in more species and systems, because it may indicate that the expected size distribution for a healthy population varies predictably among habitat types. Likewise, it would be interesting to investigate whether the size of lakes and ponds influence size distributions.

5 | CONCLUSIONS

Based on both our simulations and the large collection of datasets we assembled, it appears that turtle size distributions are typically skewed towards adults, with few juveniles. Therefore, detecting relatively few juveniles in field surveys should be expected, and few juveniles does not necessarily indicate a declining population. Nevertheless, we want to stress that threats to early life stages are still important considerations for conservation. Turtles have likely evolved to tolerate high egg and juvenile mortality followed by low adult mortality, but increased predation on nests and juveniles can still result in unstable recruitment levels (Congdon et al., 1993), especially when in tandem with reduced adult survival (e.g. overexploitation by humans). Returning to the hypothetical female from the introduction that lays 600 eggs over its lifetime, if 95% of nests are raided (Thompson, 1983), that would only leave 30 juveniles, two of which need to survive to adulthood to replace that female and her mate. Thus, increased nest predation can result in a decreased proportion of juveniles, but we should generally expect low proportions of juveniles, even for stable populations, and there are numerous sources of variation. We, therefore, make the following recommendations for improving the rigour of future studies of freshwater turtle population dynamics:

1. Care should be taken to not over-interpret a low number of juveniles. Low recruitment certainly can be a serious conservation concern, and while a low number of juveniles may be reflective of a population that is in decline, it is not inherently indicative of a population that is declining due to high egg and juvenile mortality, and additional possibilities such as methodological constraints should be considered. Indeed, due to turtles' long lifespans, only low levels of annual recruitment are required to maintain a stable population, and adult mortality is often a more pressing concern for conservation. Examining trends in juvenile abundance over time will be more effective in determining whether recruitment is being lost.
2. Researchers should be especially cautious about the interpretations from small datasets and, whenever possible, should strive for capturing at least 50–100 individuals before drawing conclusions. In some cases, this sample size may be impossible due to extremely small population sizes, but that itself may be indicative of large problems.
3. When making comparisons among sites or for populations over time, consistent methodologies should be followed as much as possible, and the sampling design should adhere to previously recommended best practices such as including multiple trap types and rotating the locations of traps within a waterbody (Hollender et al., 2022).
4. Careful consideration should be given to the types of traps being used, and when assessing studies, sites or populations over time, the biases of those methods should be considered. Ideally, if multiple methods are used, capture method should be included as a factor in statistical analyses.
5. More research on hatchling and juvenile turtles is critical. To fully understand reported size distributions and whether they are under-representing juveniles, we need more information on juvenile survivorship, movements, habitats and cryptic behaviours. Long-term datasets will also be extremely valuable.

AUTHOR CONTRIBUTIONS

Donald T. McKnight, Deborah S. Bower and James U. Van Dyke designed and led the study. Donald T. McKnight collated data and led the analyses and writing. Donald T. McKnight, Deborah S. Bower, Ellen Ariel, Stephen Beatty, Simon Clulow, Marilyn Connell, Annette R. Deppe, Sean Doody, Alastair Freeman, Arthur Georges, Samantha L. Hannabass, Ethan C. Hollender, Hunter Howell, Aaron Krochmal, Day B. Ligon, Eric Munscher, Eric J. Nordberg, Timothy C. Roth, Anthony Santoro, Jason Schaffer, Angela Simms, Ricky-John Spencer, Paul Stone, Kameron C. Voves, Andrew D. Walde, Skye Wassens, Michael A. Welsh, Nick S. Whiterod, Wytamma Wirth and James U. Van Dyke provided data and edited the manuscript.

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ACKNOWLEDGEMENTS

We would like to thank Bruce Chessman, Justin Congdon and William Hopkins for providing data and comments on this paper, as well as Mike Thompson for additional comments. We would additionally like to thank Tiaro & District Landcare volunteers and Queensland Parks and Wildlife Service (QPWS) staff and volunteers, traditional land owners and countless other volunteers, students and field assistants for helping to collect these data. The datasets used in this study were generated with funding from the following sources: ARC Linkage Grant LP200200884, Arizona Game & Fish Department, Commonwealth Environmental Water Office, Department of Florida Fish and Wildlife, Felburn Foundation, Florida Department of Environmental Protection, Jane Fenwick Foundation, Kansas Department of Wildlife and Parks, National Science Foundation grants (DEB-74-070631, DEB-79-06301, BSR-84-00861, and BSR-90-1977), New Mexico Department of Game and Fish, Office of Biological and Environmental Research, U.S. Department of Energy: Financial Assistant Award No. DE-FC09-96SR18546, Oklahoma Department of Wildlife Conservation, Texas Parks and Wildlife Department, Turtle Survival Alliance, United States Forest Service, University of New England Faculty of Science, Agriculture, Business and Law and the Commonwealth Environmental Water Office. Additional support was provided by Tiverton Agricultural Impact Fund, Winton Wetlands, Wodonga Council, Greening Australia and North East Water. Data were collected under the following permits: Department of Biodiversity, Conservation and Attractions Reg. 25 Licence FO25000094-3, 4 and 6, and Reg. 27 Licence No. BA27000339, Department of Environment and Science Queensland Government WISP15327814, Department of Fisheries/ Department of Primary Industries and Regional Development, WA exemption No.'s 2829, 3137, 3440, 3570, and 3660, Department of Parks and Wildlife Reg 17 Permit No. 01-000091-1 and FO25000063, DPI P11/0043-3.0, Florida Department of Environmental Protection, Division of Recreation and Parks Scientific (Non-Commercial) Research/ Collection Permit #03102310, Florida Fish and Wildlife Conservation Commission Permit Number LSSC-23-00007, New South Wales Government Department of Planning, Industry and Environment Scientific Licence No: SL1022308, OEH: SL100441, Texas Parks and Wildlife Scientific Permit Number SPR-0212-019, QLD Government Department of Agriculture, Fisheries and Forestry 181502, QPWS Scientific Purposes Permits # WITK03617606 and WISP03129805. Data were collected with the following animal ethics approvals: Charles Sturt Animal Care and Ethics Committee Protocols A16054, A19028, James Cook University Animal Ethics Permit A1082, Macquarie University ACEC approval A-2019-015, Missouri State University Institutional Animal Care and Use Committee Protocol 17-028, Murdoch University AEC, University of New England AEC19-081, AEC 14-116. Open access publishing facilitated by La Trobe University, as part of the Wiley - La Trobe University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

All authors affirm that they have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad repository: https://doi.org/10.5061/dryad.47d7wm3s2 (McKnight et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Simulation to calculate juvenile survivorship for a stable population.

Supporting Information S2. Metadata on the turtle populations used, including sample size, researchers involved and dates.

Supporting Information S3. Illustration and justification for size adjustments.

Supporting Information S4. Details on statistical model inputs, as well as additional figures.

How to cite this article: McKnight, D. T., Bower, D. S., Ariel, E., Beatty, S., Clulow, S., Connell, M., Deppe, A. R., Doody, S., Freeman, A., Georges, A., Hannabass, S. L., Hollender, E. C., Howell, H., Krochmal, A., Ligon, D. B., Munscher, E., Nordberg, E. J., Roth, T. C., Santoro, A., … Van Dyke, J. U. (2025). Does a lack of juveniles indicate a threat? Understanding body size distributions in a group of long-lived vertebrates. *Journal of Animal Ecology*, *00*, 1–21. https://doi.org/10.1111/1365-2656.70093