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RESEARCH ARTICLE

The ecology and morphology of Australia's desert turtle (*Emydura macquarii emmotti*)

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Abstract

Cooper Creek is one of Australia's largest unregulated river systems and one of the world's most variable large river systems. It is a dynamic environment that oscillates between booms and busts; yet, many species thrive in it. One of these species, the Cooper Creek turtle (*Emydura macquarii emmotti*) has received little attention, despite being one of Australia's largest freshwater turtles and living further inland than any other Australian turtle. We conducted surveys for *E. m. emmotti* in 2001–2004, 2019, and 2022, focussing predominantly on the Waterloo waterhole. Waterloo had a large population of *E. m. emmotti* (508 estimated individuals; 95% CI = 447–596) with an estimated density of 64.8 turtles/ha (95% CI = 57.0–76.2) and estimate biomass of 74.4 kg/ha (95% CI = 57.6–100.3 kg/ha). Juveniles were highly abundant in all years, representing up to 63.6% of captured individuals. It was slightly (but not significantly) male-biased in 2001–2004 and significantly female-biased in 2019. All sizes and sexes used the floodplain during a flooding event in 2022, but more males than females were captured on the floodplain, and there was evidence of male-biased dispersal across the years. Compared to Murray River turtles (*Emydura macquarii macquarii*), *E. m. emmotti* exhibited megacephaly across all ages and sexes, with particularly pronounced megacephaly in adult females. Algae were present on many individuals (including on the skin and plastron) but was relatively more abundant on juveniles. Leeches were not detected on any of the 66 turtles that were examined for them. The following injuries/malformations were noted: missing or injured limbs (3.2%), missing or injured eyes (1.3%), damaged shells (8.0%), scute/shell anomalies and malformations (10.6%), and marginal scute seams extending into the costals (67.4% of adults, 1.2% of juveniles). This paper presents some of the first work on this unusual turtle and makes recommendations for future research.

KEYWORDS
Chelidae, Cooper Creek, floods, Megacephaly, sexual dimorphism

INTRODUCTION

Biota inhabiting unregulated river systems in Australia's arid desert must contend with a dynamic and unpredictable boom–bust system that oscillates between periods of bountiful nutrients and periods of extremely limited resources (Bunn et al., 2006; Puckridge et al., 2000). The inaptly named Cooper Creek is a large, dryland distributary river system that has its headwaters in tropical central Queensland and subsequently breaks into a vast array of ephemeral channels and associated temporary and permanent waterholes before emptying into Lake Eyre (Kati Thanda) in South Australia. As one of Australia's largest unregulated rivers, Cooper Creek experiences natural episodes of high flow and extensive flooding (Gibling et al., 1998), often at some distance, from the source (i.e., rainfall that is typically associated with the tropical monsoonal weather systems). Between those episodes (most of the time), the system comprises a series of scattered, disconnected waterholes embedded in an arid landscape with an average rainfall less than 200 mm/year (Kotwicki, 1986), making Cooper Creek among the world's most variable and unpredictable large river systems (Kingsford, 2017; Puckridge et al., 1998).

Aquatic animals in Cooper Creek depend on sporadic local rainfall and flows from the north, and during dry periods, both the size and structure of the fish community changes dramatically as aquatic production, available nutrients, and food become limited (Arthington et al., 2005; Balcombe et al., 2015; Leigh et al., 2010). Conversely, the episodic flooding is accompanied by boom periods characterized by access to nutrients previously inaccessible to aquatic organisms, a dramatic increase in primary productivity, opportunistic reproduction, and rapid recruitment at almost all levels of the food chain (Balcombe & Arthington, 2009). As the waters recede, many invertebrates and fish retreat to the permanent and semi-permanent waterholes, resulting in high quantities of standing crop available to higher-level consumers, such as waterbirds and turtles. While the responses of Cooper Creeks' fish community to flooding are fairly well-understood, the responses of the endemic Cooper Creek turtle (*Emydura macquarii emmotti*) are poorly studied (Georges & Guarino, 2017). Turtles often comprise a large portion of the vertebrate biomass in aquatic ecosystems and serve a key role as scavengers (Iverson, 1982; Lovich et al., 2018; Santori et al., 2020; Thompson, 1993). Given their large size, *E. m. emmotti* may be a particularly important scavenger in Cooper Creek. The range of this species extends from the upper reaches in central Queensland to the lower reaches near the systems' terminal destination of Lake Eyre in South Australia (Cann & Sadlier, 2017). This contrasts with the distribution of the Eastern long-necked turtle (*Chelodina longicollis*), which also occupies Cooper Creek, but is restricted to the upper reaches adjacent to the coastal catchment of the Fitzroy–Dawson River (Kingsford et al., 2006). The Cooper Creek turtle is also found in the Diamantina River, which also flows into Lake Eyre.

With a recorded size of 368 mm (straight-line carapace length) and 7.25 kg, *E. m. emmotti* is one of Australia's largest chelid turtles by weight (Cann & Sadlier, 2017; McCord et al., 2003). They also appear to achieve high densities during dry periods (Kingsford et al., 2006) and likely constitute a substantial biomass. Likewise, they reportedly have enlarged heads (megacephaly; Legler & Georges, 1993), particularly in females, but this has not been quantified beyond a handful of individuals (Cann & Sadlier, 2017; McCord et al., 2003).

A high proportion of juveniles exist in some populations of *E. m. emmotti* (Georges & Guarino, 2017; Thompson, 1983), and there is some evidence that the permanence of each waterhole dictates population structure and dynamics (Georges & Guarino, 2017; White, 2002). Additionally, a study of *E. m. emmotti* sex ratios found that five populations were unbiased, five were male-biased, and one was female-biased (Georges et al., 2006). Much of our knowledge of this turtle is, however, based on limited observations and anecdotes, and further research is required to better understand its ecology (Cann & Sadlier, 2017; Georges & Guarino, 2017; Kingsford et al., 2006). Here, we build on existing knowledge of this exceptional riverine turtle with new insights on the ecology and morphology of *E. m. emmotti* in the iconic Cooper Creek drainage. We also highlight many key areas for future research.

METHODS

Surveys and general data

Our results are a combination of two survey efforts: a broad study across multiple waterholes conducted in 2001–2004 and a focused study at the Waterloo waterhole on the Noonbah cattle station (–24.224059°, 143.302046°) in 2019 and 2022 (with some efforts at the nearby Fishhole [–24.094372°, 143.383412°] and Teatree [–24.182270°, 143.355543°] waterholes). The 2001–2004 study also included repeated surveys at Waterloo, Fishhole, and the Broadwater waterholes (–24.102861°, 143.353720°). Fishhole is ~15 km upstream of Waterloo, and Broadwater is ~13 km upstream of Waterloo and ~3 km west of Fishhole (all distances are straight-line distances). Some of the key results of the 2001–2004 study have been previously reported (Georges et al., 2006; Goodsell, 2002; White, 2002). Therefore, we will restrict our attention to a few additional aspects of that broad study and focus on the results from Waterloo, Fishhole, and Broadwater (particularly Waterloo to allow comparisons with the 2019/2022 study). All three waterholes are located on the Thomson River upstream of where it joins the Barcoo River to form Cooper Creek.

In 2001–2004, a combination of conventional baited hoop traps (Legler, 1960) and baited snorkel traps (hereafter" cathedral traps"; Kuchling, 2003) was used, whereas fyke nets (Vogt, 1980) and baited cathedral traps were used in 2019, and fyke nets and hoop traps were used in 2022. All traps were baited with meat (e.g., ox liver, sheep, kangaroo, fish, and crawfish depending on availability). In 2019, Waterloo was isolated, and water levels were low. This allowed some fyke nets to be placed in the centre of the channel with long leads extending to either shore. These fyke nets were paired with one net facing upstream while the other faced downstream (thus, turtles moving in either direction would be captured). Traps were moved periodically to maximize capture success (Hollender et al., 2022). We surveyed turtles from 7 to 20 December 2019 and from 25 April to 4 May 2022.

For all individuals, callipers were used to measure the straight midline carapace length (CL) and straight midline plastron length (PL; to the nearest 0.1 mm in 2001–2004 and the nearest 1 mm in 2019/2022). In 2001–2004, weight (g) was measured with an electronic scale for individuals <3 kg (to the nearest 1 g) and with a Salter® spring scale for individuals >3 kg (to the nearest 10 g). In 2019, weight was measured with one of the following Pesola® spring balances 100 g (to the nearest 1 g), 1 kg (to the nearest 10 g), 5 kg (to the nearest 50 g), or 10 kg (to the nearest 100 g). In 2022, weight was measured with an electronic scale (to the nearest 1 g). In 2019/2022, injuries and shell anomalies (e.g., abnormal numbers of scutes) were recorded. Shell terminology follows that of Zangerl (1969) with the exception of our reference to costal scutes and pleural bones (following Pritchard & Trebbau, 1984), we marked all individuals by using a rotary tool, hacksaw, or file to notch a unique combination of marginal scutes (Waudby et al., 2022).

Males were easily identified by their large tails at 180 mm CL, whereby the anterior margin of the cloacal aperture lay well outside the margin of the carapace when the tail was extended (Georges et al., 2006). Females mature at a larger size and presumably at a greater age than males. Using only sexually mature individuals for population demographics and sex ratios can lead to inaccurate results because the age cohorts for mature males and mature females may not be the same (Georges et al., 2006; Gibbons, 1990). Therefore, we classified turtles as females if they were ≥180 mm CL and did not have enlarged tails, and we classsified all turtles <180 mm CL as juveniles. Based on previous results (Georges et al., 2006; White, 2002), males and females at Waterloo have similar growth curves up to 180 mm CL (males reach 180 mm at roughly age 12 on average and females reach 180 mm at roughly age 11 on average). Therefore, this cut-off allowed us to compare similar age cohorts (with the caveat that the female category included both subadults and mature adults).

Additionally, for haphazard subsets of individuals, we recorded straight carapace width at the widest point and shell height at the highest point as well as the head measurements, algae coverage, leeches, and marginal scute seams described as follows. Those metrics were recorded either as time allowed (i.e., on slow days, we would record them for all turtles in a given trap or traps) or if individuals were captured from size-classes for which we had little data. In all cases, decisions about whether to measure those traits were made before examining them.

All analyses were conducted in R v4.03 (R Core Team, 2017). For all tests, we assessed significance at $\alpha = 0.05$. Chi-square tests included a continuity correction (the default in chisqu.test() function).

Waterloo: Population demographics

In December 2019, our capture rates in the Waterloo waterhole were sufficient to calculate a population estimate. Because this was a short-term study in an entirely closed system, we used the Schumacher–Eschmeyer method (Schumacher & Eschmeyer, 1943) via the FSA package (Ogle et al., 2022), with each day included as a sampling period. There are often differences in the catchability of different sexes and size-classes, and those differences can result in inaccurate sex ratio and population size estimates (McKnight & Ligon, 2017). Therefore, we ran a separate estimate for males, females, juveniles ≥100 mm CL, and juveniles <100 mm CL (initial assessments suggested that there was a large difference in the catchability of those size-classes [Table 1]). We summed those estimates and their confidence intervals to produce a total estimate for the population. Likewise, we based the sex ratios on the estimated numbers of males and females, rather than on the numbers of captured males and females (McKnight & Ligon, 2017). Similarly, for each sex/age-class, we calculated biomass by taking the mean mass of individuals in that sex/age-class and multiplying it by the estimated population size. Confidence intervals were calculated by multiplying the confidence intervals for the population estimates by the confidence intervals for the mean masses.

We used chi-square tests of goodness of fit to see whether the sex ratio differed significantly from 1:1, and we used chi-square tests of association to compare the ratio of juveniles to males+females between cathedral nets and fyke nets in Waterloo (2019), to compare the ratio of juveniles to males+females between Waterloo (2001–2004) and Waterloo (2019; cathedral nets only), to compare the ratio of all males and females marked in Waterloo 2001–2004 to the ratio of the males and females that were marked in Waterloo in 2001–2004 and subsequently recaptured in Waterloo in 2019/2022, and to compare the ratio of all males and females marked in Waterloo, Broadwater, or Fishhole in 2001–2004 to the ratio of males and females that were detected migrating among any of the three waterholes.

TABLE 1 Demographic information for each age/size-class of *Emydura macquarii emmotti* in the Waterloo waterhole in 2019 (7.84 ha surface area; note that mass was not recorded for a few individuals).

Sex and size categories	# of individuals marked	# of individuals recaptured	# of recapture events	Estimated population size (95% CI)	Total recorded mass (kg)	Estimated biomass (kg/ha; 95% CI)
Males	55	26	101	56 (52–61)	90.6	11.8 (10.0–14.0)
Females	101	21	79	123 (99–162)	367.9	57.1 (43.0–80.1)
Juveniles (≥100 mm)	146	84	340	143 (135–153)	36.4	4.5 (3.9–4.8)
Juveniles (<100 mm)	126	11	65	186 (161–220)	5.0	1.1 (0.8–1.4)
Total	428	142	585	508 (447–596)	499.9	74.4 (57.6–100.3)

Effects of flooding

In April 2022, a large rainfall event caused the Thomson River to spill its banks and inundate the surrounding floodplain (stranding us on a newly formed island). The Stonehenge Weather station (~15 km downstream of Waterloo) recorded 78 mm of rainfall on 24–25 April 2022 with water levels in the Thompson River rising from 0.62 m (23 April 2022) to a peak of 5.22 m (28 April 2022). By 4 May 2022 (our last day of trapping), water levels had dropped to 4.19 m, which still left large areas inundated, but allowed many previously flooded sections to dry or recede to only a few centimetres (Queensland Government, accessed 2 December 2022, https://water-monitoring.information.qld.gov.au/). We took advantage of this opportunity and, as possible, deployed fyke nets and hoop nets on the floodplain around Waterloo and along the edges of the main channel. It was not possible to use cathedral nets due to the current (including on the floodplain). We frequently had to reposition nets as water levels changed. When possible, we placed fyke nets facing upstream (so that anything moving with the current would enter the trap), and as water levels on the floodplain lowered, we attempted to cut off deep sections flowing from the floodplain to the main channel to capture individuals as they exited the floodplain. We used chi-square or Fisher's exact tests of association to compare the sex ratio of turtles in Waterloo in 2019 to the sex ratios of all turtles captured on the floodplain in 2022 and to compare the sex ratios of all turtles that were captured in 2019 and individuals that were recaptured on the floodplain in 2022.

Algae and leeches

In December 2019, we recorded observations of algal loads from a haphazard selection of turtles (112 juveniles, 61 females, and 28 males). We scored the per cent of area covered by algae separately for the carapace, plastron, and skin, and recorded the scores as follows: none (0%), very low (present but <5%), low (6%–33%), medium (34%–67%), and high (68%–100%). If individuals were currently moulting their scutes, we based the percentages on the unmolted scutes. To examine the relationship between size and algal load, we used negative binomial models (separately for carapace, plastron, and skin), with CL as the predictor variable, and the median of the algae category as the response variable (e.g., a turtle scored as "medium" would be entered as 50.5). In 2022, we also looked for and recorded the presence or absence of leeches on 66 turtles (32 males, 9 females, and 25 juveniles).

Head and shell dimensions

To examine megacephaly, we took five head measurements: head width (HW; measured from the centre of the tympanic membrane on each side [the widest point]), head height (measured to pass through the centre of the tympanic membrane [the tallest point]), head length (measured from the tip of the snout to the rear of the sagittal crest), upper jaw width (measured at the widest point of the keratin beak), and interocular width (the bone between the eyes measured at the narrowest point). We recorded these measurements on between 53–60 males, 63–74 females, and 101–145 juveniles (sample sizes are presented as ranges because, due to time constraints, not all measurements were taken from all individuals; see Tables S1 and S2). To provide a point of comparison, we also collected the same measurements from 27–36 males, 32–44 females, 16–19 hatchlings, and three ~1–2-year-old *E. m. macquarii* in the Murray and Lower Murray Rivers. The adults and 1–2-year-olds were collected with baited fyke nets, hoop nets, and cathedral nets from waterbodies around Albury (Victoria) and Pike floodplain near Renmark (South Australia). For the hatchlings, we collected eggs from wild nests around Gunbower (New South Wales), incubated them in captivity at 28°C, and measured the hatchlings. Additionally, for *E. m. emmotti*, we also measured carapace width (at the widest point) and shell height (at the highest point).

For all measurements, we examined regressions of CL against measurements calculated as a proportion of CL (e.g., carapace length against head width/CL). Additionally, within each subspecies, we compared males and females using linear models with the shell or head measurement as the response, and CL and sex (with an interaction) as predictors. We examined these trends both using all males and females and excluding females that were larger than the largest male. The conclusions were the same for both subsets, so only the full data are presented here (all results are available in Tables S3–S9). We also examined regressions on log10 transformed data as an indication of whether growth was allometric or isometric. Finally, we used linear models to compare 0–2-year-olds of both species, with head metric as the response, and CL and subspecies (with an interaction) as predictors (we limited the *E. m. emmotti* data to individuals equal to or smaller than the largest juvenile *E. m. macquarii* we sampled [CL ≤ 68.8 mm]).

Marginal scute seams

On multiple *E. m. emmotti* individuals, we observed that the seams between the marginal and costal scutes included an extension of the marginal costal seam laterally towards the vertebral column, sometimes for several

FIGURE 1 Photos of *Emydura macquarii emmotti* from the Waterloo waterhole. (a) A megacephalic female. (b) An adult female. Large marginal seam extensions are visible on right marginals 5, 6, and 7. (c). A young turtle with plastron and skin covered in algae. (d). A juvenile missing a large chunk of its carapace. (e). Extensions on marginal scute seams. Additional photos, including photos of heads, deformities, hatchlings, and scute seam extensions, are available in the Data S1. Photos by Donald McKnight.

centimetres in extent (Figure 1). We quantified this on a selection of turtles (39 males, 47 females, and 184 juveniles). We scored each scute as 0 (no extension), 1 (very slight extension), 2 (slight), 3 (moderate), 4 (strong), and 5 (very strong). We used negative binomial models to look for correlations between CL and the number of scutes with some evidence of extensions, as well as correlations between CL and the sum of scute scores (for both models, sex was included as a factor, and only individuals >180 mm CL [the size at which they can be sexed] were included). Additionally, we looked for evidence of asymmetry by taking the absolute value of the difference in scute scores for corresponding pairs of scutes for each individual (e.g., the score of scute left 1 vs. the score of scute right 1).

RESULTS

Sizes

Between 09 and 19 December 2019, we captured 11 hatchlings that still had yolk scars, eight of which still had an egg tooth (Figure S9). The 11 hatchlings had the following dimensions (mm): CL: range = 27.2–33.9, mean = 31.7, SD = 2.0; plastron length: range = 23.4–29.0, mean = 27.2, SD = 1.7; carapace width: range = 28.2–34.0, mean = 31.5, SD = 1.8; shell height: range = 14.6–16.2, mean = 15.2, SD = 0.7. They weighed <10 g.

Across all waterholes and years (including 2001–2004), the largest individual (female) had CL of 402 mm and a plastron length of 314 mm. The mass for this turtle could not be recorded, but based on a power regression (CL against mass; $n = 620$, $R^2 = 0.974$, formula: mass = $e^{-10.45+3.25*\ln(\mathrm{CL})}$), the mass was estimated as 8421 g. The largest female for which mass was recorded was CL = 363 mm, plastron length = 297 mm, and mass = 6400 g. Only 44 females were >350 mm in CL (out of 1080 with CL measurements), and 14 were >368 mm in CL (the previous published size record).

Across all populations, the largest male had a CL of 346 mm. The mass for this turtle could not be recorded, but based on a power regression (CL against mass; $n = 660$, $R^2 = 0.949$, formula: mass = $e^{-9.163+3.012*\ln(\mathrm{CL})}$), the mass was estimated as 4659 g. The largest male for which mass was recorded was CL = 315 mm, plastron length = 257 mm, and mass = 3850 g. Only nine males were >300 mm in CL (out of 1148 with CL measurements).

Population demographics

In 2001–2004, we captured 302 individuals in Waterloo (115 males, 99 females, 87 juveniles, and 1 unknown), 378 individuals in Fishhole (114 males, 80 females, and 184 juveniles), and 262 individuals in Broadwater (97 males, 38 females, and 127 juveniles). The sex ratios were significantly skewed towards males in Fishhole (1:0.70 M:F; $\chi^2 = 5.96$; $p = 0.0146$) and Broadwater (1:0.39 M:F; $\chi^2 = 25.79$; $p < 0.0001$). The sex ratio at Waterloo was only slightly male-biased and did not differ significantly from 1:1 (1:0.86 M:F; $\chi^2 = 1.20$; $p = 0.2741$). Note that these sex ratios differ slightly from previously reported sex ratios for these sites (Georges et al., 2006) owing to differences in the means by which cohort corrections for males and females were calculated; however, the patterns remain the same. In 2019, we captured 428 individuals in Waterloo (55 males, 101 females, and 272 juveniles), 44 individuals in Fishhole (13 males, 6 females, and 25 juveniles), and 24 individuals in Teatree (2 males, 4 females, and 18 juveniles).

In 2019 at Waterloo, we recaptured 142 of the 428 turtles we marked that year (26 males, 21 females, and 95 juveniles; Table 1), which was sufficient for a population estimate. The estimated population size was 508 individuals (95% CI = 447–596). The total mass of captured individuals was 499.9 kg, and the estimated mass of the entire population was 853.5 kg. At the time of this sampling, Waterloo had a surface area of 7.84 ha, resulting in an estimated 64.8 turtles/ha (95% CI = 57.0–76.2) with an estimated biomass of 74.4 kg/ha (95% CI = 57.6–100.3 kg/ha). There were an estimated 56 males (95% CI = 52–61) and 123 females (95% CI = 99–162), resulting in a heavily female-biased sex ratio (1:2.2; M:F; 95% CI = 1:1.6–1:3.1). This bias was statistically significant based on either the number of captured males and females ($\chi^2 = 13.56$; $p = 0.0002$) or the estimated number of males and females ($\chi^2 = 25.08$; $p < 0.0001$). It also differed significantly from the sex ratio in 2001–2004 based on either the number of captured males and females ($\chi^2 = 11.68$; $p = 0.0006$) or the estimated number of males and females ($\chi^2 = 19.09$; $p < 0.0001$).

In 2019 and 2022, we recaptured 47 individuals (9 males and 38 females) from the 2001–2004 survey. Thirty-six of them could be identified from the previous survey (the others clearly had notches, but the exact identity could not be determined). These 36 turtles were sexed as 3 males, 19 females, and 14 juveniles in 2001–2004, and by 2019/2020, the 14 juveniles had matured into 5 males and 9 females (thus 8 males and 28 females in 2019/2020). Of the 36 identified turtles, 33 were previously captured in Waterloo. To compare the sex ratio of the recaptured Waterloo turtles with the sex ratio in 2001–2004, we excluded migrants and used only individuals that were large enough to be sexed (and thus included in the sex ratio) when they were captured in 2001–2004 (3 males, 19 females). The sex ratio of recaptures (1:6.33 M:F) differed significantly from the sex ratio in 2001–2004 (1:0.6 M:F; $\chi^2 = 11.28$; $p = 0.0008$) demonstrating a strong female skew in recaptured animals.

We captured a large number of juveniles (relative to adults). This was particularly pronounced in the 2019 survey of Waterloo, where 63.6% of captured individuals were juveniles. This was at least partially due to the use of large fyke nets that cut off the channel (Figure 2). The fyke nets captured a significantly higher proportion of juveniles than did the cathedral nets (fykes = 265 juveniles, 99 males + females; cathedrals = 64 juveniles, 105 males + females; $\chi^2 = 58.14$; $p < 0.0001$). The fyke nets also were able to capture substantially smaller individuals (minimum = 27.2 mm CL) than the cathedral nets captured (minimum = 61 mm CL). The proportion of juveniles captured in Waterloo in 2001–2004 (using cathedral nets; see above) was not significantly different from the results of cathedral nets in 2019 (2001–2004 = 89 juveniles, 213 males+females; $\chi^2 = 3.11$; $p = 0.0777$); however, there were clear differences in the distributions of sizes, particularly for females, which were strongly shifted towards large individuals in 2019 (Figure 2).

Movement

Using recapture data, we documented 21 instances of turtles moving among waterholes. During 2001–2004, eight individuals moved between Fishhole and Broadwater (5 males and 3 juveniles; ~3 km minimum distance moved), five moved between Waterloo and Fishhole (4 males and 1 juvenile; ~15 km minimum distance), and five moved between Waterloo and Broadwater (all males; ~13 km minimum distance). Additionally, in 2019 in Waterloo, we captured two individuals that were marked in Broadwater in 2001–2004 (both currently adult males; previously juveniles), and we captured one individual that was marked in Fishhole in 2001–2004 (male). No female migrations were documented. Using only the 2001–2004 data

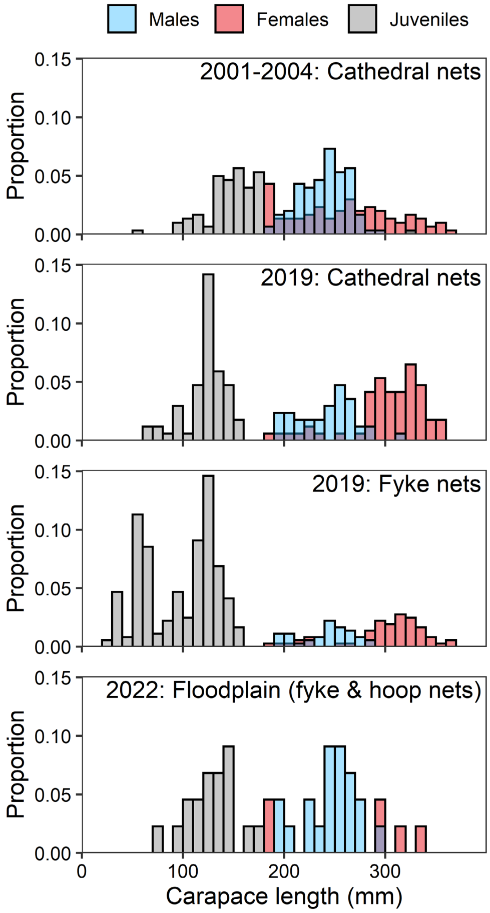

FIGURE 2 Frequency histograms of *Emydura macquarii emmotti* sizes from Waterloo in 2001–2004, Waterloo in 2019 (split by net type), and the floodplain around Waterloo in 2022. Each bar is 10 mm.

(to limit potential biases), the combined sex ratio for all three locations was 1:0.67 (326 males, 217 females), which differed significantly from the exclusively male sex ratio of known migrants (14 males, 0 females; $\chi^2 = 7.56$; $p = 0.0060$).

Effects of flooding

In 2022, we captured 44 individuals on the floodplain around Waterloo (20 males, 6 females, and 18 juveniles). During the same time, we captured 25 individuals in the main channel (12 males, 4 females, and 9 juveniles; one individual was captured in both locations). The turtles captured on the floodplain ranged from 78.6–338 mm CL (plastron length = 66–282 mm; mass = 68–5250 g) with a mean CL (±SD) of 201 ± 70 mm (plastron length = 165 ± 58 mm; mass = 1298 ± 1166 g; Figure 2).

During the 2022 flood, the sex ratios of turtles captured in the main river channel and on the floodplain were significantly male-biased compared to the sex ratios of both captured (main channel: $\chi^2 = 8.04$, $p = 0.0046$; floodplain: $\chi^2 = 14.30$, $p = 0.0002$) and estimated (main channel: $\chi^2 = 10.51$, $p = 0.0012$; floodplain: $\chi^2 = 18.36$, $p < 0.0001$) males and females in Waterloo in 2019. Eleven of the floodplain turtles were recaptures from 2019 (5 males, 1 female, and 5 juveniles). The male-biased sex ratio of these recaptures was significantly different from the female-biased sex ratio of captured (Fisher's test: $p = 0.0266$) or estimated (Fisher's test: $p = 0.0155$) turtles in Waterloo in 2019.

Algae and leeches

Smaller turtles had larger proportions of area covered by algae on their carapace ($\chi^2 = 11.40$, $p = 0.0007$), plastron ($\chi^2 = 37.28$, $p < 0.0001$), and skin ($\chi^2 = 232.37$, $p < 0.0001$) than did larger individuals. For all three body areas, relative algal coverage was substantially higher for the smallest turtles (CL ≤ 100 mm) compared to the largest turtles (CL > 300 mm; Figure 3). This difference was particularly pronounced on the skin.

We did not find any leeches on any of the 66 turtles we examined.

Head and shell dimensions

Adult *E. m. emmotti* exhibited clear megacephaly that was particularly pronounced in females. The megacephaly often reached grotesque proportions in large individuals, giving them an almost emaciated appearance, with the eyes sunken back into the skull (Figures 1 and 4, Figures S10–S12). This is partially because the interocular width had a much shallower

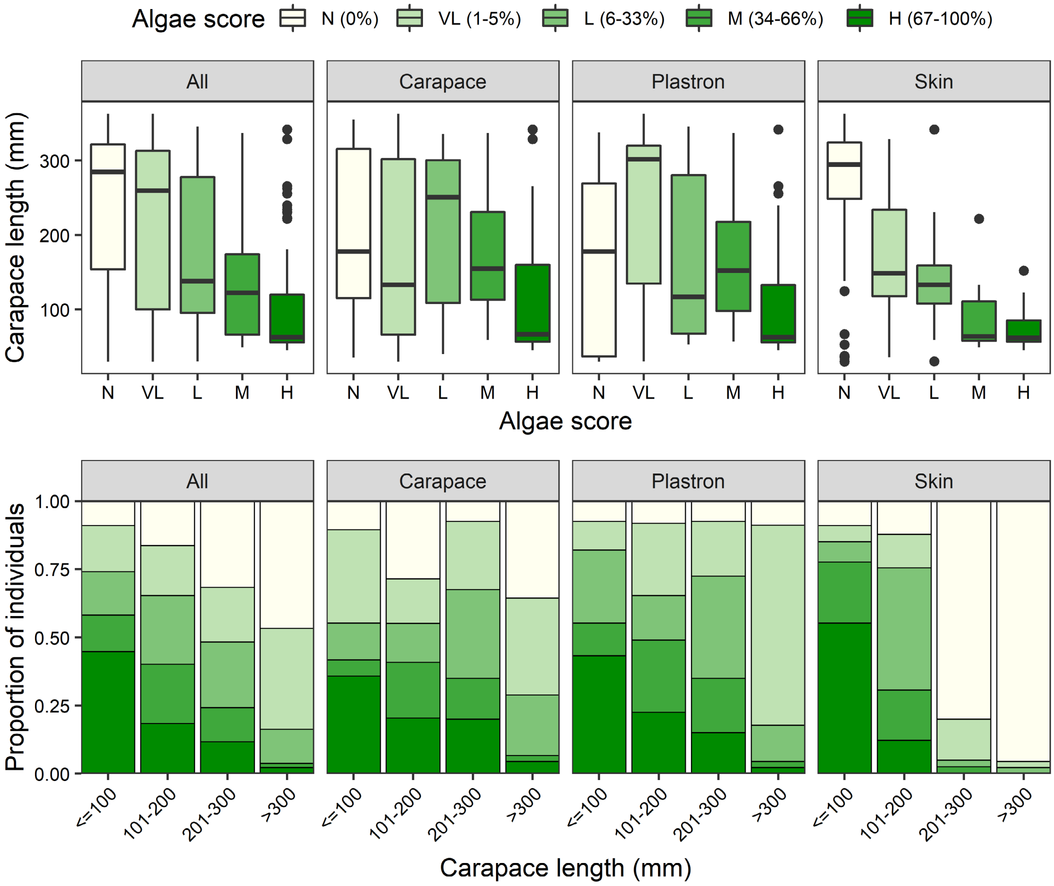

FIGURE 3 Algae scores (based on an approximate per cent of an area covered by algae). The top row shows the carapace lengths (CL) of individuals in each algae category. In the second row, individuals are binned by CL and the proportion of individuals of each CL that had each algae score is shown. The “All” column includes all data regardless of the area it came from (thus, each individual is entered three times: once for carapace, once for plastron, and once for skin).

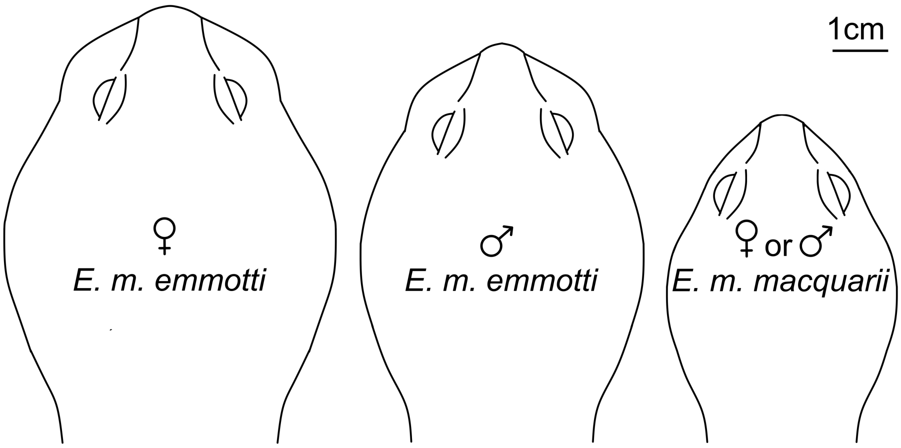

FIGURE 4 A scale comparison of average head sizes (for an individual with a 300-mm carapace length) for female *Emydura macquarii emmotti*, male *E. m. emmotti*, and female or male *Emydura macquarii macquarii* (the difference in their head sizes is small). Note the protruding upper jaws on *E. m. emmotti*. Also see Figures S10–S12.

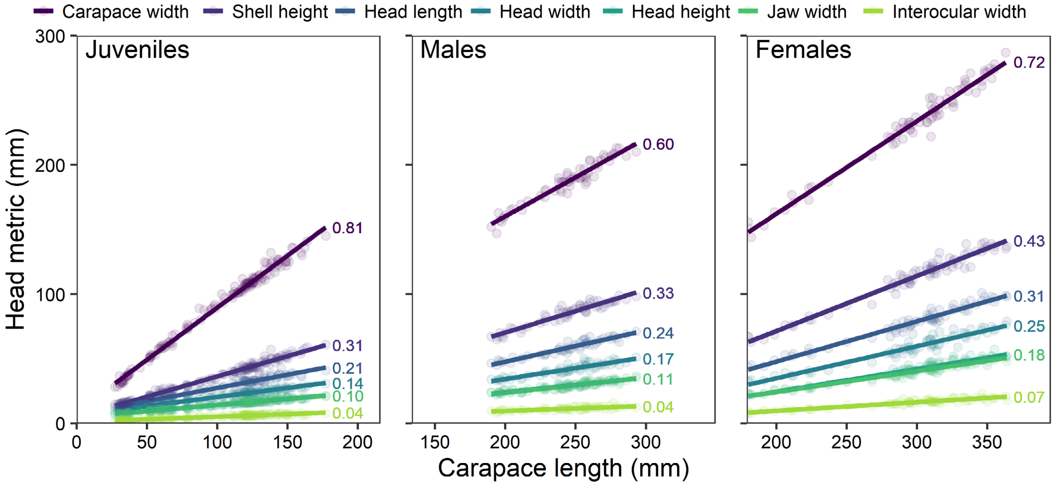

FIGURE 5 Head and shell measurements regressed against carapace length (CL) for *Emydura macquarii emmotti*. The numbers show the slope of each line. Head height and jaw width had nearly identical slopes and intercepts, so only a single mean value is displayed, but head height did have a slightly higher slope than did jaw width (full values are available in Tables S1 and S2). Note that the spread of CLs (maximum–minimum) is the same for each panel, so the slopes are comparable visually.

slope (regressed against CL) than did the other measurements (Figure 5). The upper jaw, in contrast, became enlarged, extending far past the eyes.

For carapace width, shell height, and all five head size measurements, female *E. m. emmotti* had consistently larger heads and shells (relative to CL) than did males across all adult sizes (all $p < 0.0001$), but there were also significant interactions between sex and CL (all $p < 0.0001$), with females consistently having a steeper slope (Figures 5 and 6). As an illustration, for individuals with a 300-mm CL, an average female would have a 6.1% wider carapace, 10.2% taller shell, 9.7% longer head, 16.6% wider head, 18.9% taller head, 14.1% wider upper jaw, and 21.5% wider interocular distance compared to an average male (calculated as: (female–male)/male * 100; Figure 4; additional comparisons are in Tables S1 and S2).

Furthermore, examination revealed that, as adults, males exhibited isometric head growth (i.e., head sizes maintained a consistent proportion with CL), whereas females exhibited allometric growth, with head sizes becoming disproportionately larger with increasing CLs (Figure 6). The log-transformed plots (for all five measurements) confirmed that a line with a

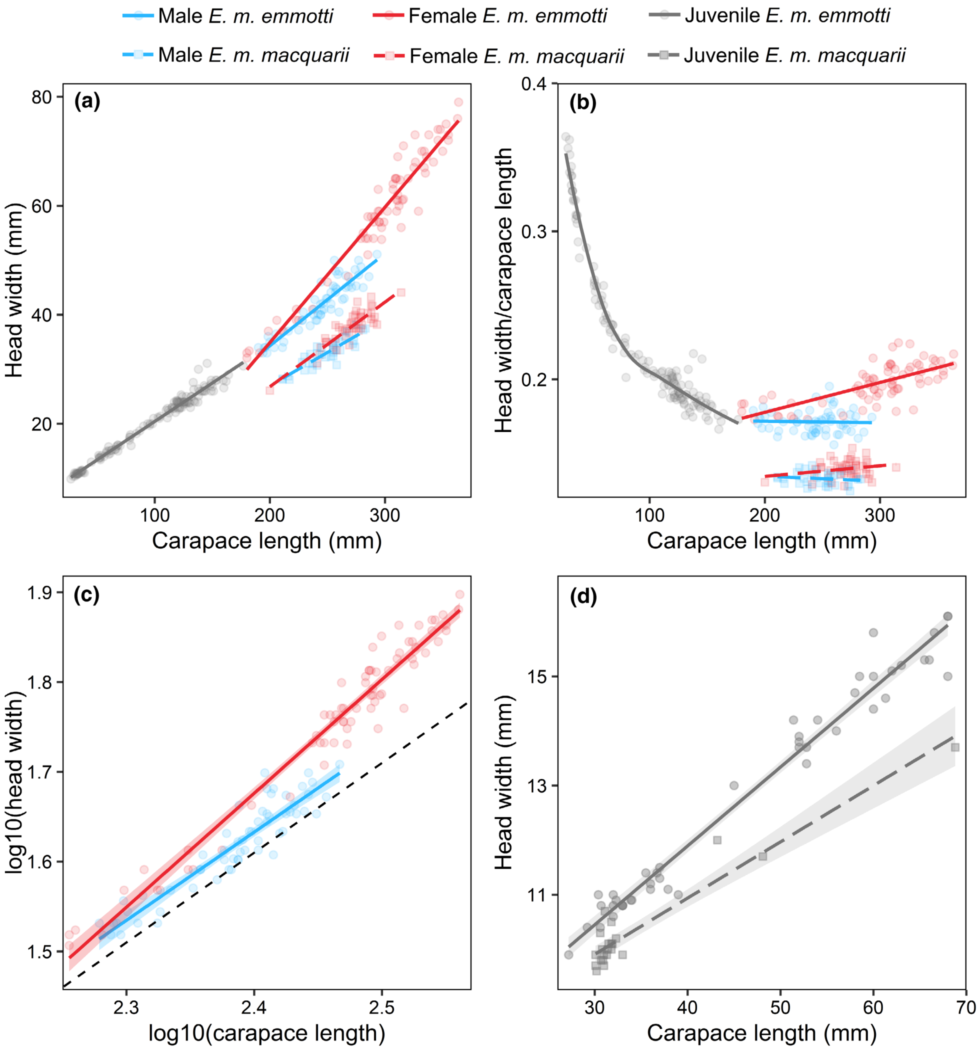

FIGURE 6 Regressions of head width and carapace length (CL) for *Emydura macquarii emmotti* and *Emydura macquarii macquarii*. (a) Raw measurements. (b) Head width divided by CL (thus illustrating how the proportions change over different body sizes; note that a smoothed line is shown for juveniles, and linear regressions are shown for all others). (c) Male and female *E. m. emmotti* (log10 transformed). The dotted line shows a slope of 1 and was positioned (via the intercept) parallel to the male line to illustrate the isometry in males and allometry in females (95% confidence intervals are shown but are very narrow). (d) 0–2-year-old turtles of both subspecies (note that these *E. m. macquarii* are not included panels A or B for increased readability). Additional graphs for other measurements are available in Figures S1–S8.

slope of one was contained within the 95% confidence intervals for males but not for females (females had slopes > 1; Data S1). Juveniles also exhibited allometric growth, but in the opposite direction. Hatchlings had extremely large heads (relative to body size), and older juveniles had comparatively smaller heads (Figure 6). Interestingly, for adults, shell height followed the same patterns as the head measurements (positive allometry for females and isometry for males), but for carapace width, both sexes showed negative allometry (i.e., slopes significantly < 1 on a log–log scale). Thus, both sexes become increasingly elongated over time.

All five head size measurements were substantially larger (relative to CL) in *E. m. emmotti* males and females compared to *E. m. macquarii* males and females (Figures 4 and 6). The difference was so pronounced that it did not warrant statistical analysis. As an illustration, for individuals with a 300-mm CL, an average female *E. m. emmotti* would have a 34.1.% longer head, 41.4% wider head, 39.7% taller head, 40.3% wider upper jaw, and

31.2% wider interocular distance than an average female *E. m. macquarii* (calculated as: [*E. m. emmotti*-*E. m. macquarii*]/*E. m. macquarii* * 100).

Unlike *E. m. emmotti*, *E. m. macquarii* exhibited only a slight difference in head size (relative to body size) between males and females, with females having slightly larger heads than males (Figure 6). The difference was strongest for head width ($F=22.82$; $p<0.0001$), with a slightly significant difference for head height ($F=4.52$, $p=0.0379$) and upper jaw width ($F=4.77$, $p=0.0331$), and no significant difference for head length ($F=1.09$, $p=0.3018$) or interocular width ($F=1.70$, $p=1.970$). There was a nearly significant interaction with sex for head width ($F=3.80$, $p=0.0551$) that became slightly significant when excluding females larger than the largest male ($F=5.90$, $p=0.0179$), but no other interactions were significant. All measurements for *E. m. macquarii* exhibited isometric growth, but head width was nearly allometric (i.e., a line with a slope of 1 was almost outside of the 95% confidence intervals on a log–log scale). It should be noted that more data were available for head width than for the other measurements, but subsetting to only turtles that also had the other head measurements recorded yielded similar results ($F=14.80$, $p=0.0003$).

For turtles ≤68.8 mm CL (~0–2-year-olds), *E. m. emmotti* had significantly larger heads (relative to body size) than did *E. m. macquarii* for all measurements (all $p<0.0002$) except head height ($F=1.92$, $p=0.1715$; Figure 6). Interactions between subspecies and carapace length were significant for all measurements (all $p<0.01$) except for interocular width ($F=0.27$, $p=0.0845$). For head height, hatchlings were similar between subspecies, but *E. m. emmotti* quickly became larger.

Full statistical outputs and additional regressions, figures, and comparisons (including regressions based on plastron length) are available in the Data S1.

Injuries and shell anomalies

For individuals captured in 2019/2022 (males = 99, females = 121, juveniles = 335), 18 were missing a leg ($n=2$), foot ($n=8$), part of a foot ($n=5$), or webbing/toes ($n=3$). There were significantly more injuries on the rear limbs ($n=14$) than on the front limbs ($n=4$; $\chi^2=5.56$; $p=0.0184$). Six individuals were missing an eye or had injured eyes. A seventh individual was missing part of the upper and lower left eyelids. Most injuries appeared old.

Shell injuries (i.e., damaged or missing scutes, breaks in the shell, and scutes with natural notches in them) were harder to quantify and categorize, and in some cases, we could not distinguish between congenital malformations and injuries. Nevertheless, 44 individuals were noted with some form of shell damage: 23 had natural notches on or were missing 1–2 contacting marginal scutes, three had remodelled breaks, three were missing the edges and centre of multiple rear marginal scutes giving them a skeletal appearance (Figure S13), one was missing a "chunk" out of the rear plastron lobe, and the remaining 14 turtles were missing all or part of at least three consecutive marginal scutes (and sometimes part of the costals) giving the appearance that a chunk had been taken out of them (Figure 1). Thirteen of these "chunks" were from the rear of the carapace, and one was from the middle.

Fifty-nine turtles (10.6%) had some form of shell or scute malformation (e.g., unusual numbers or shapes of scutes). Two females had unusually shaped shells (Figure S14), and one juvenile was noted as having unusual scutes, but no other notes were recorded. The remaining turtles had malformations on the following scutes: cervical = 1, marginals = 18, costals = 23, and vertebrals = 25 (some turtles had malformations on multiple scute types). For both vertebrals and costals, most malformations occurred

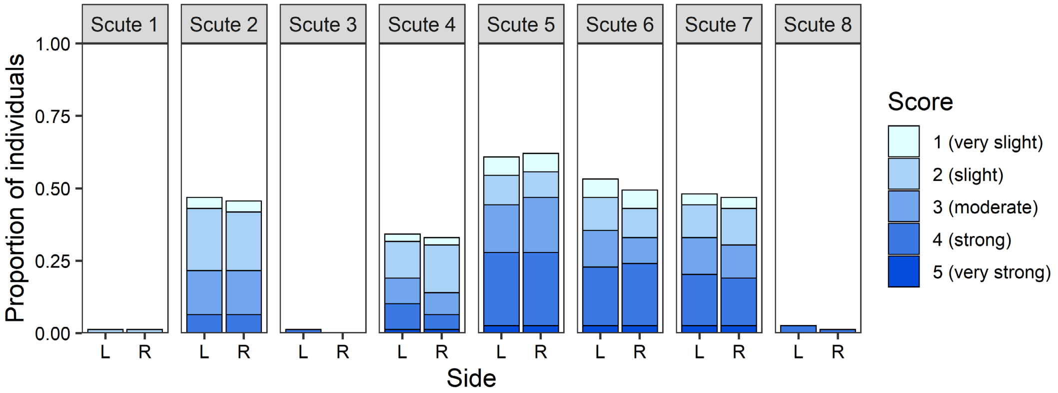

FIGURE 7 Frequency of extensions in the seams of the marginal scutes (extending into the costal scutes). Because of the effects of size and maturity (Figure 8), only sexually mature adults (males > 180 mm carapace length [*n* = 39]; females > 250 mm carapace length [*n* = 40]) were included in this figure. Scutes 9–12 did not have seam extensions. Scute counts begin at the front of the carapace.

on the first scute (17 for vertebrals and 11 for costals [for 3 individuals, the location of the costal malformation was not noted]), with splits creating an extra scute being particularly common (Figure S15). Additional photos and details on the injuries and malformations are available in the Data S1.

Marginal scute seams

Extensions in the seams of the marginal scutes (extending into the costal scutes) were common on scutes 2, 4, 5, 6, and 7 (counting from the front); rare on scutes 1, 3, and 8; and absent from scutes 9–12 (Figure 7; Figures S16 and S17). They were particularly prominent on scutes 5–7. There was a clear relationship between size and both the frequency and intensity of extended marginal scute seams. Out of 184 juveniles examined, only one individual (CL = 120 mm) had at least one extended marginal scute seam (and those seams were only slightly extended). In contrast, 35 out of 47 females (74.5%) and 23 out of 39 males (58.9%) had at least one extended scute seam. Furthermore, among males and females, there was a strong positive correlation between CL and both the number of scutes with at least some degree of seam extensions ($\chi^2 = 25.55$, $p < 0.0001$) and the sum of the scores per scute ($\chi^2 = 26.37$, $p < 0.0001$; Figure 8). Interestingly, after accounting for CL, males had more extended scute seams ($\chi^2 = 16.39$, $p < 0.0001$) and higher sums of scores per scute ($\chi^2 = 12.13$, $p = 0.0005$) than did females.

There was a high degree of symmetry between the left and right marginal scutes (Figure 7). For the 59 turtles (males, females, and the juvenile) with at least one extended scute seam, 44 (74.6%) had identical scores for all corresponding left and right scutes (e.g., scute left 1 received the same score as scute right 1). For the 15 asymmetric turtles, eight only differed by one scute between the left and right, three differed by two scutes, three differed by three scutes, and only one differed by four scutes. The mean difference between the scores for pairs of left and right scutes for those 15 individuals was 0.51.

DISCUSSION

Population demographics, movements, and flooding

Using large fyke nets that completely cut off the channel allowed us to quickly capture a large portion of the turtles in Waterloo in 2019 (428 individuals out of an estimated 508 individuals) and capture the full-size range

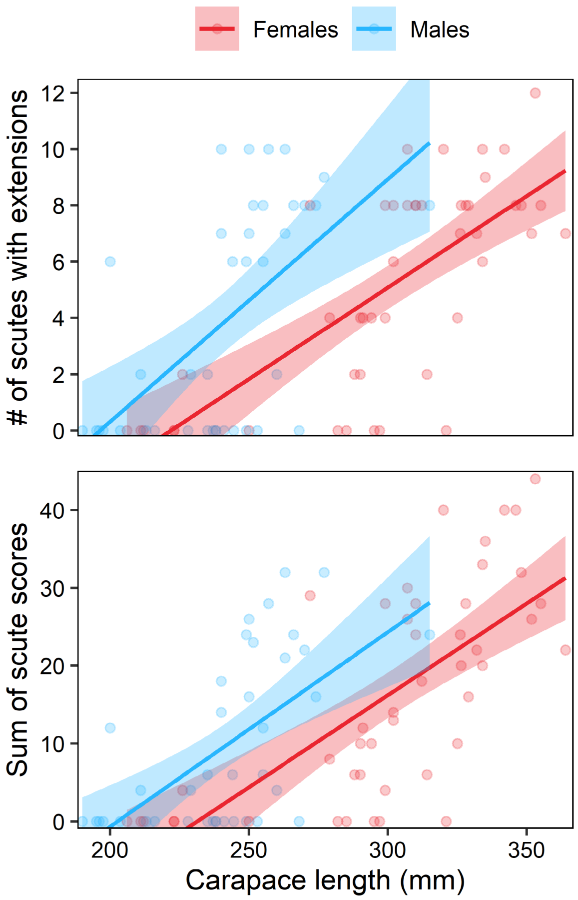

FIGURE 8 Regressions of *Emydura macquarii emmotti* carapace length (CL) and the number of marginal scutes with extensions in their seams (top) and the sum of the score of the seam extensions (bottom; each scute was rated as 0–5). Juveniles (turtles < 180smm CL are not shown).

of individuals. Furthermore, partitioning our estimates by size and sex confirmed that our trapping provided a comprehensive and accurate picture of the turtle population at that time. Perhaps most notably, the population consisted predominantly of juvenile turtles, with large numbers of juveniles also captured at the other sites and in the 2001–2004 survey. Thompson (1983) also noted that Cooper Creek had a high number of juveniles compared to *E. m. macquarii* populations in the Murray River and suggested that this was a result of differences in nest predation rates by invasive foxes (*Vulpes vulpes*), which are common and abundant around the Murray River, but rare or absent around Cooper Creek. Subsequent research also found low proportions of juveniles in the Murray River (Chessman, 2011; Van Dyke et al., 2019); however, the role of foxes in that trend is not universally accepted (Chessman, 2021). It would be useful to systematically examine nest predation rates by natural nest predators at Cooper Creek. Additionally, the age-based survivorship rates of Cooper Creek turtles should be examined, because this high abundance of juveniles at Waterloo suggests that either few juveniles survive all the way to adulthood (coupled with high reproduction rates producing many juveniles), or adult mortality is very high (coupled with high survivorship to maturity), or source–sink dynamics are occurring with high productivity and subsequent dispersal from some waterholes (Georges & Guarino, 2017; White, 2002), or some combination of those possibilities.

Based on the population estimates and mean mass of captured individuals, we calculated a turtle biomass of 74.1 kg/ha (95% CI = 61.7–93.7) for Waterloo in 2019. Few biomass estimates are available for Australian freshwater turtles. Georges (1984) calculated a biomass of 28.8 kg/ha of a population of small *E. macquarii* on Fraser Island, and Kennett (1994) reported biomasses of 8.1–17.3 kg/ha for *Chelodina rugosa* and 105.3–170 kg/ha for *Elseya dentata*. Iverson (1982) reported that the biomasses for populations of 16 aquatic turtle species (none from Australia) ranged from 10.2–384.2 kg/ha with a mean of 137.5 ± 124.8 kg/ha; however, that estimate was skewed by a few large, herbivorous species. Therefore, we reanalysed his data by calculating the median for aquatic species using the data from Table 1 in Iverson (1982) (when multiple populations were available per species, we used the median value per species; we considered both *Kinosternon scorpiodes* subspecies to be semi-aquatic, rather than aquatic). This produced a median value of 46.5 kg/ha, suggesting that the Waterloo *E. m. emmotti* population has a moderate to high biomass compared to other aquatic turtle species.

The biomasses and densities of fish communities in Cooper Creek reach extraordinarily high densities following floods (due to the productivity of the floodplain), followed by large declines in biomass, density, and species richness as resources in the waterholes decrease (Arthington et al., 2005; Balcombe et al., 2015; Balcombe & Arthington, 2009). For example, in March 2004, following a large flooding event in January and February, four waterholes near Windorah had a total fish biomass of 12 288 kg/ha (Balcombe et al., 2015). This declined over time and by December 2004 had dropped to 2913 kg/ha (Balcombe et al., 2015). Unlike fish, turtles' longevity and slow growth rates likely make them less prone to such rapid and extreme fluctuations in demographics, and they may represent a comparatively stable biomass that can lock up nutrients for much longer periods.

Nevertheless, floods do appear to play a role in the ecology of *E. m. emmotti*. Many species of fish use the Cooper Creek floodplains (Balcombe et al., 2007), and several previous works have stated that *E. m. emmotti* likewise utilizes the floodplain (Georges & Guarino, 2017; Kingsford et al., 2006), including an observation of turtles “walking just in front of a flood” (Georges & Guarino, 2017). Our study is the first to confirm this behaviour quantitively, as well as the first to document the demography of turtles using the floodplains. Several other freshwater turtle species alter their behaviour following flooding and/or make use of flooded habitats (Bodie & Semlitsch, 2000; Doody et al., 2002; McKnight et al., 2023; Ocock et al., 2018), but the importance and use of floodplains is poorly understood for most turtle species and should be the topic of future research. Floodplains are often highly productive (Junk et al., 1989) and likely represent critical foraging opportunities for species like *E. m. emmotti*. They may also present a risk, however, as turtles could become stranded away from the permanent pools and die when the water dries. Trophic studies of turtles on floodplains should be a priority for future research.

Interestingly, while both sexes and a wide range of turtle sizes were captured on the floodplain and in the channel around Waterloo in 2022, the sex ratio was strongly male-biased, compared to the female-biased sex ratio in Waterloo in 2019. Additionally, we documented 17 males (but no females) that moved between waterholes. Furthermore, in Waterloo in 2019 and 2022, the sex ratio of recaptures from 2001–2004 was strongly female-biased, even though the sex ratio at Waterloo in 2001–2004 was slightly male-biased. Taken together, these results suggest a male-biased dispersal pattern in which males make use of floods to migrate among waterholes, while females generally remain in their waterhole and make more limited use of the floodplain. Similar patterns of male-biased dispersal have been observed in *Chelodina expansa* (Bower et al., 2012) and *E. m. macquarii* in the Murray River (Van Dyke et al., n.d.). It should be noted, however, that male-biased mortality rates would also explain some (but not all) of the patterns we observed, and robust movement studies that track individuals would be valuable. Additionally, during the 2022 flood, we also caught more males than females in the main channel of Waterloo. Turtles were, however, actively moving in and out of the floodplain, and this may indicate a general increase in activity for males during flooding. More work is needed to clarify this.

Beyond a change in the sex ratio at Waterloo over time, the size distribution also shifted. In 2001–2004, a large portion of females were <280 mm CL, whereas in 2019, regardless of the trapping method, almost all females were >280 mm CL. Unlike fish populations that change rapidly in response to floods, the turtle populations may fluctuate on longer timescales with both male-biased movement patterns and high juvenile growth/survival during good years affecting the population structure (both sex ratio and size distribution) for years to come. Collecting data annually over a long time period will be required to properly examine this.

Algae and leeches

Epizootic algae are common on many turtle species, and some *Basicladia* species specialize on turtles (Proctor, 1958). Many *E. m. emmotti* had algae growing on them, but it was generally present as a thin layer, rather than the thick, filamentous "mossback" coating that is common on many species (Burgin & Renshaw, 2008; Skinner et al., 2008). Several studies have found less algae on smaller turtles (Akgul et al., 2014; Edgren et al., 1953; Proctor, 1958), while others failed to find a relationship between size and algae (Gibbons, 1968). In contrast, we found very little algae on large adults, while very young turtles were often almost completely coated. This could represent a difference in habitat choice among age groups (e.g., juveniles spending more time in shallow, warm environments) and could provide camouflage benefit to young individuals; it should be investigated further. Interestingly, algae were not restricted to the carapace but were also common on the plastron and skin. Indeed, the relationship with size was clearest for algae on the skin, with 91.0% of turtles <100 mm having at least some algae and 55.2% having high algal loads (i.e., ≥67% of skin covered), compared to turtles >200 mm in which only 11.8% had any algae and none had high loads (seven had very low loads [<5% covered], two had low loads [6%–33% covered], and one had a medium load [34%–66%]).

Leeches are also common on aquatic turtles, yet we failed to find any. *Emydura macquarii krefftii* in Townsville, Queensland, have very high levels of leeches, with 98.8% of individuals harbouring them and 92.9% hosting more than five leeches (McKnight et al., 2021). In contrast, leeches were only found on 34.5% of *E. m. macquarii* in Victoria, and only 10.7% of individuals had more than five leeches (Chessman, 1987). Meanwhile, 0%–5.5% of *Emydura victoriae* [*australis*] and 12.3%–83.3% of *Chelodina burrungandjii* in the Kimberley had leeches (Skinner et al., 2008). It is unclear why leech levels are so low in Cooper Creek.

Head and shell dimensions

Cooper Creek turtles have substantially larger heads (relative to body size) than *E. m. macquarii*, and this difference appears to start early; even hatchling *E. m. emmotti* have relatively larger heads than hatchling

E. m. macquarii. Furthermore, as adults, there is a pronounced sexual dimorphism in head size in *E. m. emmotti*, whereas there is only a slight difference between the sexes in *E. m. macquarii*.

Sex-specific megacephaly has been reported in several other turtles (with North American map turtles [*Graptemys* spp.] and diamond-backed terrapins [*Malachelys terrapin*] probably being the most well-known examples; Ernst & Lovich, 2009; Lindeman, 2000, 2013). Lindeman (2000) reported that the ratios of head width to plastron length (based on the predicted head width for the maximum plastron length for the species) for females of 15 *Graptemys* species ranged from 0.119–0.263. Following the same procedure, we calculated a ratio of 0.248 for *E. m. emmotti*, placing it on the high end of the spectrum. It should be noted, however, that Lindeman (2000) included unsexed juveniles in his regressions, whereas we only used adult or subadult females. Nevertheless, it is clear that *E. m. emmotti* have relatively large heads even when stacked against the infamously big-headed *Graptemys* spp. It is also worth noting that in *Graptemys* spp. and *M. terrapin*, females are often at least twice the CL and many times the mass of males (Ernst & Lovich, 2009; Lindeman, 2013), whereas the difference in adult body sizes was comparatively small in *E. m. emmotti*, with the largest female being only 1.16 times the CL and 1.8 times the mass (estimated) of the largest male. Additionally, both sexes of *E. m. emmotti* were megacephalic compared to *E. m. macquarii*, and the shells of female *E. m. emmotti* were both wider and taller than the shells of males (relative to CL), with the patterns for shell height closely matching the patterns for head measurements (see Data S1).

Several other *Emydura* species are megacephalic in at least some populations (e.g., *E. m. krefftii*, *E. subglobosa worrelli*, *E. tanybaraga*, and *E. victoriae*; Cann & Sadlier, 2017; Legler & Georges, 1993). However, few head measurements have been published. Trembath et al. (2004) reported that female *E. m. krefftii* in Townsville, Queensland, had larger heads (relative to mass) than did males, and both sexes exhibited roughly isometric growth. Because they reported regressions against mass, it is hard to make direct, meaningful comparisons, but their data suggest a lower degree of megacephaly and sexual dimorphism than we documented in *E. m. emmotti*, which is consistent with our personal observations of Townsville *E. m. krefftii* (DTM and DSB, pers. obs.). In contrast, a study on *E. victoriae* in the Daly River documented pronounced megacephaly in adults (Welsh et al., 2017). Applying the same maximum size ratios used earlier (but for CL) to their data and ours suggests a maximum head width/CL ratio of 0.213 for *E. m. emmotti* and 0.250 for *E. victoriae*. Interestingly, unlike *E. m. emmotti* and *E. m. krefftii*, head sizes in male and female *E. victoriae* were not significantly different after accounting for body size.

The cause of such pronounced megacephaly in *E. m. emmotti* is not immediately clear. In *Graptemys* spp. and *M. terrapin*, megacephaly is associated with a diet that specializes on hard-shelled organisms such as molluscs (Ernst & Lovich, 2009; Lindeman, 2000, 2013). The diet of *E. m. emmotti* is, however, currently unknown. *Emydura m. macquarii* in Victoria and New South Wales are opportunistic omnivores that consume a large quantity of algae, as well as carrion, macrophytes, and invertebrates (Chessman, 1986; Petrov et al., 2018). *Emydura m. krefftii* in the Fitzroy River are likewise omnivorous (Rogers, 2000). *Emydura m. macquarii* do, however, switch from an algae-dominated diet to a more carnivorous diet when the water is turbid and primary productivity is low (Petrov et al., 2020), and turbidity in Cooper Creek is very high (Bailey, 2001), which could incline *E. m. emmotti* towards carnivory. A stable isotope study showed that algae is a key primary producer in Cooper Creek, but it did not determine whether *E. m. emmotti* eats the algae itself or simply eats organisms (such as crayfish) that eat the algae (Bunn et al., 2003).

It is unclear why a generalist (and particularly one that consumes large quantities of algae) would develop such large heads, making it likely that the diet of *E. m. emmotti* differs from that of the other subspecies. Consistent with the dietary hypothesis, a study on the diets of a megacephalic population of *E. victoriae* found that large adults specialized on molluscs, while *E. subglobosa worrelli* at the same location did not exhibit megacephaly and were generalist omnivores (Welsh et al., 2017). Amusingly, Cann and Sadlier (2017) observed a megacephalic *E. victoriae* [*australis*] awkwardly attempting to eat weeds and commented, “what a tremendous disadvantage the ‘boofheaded’ state becomes.” Additional studies quantifying the diets and degrees of megacephaly across *Emydura* species and populations (including New Guinea populations) would be fruitful.

Injuries, shell anomalies, and marginal scute seams

Anomalous numbers and arrangements of scutes are common in turtles, and the frequency we observed (10.6% of individuals) is not unusual (Cherepanov, 2014; MacCulloch, 1981; McKnight & Ligon, 2014). The “extensions” in the seams of the marginal scutes are not, however, features that have been widely reported. We have occasionally seen small extensions in particularly large *E. m. macquarii*, but not with the frequency or prominence with which they were observed at Cooper Creek (McKnight, pers. obs.). Likewise, there are some photos of northern *Emydura* species with similar features (Cann & Sadlier, 2017), but the frequency and relevance of the trait have not been discussed. In *E. m. emmotti*, the feature usually only developed in adult turtles, becoming particularly prominent in the largest individuals. However, females generally did not start developing seam extensions until they reached sexual maturity (i.e., subadult females did not develop them as frequently or strongly as did males of the same size). Our sample size of subadult females was, however, limited and should be expanded in the future. Nevertheless, even within adult females, there were clear linear trends, suggesting that females begin developing seam extensions at larger sizes than do males, and when comparing males and females of the same size, the males will generally have more prominent seam extensions. Perhaps this feature is driven by age rather than size.

We also found multiple turtles that were missing limbs or chunks out of their shell, with most injuries occurring on the rear of the shell. The bias towards the rear could indicate that they are usually attacked from behind, or it could be a survivorship bias if attacks to the front often injure the head and neck, making them harder to survive. Hollender et al. (2018) found a similar result for species that are prone to boat strikes and proposed that the preponderance of injuries to the turtles' posterior suggested that either injuries to the anterior were harder to survive or that turtles were being hit while in the process of diving.

The cause of the injuries we observed is not entirely clear. Boating is uncommon in our waterholes, and none of the injuries looked like propeller strikes. Also, because damaged shells and missing limbs were observed on males, females, and juveniles, they are unlikely to be from terrestrial predators (these turtles do not generally move around on land except for nesting females). It therefore appears likely that these injuries are from predators in the waterholes. In addition to avian predators such as herons and egrets, Cooper Creek contains large crawfish (*Cherax destructor* and *C. quadricarinatus*), several large predatory fish (e.g., *Macquaria ambigua*), and, of course, giant, big-headed turtles, any of which could take a bite out of a young *E. m. emmotti*. The role of *E. m. emmotti* has been largely neglected in studies of Cooper Creek's foodwebs, and these magnificent, ugly turtles should be a priority in the future.

AUTHOR CONTRIBUTIONS

Donald T. McKnight: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Arthur Georges:** Conceptualization (equal); data curation (equal); formal analysis (supporting); funding acquisition (equal); investigation (equal); methodology (equal); project administration (supporting); resources (equal); supervision (equal); writing – review and editing (equal). **Fiorenzo Guarino:** Investigation (equal); project administration (equal); writing – review and editing (supporting). **Deborah S. Bower:** Conceptualization (equal); data curation (supporting); formal analysis (supporting); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (lead); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

The data are currently being used for other long-running projects, but they can be made available upon reasonable request.

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SUPPORTING INFORMATION

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

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