Received: 1 May 2023 | Revised: 15 October 2023 | Accepted: 26 October 2023

DOI: 10.1111/aec.13456

RESEARCH ARTICLE

Climate change affects the early-life history of a freshwater turtle in a severely drying region

Anthony Santoro[1,2] | **Jane M. Chambers**[1] | **Brendan Ebner**[3,4] | **Stephen J. Beatty**[2]

[1]Environmental and Conservation Sciences, Murdoch University, Murdoch, Western Australia, Australia

[2]Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute, Murdoch University, Murdoch, Western Australia, Australia

[3]TropWATER – Centre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Townsville, Queensland, Australia

[4]CSIRO Land and Water, Atherton, Queensland, Australia

Correspondence
Anthony Santoro, Environmental and Conservation Sciences, Murdoch University, 6150 Murdoch, WA, Australia.
Email: anthony.santoro@murdoch.edu.au

Abstract

Freshwater turtles are one of the most threatened vertebrate groups. Climate change is a major threat to these species, with impacts affecting all life-history stages. There is currently a limited understanding of how changes in climate may alter the environmental triggers for hatching and emergence from the nests of freshwater turtle hatchlings. This precludes making predictions about how climate change may impact freshwater turtle recruitment success. The south-western snake-necked turtle (*Chelodina oblonga*) is endemic to south-western Australia, a global biodiversity hotspot that has undergone severe climatic drying. Recruitment failure is thought to be occurring in many populations of the species. However, there is little understanding as to how environmental change may be influencing recruitment. This study aimed to: (1) determine the incubation duration and hatching and hatchling emergence success of *C. oblonga*, (2) determine if the species exhibits hatching or emergence synchrony and/or delayed emergence and (3) quantify the effects of temperature and rainfall on hatchling emergence. Using this information, the study assesses how climatic drying and warming may be impacting *C. oblonga*'s early life-history. Between 2018 and 2020 nest sites were monitored around a large urban wetland with weekly assessments of egg and hatchling status. Incubation duration and hatching and hatchling emergence success were calculated, and generalized linear models were built to determine how temperature and/or rainfall predicted emergence. Hatchlings either emerged shortly after hatching or overwintered in the nest, and both hatching and emergence were asynchronous. Both emergence periods were positively associated with temperature and rainfall. This study reveals that incubation duration, hatching success, hatchling emergence and survival are all likely to be impacted by recent and projected climate change, and especially drying. Warming and drying are predicted for many temperate regions globally, and it is therefore important that their impacts on the early life history of freshwater turtles be better understood.

KEYWORDS
Chelonia, egg incubation, hatchling emergence, over-wintering, reptile

INTRODUCTION

Freshwater turtles are one of the most threatened vertebrate groups globally, with ~60% of species listed as threatened or worse (Lovich et al., 2018; Stanford et al., 2020). The primary causes threatening freshwater turtles include climate change, loss or modification of habitat, predation, pollution and overharvesting for the pet trade (Gibbons et al., 2000; Klemens, 2000; Stanford et al., 2020). Due to these multifaceted threats, it is imperative to develop comprehensive strategies to mitigate their impacts and ensure the continued survival of freshwater turtles.

Understanding the early life history of freshwater turtles is pivotal for their conservation. This critical phase encompasses crucial developmental milestones, from egg incubation to hatching and emergence from the nest, and significantly influences their survival and population dynamics (Valenzuela, 2001; Micheli-Campbell et al., 2011; Knoerr, Graeter, et al., 2021; Knoerr, Tutterow, et al., 2021). Each stage is fraught with challenges, and even small variations can have profound impacts on survival rates (Chessman, 2018; Janzen et al., 2007; Zappalorti et al., 2017). By understanding the early life history phase of turtles, insights into their vulnerabilities can be attained and targeted conservation measures developed.

Incubation

One of the fundamental aspects of freshwater turtle early life history is egg incubation. The development of embryos during this phase ultimately determines the hatchling's condition and chances of survival (Booth et al., 2004; Micheli-Campbell et al., 2011). The environmental conditions surrounding the eggs, including temperature and humidity, play a pivotal role in shaping embryonic development (Zhu et al., 2006). Higher temperatures tend to accelerate development, while lower temperatures slow it down (Ewert, 1979, 1985). Longer incubation periods may result in higher vulnerability to predation (Riley & Litzgus, 2014), while shorter durations might hinder the development of vital physiological and anatomical traits (Colbert et al., 2010). The duration of incubation can vary widely among species, and understanding these differences is essential for assessing the vulnerability of turtle populations to climate change and crafting effective conservation strategies that promote the survival of these species.

Hatching and emergence of success

Hatching success (i.e., the proportion of eggs that successfully produce hatchlings) and hatchling emergence success (i.e., the proportion of hatchlings that successfully emerge from the nest) are also pivotal aspects of freshwater turtle early life history. Factors such as predation, disease and environmental conditions can profoundly influence hatching and emergence success rates (Carranco et al., 2022; Knoerr, Graeter, et al., 2021). High hatching and emergence success contributes to a larger population of juvenile turtles, contributing to the long-term viability of the overall population (Carstairs et al., 2019; Knoerr, Graeter, et al., 2021; Knoerr, Tutterow, et al., 2021). Conversely, low hatching and emergence success rates can negatively impact the viability of populations. Therefore, studying hatching and emergence success is essential for assessing the overall reproductive potential and viability of freshwater turtle populations.

Emergence timing, strategies and triggers

Freshwater turtle hatchlings experience much higher natural mortality rates compared to older age classes (Iverson, 1991; Wilbur, 1975). Survival rates of hatchlings following emergence from the nest are affected by several factors that vary temporally, including the availability of food resources (Gibbons & Nelson, 1978), the abundance of predators (Janzen et al., 2000; Paterson et al., 2012, 2014), dispersal opportunities (Doody et al., 2001; Nagle et al., 2004) and the thermal environment (Moran et al., 1999). Because of this, intraspecific and interspecific variations in the timing of hatchling emergence are common (Gibbons & Nelson, 1978; Riley et al., 2014), and there are three broad strategies:

1. Emerge in autumn and hibernate on land (then remain on land for terrestrial turtles) (Burke & Capitano, 2011) or emerge in autumn and hibernate on land until spring and then enter aquatic habitat (aquatic species) (Draud et al., 2004; Muldoon & Burke, 2012; Paterson et al., 2012)
2. Emerge in autumn, enter aquatic habitat and hibernate before subsequently increasing activity in spring (Carroll & Ultsch, 2007; Costanzo et al., 1995)
3. Hibernate in or below the nest until spring, then emerge and enter aquatic habitats (Baker et al., 2003; Costanzo et al., 1995; Nagle et al., 2004; Pappas et al., 2000)

If environmental conditions are favourable upon hatching and food and habitat are available, immediate emergence should be favoured (i.e. strategies 1 and 2) (Gibbons & Nelson, 1978). On the other hand, overwintering within the nest (i.e. strategy 3) may provide survival advantages via reduced exposure to low temperatures, dry wetlands, seasonally low food availability and/or above-ground predation risk. In contrast, spring is characterized by increasing temperatures and food resources that are likely more favourable for dispersal and growth (Gibbons, 2013; Gibbons & Nelson, 1978; Nagle et al., 2004; Wilbur, 1975). However, factors such as desiccation, flooding, freezing and predation can impact the survival rates of hatchlings overwintering in the nest (Breitenbach et al., 1984; Costanzo et al., 1995, 2008; Packard et al., 1989; Storey et al., 1988). Studying emergence timing is crucial for conservation, as it enables us to anticipate the presence of juvenile turtles in terrestrial habitats, assess their vulnerability to predation and implement management strategies to protect them during this vulnerable phase.

A range of interspecific differences in emergence strategies exist. Hatchlings of some species emerge synchronously (Congdon et al., 1983; Nagle et al., 2004; Tucker, 1999). This synchrony provides advantages including reduced individual energy expenditure during digging from nest chamber to surface (Carr & Hirth, 1961; Rusli et al., 2016), dilution of predator risk per capita via swamping (Spencer et al., 2001), reduced time a predator can smell hatching eggs and predate a nest (Doody, 2011) and preventing mortality due to enhanced environmental extremes of breached nests (Baker et al., 2006; Nagle et al., 2004). This study hereafter defines emergence synchrony as all hatchlings from a nest emerging within a 24-hour period (Baker et al., 2013; Geller et al., 2020).

In contrast, hatchlings of many species emerge asynchronously (Glen et al., 2005; Houghton & Hays, 2001; Lindeman, 1991; Nagle et al., 2004). Asynchronous emergence has been attributed to variation in incubation rates through differences in temperature and soil moisture throughout the nest microenvironment (Houghton & Hays, 2001). Asynchronous emergence has been suggested to be a superior strategy to synchrony when predators are prey-switching generalists (Ims, 1990). Identifying the emergence strategy implemented by a species enables an understanding of the key environmental influences, including the drivers of mortality in its early life-history phase.

Emergence from the nest by hatchling turtles is usually triggered by physical or biological factors. Physical factors often include rainfall and temperature, with rainfall suggested to trigger some species by softening the soil above the nest chamber, thus facilitating excavation for emerging hatchings (DePari, 1996; Doody et al., 2001; Moll & Legler, 1971; Nagle et al., 2004; Santidrián Tomillo et al., 2015). Temperature change may also trigger emergence, often by a temperature increase (Gibbons & Nelson, 1978; Tucker, 1999) or further increases or decreases in temperature once a threshold has been reached (Moran et al., 1999; Nagle et al., 2004). Increases in temperature following cold winters may indicate more favourable foraging and growing conditions for hatchlings and trigger their emergence (Gibbons & Nelson, 1978). Biological factors can include hatchlings possessing an internal clock that triggers their emergence (Lindeman, 1991; Moran et al., 1999) or the relative risk of predation (Riley et al., 2014). While several aspects of the effects of climate change on chelonians have been researched (Butler, 2019), there remains a paucity of studies that have assessed how changing temperature and rainfall patterns will impact the timing and success of hatchling emergence in freshwater turtles (for marine turtles, see Hill et al., 2015; Laloë et al., 2021).

Chelodina oblonga is one of two freshwater turtle species native to the south-west of Western Australia. Its reproductive ecology remains largely unstudied, and only two relevant natural history-based studies have been conducted in the past 55 years (Burbidge, 1967; Clay, 1981). Nesting occurs in spring and summer (Burbidge, 1967; Clay, 1981). An average clutch size of eight eggs was reported for the spring reproductive season and four eggs for the summer season (Clay, 1981). The egg incubation period ranged from 200 to 230 days (Burbidge, 1967; Clay, 1981). There was some variation in the reported hatchling emergence timing. Burbidge (1967) reported that hatchlings generally emerge in May, but that under certain conditions, hatching may be delayed, or the hatchlings may remain in the nest, emerging as late as August. Clay (1981) reported that all hatchlings emerged in mid-August, regardless of when they were laid. This suggests the duration hatchlings remain within the nest is substantially greater for nests made in spring than summer. After emergence, hatchlings are thought to head straight to nearby wetlands.

Chelodina oblonga populations in urban wetlands appear to be declining, with recruitment hindered for at least a decade (Santoro et al., 2020). Furthermore, the climate of southwestern Australia has dried dramatically, with the onset coinciding with the period when the aforementioned pioneering natural history studies were conducted on *C. oblonga* (McFarlane et al., 2020). A contemporary understanding of hatching and emergence success is needed to provide an indication of recruitment potential and identify whether interventions are required. By comparing this information to historical studies, an insight as to whether the change in climate that has occurred over the past ~50 years may have caused changes in the timing of hatching and hatchling emergence. Finally, a current quantitative basis for understanding and predicting the key environmental cues for emergence is required to help understand how climate change may be impacting the recruitment rates of this prominent wetland vertebrate.

This study aims to determine: (1) the number of days from laying to hatching (incubation duration), (2) the percentage of eggs that hatch successfully (hatching success), (3) the percentage of hatchlings that emerge successfully (emergence success), (4) when hatchlings emerge from the nest (emergence timing) and (5) whether hatchlings emerge due to environmental (rainfall, temperature) or biological reasons (emergence trigger).

Using this information, the study aimed to compare how these factors may have changed over time by comparing them to studies on the species that were undertaken prior to the climate drying of the region.

METHODS

Study site

The study was conducted in Bibra Lake, located within the Beeliar Regional Park, Perth, Western Australia (Figure 1). Bibra Lake is a surface expression of the local unconfined aquifer, with water levels recharged by rainfall (Davis & Froend, 1999). Southwestern Australia is a global biodiversity hotspot (Myers et al., 2000) and has a Mediterranean climate with hot, dry summers and cool, wet winters (Sturman & Tapper, 1996). The average annual rainfall for the region has declined from ~900 mm for the period between 1920 and 1975 to ~711 mm between 2011 and 2020 (Water Corporation, 2021). Historically, rain has fallen predominantly during the winter months (June–August); however, it now occurs over a wider time-period, with significantly decreased rainfall during winter and increased rainfall during summer (McFarlane et al., 2020). Groundwater levels in Perth have declined over the last few decades as a result of reduced rainfall and groundwater extraction for human use (Dawes et al., 2012), resulting in permanent wetlands becoming seasonal and seasonal wetlands being dry for increasingly long periods (Sim et al., 2013). The average maximum temperature in Perth has increased from 24.4°C between 1970 and 1979 to 25.6°C between 2010 and 2019 (Bureau of Meteorology, 2021).

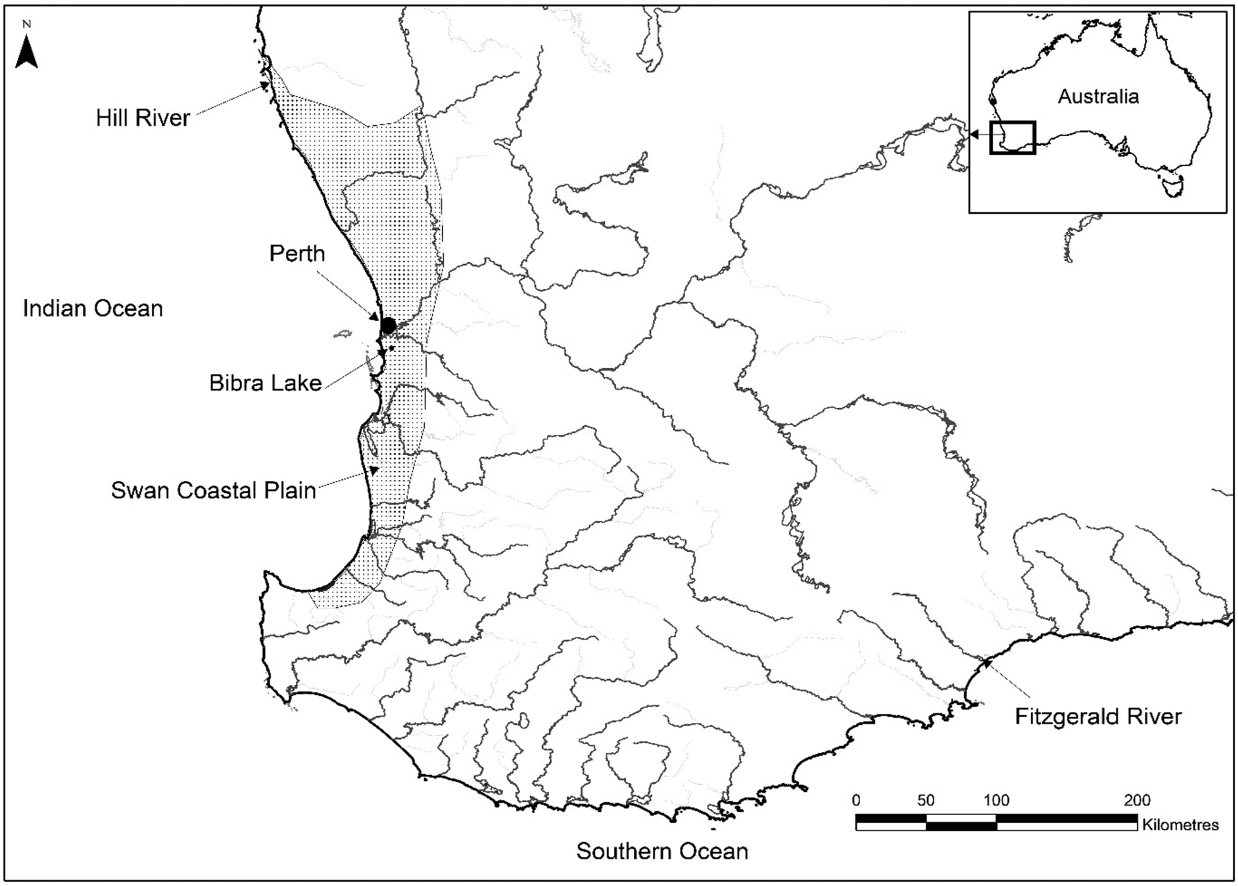

FIGURE 1 Map of southwestern Western Australia, highlighting the study location (Bibra Lake), within the Swan Coastal Plain (shaded zone), and the limits of *Chelodina oblonga*'s geographical range – the Hill and Fitzgerald Rivers.

Nest location/identification

Nests were located opportunistically while radio-tracking was being conducted as part of a parallel study on the ecology of adult turtles over a two-year period and through the 'Turtle Tracker' program in 2019 (Santoro, 2022). The 'Turtle Tracker' program involved trained volunteers searching the terrestrial environment surrounding Bibra Lake during the spring nesting season (September–November). Female turtles were observed from a distance until nesting was completed. Once nesting was completed, nests were carefully excavated, eggs removed and numbered with pencils and then placed back in the nest, and protected with a nest cage (19 nests). Six nests were also created artificially using eggs extracted directly from recently deceased female turtles (killed in wildlife–vehicle incidents or predation) in both nesting seasons.

Natural nests were laid between the 19th October and 3rd December 2018, and the 25th September and 11th October 2019 (Table 1). The methods used for nest location resulted in all but one nest (3rd December 2018) being from the spring nesting period. Artificial nests were created with eggs extracted from females injured or killed during nesting migrations between the 18th October and 24th November 2018, and the 25th September and 18th November 2019 (Table 1).

Nest monitoring – Incubation duration, hatching success, emergence timing and success

Eight and 17 nests were monitored in 2018/19 and 2019/20, respectively (Table 2). No non-invasive methods for checking egg/hatchling chronology in natural nests were found in the literature. Therefore, the following protocols were used. In 2019, nests were carefully excavated to monitor egg and hatchling progress approximately weekly between May and September. In 2020, 14 hatchlings from two natural nests emerged prior to the first nest check on the 27th March, which is over a month earlier than previously reported (Burbidge, 1967). Thus, in 2020, nests were checked approximately weekly from the 27th of March to September. Whether these 14 hatchlings emerged within the week prior to the 27th of March 2020 (Table 2) could not be confirmed, so they were removed from emergence analysis.

Each week, each egg/hatchling was assessed and placed into one of the following status categories: intact, cracked, hatchling or emerged. In October of both years, any unhatched eggs were cut open for assessment and placed into one of the following categories: infertile (egg did not contain an undeveloped embryo) or undeveloped hatchling (egg contained an embryo/hatchling that did not complete development). Twelve (4%) hatchlings became highly active during the nest monitoring process and these hatchlings were released rather than reburied (Table 2). Hatchlings that were released were not included in the emergence analysis.

Triggers of hatchling emergence

Environmental parameters

Temperature and rainfall are key environmental parameters that are known to influence hatchling emergence in other freshwater turtle species (DePari, 1996; Doody et al., 2001; Gibbons & Nelson, 1978; Moll & Legler, 1971; Moran et al., 1999; Nagle et al., 2004; Santidrián Tomillo et al., 2015; Tucker, 1999). These data were sourced from the Australian

TABLE 1 Dates nests were laid, dates of earliest and latest hatching and emergence, lengths of incubation and time from hatching to emergence for *Chelodina oblonga* nests.

							Incubation (days)					Emergence (days)	
Year	Natural/ artificial	Nest	Laid	Hatched	First hatchling	Last hatchling	Mean (SE)	Range	Emerged	First emerge	Final emerge	Mean (SE)	Range
2018	Natural	Hope Rd	21/10/18	9	<8/5/19	14/5/19	203 (1)	199–205 (6)	9	22/5/19	5/6/19*	16 (2)	8–22
		Ice Rink	19/10/18	7	<8/5/19	8/5/19	201 (0)	201 (na)	7	5/6/19	3/9/19	71 (16)	28–118
		Roe 8	3/12/18	11	14/5/19	5/6/19	174 (2)	162–184 (22)	7	21/5/19	31/5/19	1 (1)	0–7
	Artificial	Adventure World	22/10/18	11	<8/5/19	18/6/19	204 (4)	198–239 (41)	10	5/6/19	26/8/19	69 (11)	28–110
		Native Arc	18/10/18	7	5/6/19	18/6/19	240 (4)	230–257 (27)	4	5/6/19	22/8/19	34 (20)	0–72
		North Lake	24/11/18	4	<8/5/19	28/5/19	175 (6)	165–185 (20)	3	5/6/19	26/8/19	49 (21)	28–90
		ALL	NA	49	<8/5/19	18/6/19	200 (3)	162–257	40	21/5/19	3/9/19	41 (6)	0–118
2019	Natural	AW Bus	4/10/19	7	<27/3/20	NA	175 (0)	175 (na)	7	<27/3/20	NA	0	0
		AWPL2	4/10/19	3	27/4/20	11/5/20	213 (4)	206–220 (14)	2	11/5/20	18/5/20	11 (4)	14–21
		Big Play	11/10/19	10	<27/3/20	11/5/20*	193 (6)	168–213* (45)	2	NA	NA	NA	NA
		Cnr Gwil Prog	4/10/19	4	<27/3/20	8/6/20	209 (15)	199–248 (49)	1	18/8/20	NA	120	120
		Dirt Carpark	4/10/19	7	<27/3/20	13/4/20	180 (3)	175–192 (17)	5	6/4/20	NA	10	10
		Gazeebo	11/10/19	7	<27/3/20	<27/3/20	<168	<168 (na)	7	<27/3/20	<27/3/20	NA	NA
		Ice Park	4/10/19	4	<27/3/20	6/4/20	180 (3)	175–185 (10)	4	6/4/20	13/4/20	9 (1)	7–10
		Native ARC	4/10/19	5	6/4/20	26/5/20	201 (10)	185–235 (50)	4	13/4/20	13/7/20	26 (15)	7–69
		Park Bench	30/9/19	8	<30/3/20	27/4/20	195 (3)	182–210 (28)	3	20/4/20	5/5/20	17 (5)	7–22
		South NARC	4/10/19	7	<27/3/20	11/5/20	201 (8)	175–220 (45)	6	13/4/20	18/8/20	73 (14)	17–99
		South Play	25/9/19	5	11/5/20	2/6/20	238 (4)	229–251 (22)	3	7/9/20	14/9/20	119 (0)	119
		Style Wallia	4/10/19	10	6/4/20	20/4/20	195 (2)	185–199 (14)	7	20/4/20	7/9/20	84 (24)	7–140
		Wetlands Centre	25/9/19	9	<27/3/20	6/4/20*	193 (1)	184–194* (10)	0	NA	NA	NA	NA
		White Pickett	4/10/19	1	13/4/20	NA	192	192 (0)	0	NA	NA	NA	NA
	Artificial	Hope Rd	18/11/19	3	5/5/20	2/6/20	178 (9)	169–197 (28)	1	5/5/20	NA	0	0
		South Play Art	25/9/19	1	6/4/20	NA	194	NA	0	NA	NA	NA	NA
		ALL	NA	91	<27/3/20	8/6/20	195 (2)	168–251	52	<27/3/20	14/9/20	54 (9)	0–140

*Nest predated.

TABLE 2 Summary information of the fate of each egg within natural and artificial *Chelodina oblonga* nests.

				Outcome						
				Hatchlings			Eggs			
Year	Natural/ artificial	Nest	Number of eggs	Emerged	Released	Dead	Undeveloped hatchling	Infertile	Depredated	Unknown
2018	Natural	Golf Course 1	2[b]	0 (0%)	0	0	0	2 (100%)	0	0
		Hope Rd	10	5 (50%)	2 (20%)	0	1 (10%)	0	0	2[a]
		Ice Rink	11	7 (64%)	0	0	0	4 (36%)	0	0
		Roe 8	14	7 (50%)	0	4 (28%)	0	3 (22%)	0	0
		Mean ± SE	9 ± 3	5 ± 2 (41% ±14%)	1 ± 1 (5% ±5%)	1 ± 1 (7% ±7%)	0 ± 0 (3% ±3%)	2 ± 1 (40% ±21%)	0 ± 0	1 ± 1
	Artificial	Adventure World	22 (10 + 12)	10 (45%)	0	1 (4%)	6 (26%)	5 (22%)	0	0
		Golf Course 2	11	0 (0%)	0	0	0	11 (100%)	0	0
		Native Arc	9	4 (44%)	0	3 (33%)	0	2 (22%)	0	0
		North Lake	10	3 (30%)	0	1 (10%)	1 (10%)	5 (50%)	0	0
		Mean ± SE	13 ± 3	4 ± 2 (30% ±10%)	0 ± 0 (0% ±0%)	1 ± 1 (12% ±7%)	2 ± 1 (9% ±6%)	6 ± 2 (49% ±18%)	0 ± 0	0 ± 0
	Total	8	89	36	2	9	8	32	0	2
2019	Natural	AW Bus	12	7 (58%)	0	0	0	5 (42%)	0	0
		AWPL2	11	2 (18%)	0	1 (9%)	2 (18%)	6 (54%)	0	0
		Bibra Dr Trail	7	0 (0%)	0	0	2 (28%)	5 (72%)	0	0
		Big Play	17	2 (12%)	1 (6%)	1 (6%)	2 (12%)	2 (12%)	6 (36%)	3 (18%)
		Cnr Gwil Prog	11	1 (9%)	1 (9%)	2 (18%)	0	6 (54%)	0	1 (9%)
		Dirt Carpark	12	5 (42%)	0	2 (17%)	0	4 (33%)	0	1 (8%)
		Gazeebo	7	7 (100%)	0	0	0	0	0	0
		Ice Park	13	4 (31%)	0	0	4 (31%)	5 (38%)	0	0
		Native ARC	10	4 (40%)	0	1 (10%)	0	5 (50%)	0	0
		Park Bench	12	3 (25%)	1 (8%)	4 (33%)	3 (25%)	1 (8%)	0	0
		South NARC	10	6 (60%)	1 (10%)	0	0	3 (30%)	0	0
		South Play	7	3 (43%)	1 (14%)	1 (14%)	1 (14%)	1 (14%)	0	0
		Style Wallia	12	7 (58%)	4 (33%)	0	0	1 (8%)	0	0
		Wetlands Centre	9	0 (0%)	1 (11%)	0	0	0	8 (88%)	0
		White Pickett	13	0 (0%)	0	1 (8%)	3 (23%)	8 (61%)	0	1 (8%)
		Mean ± SE	11 ± 1	3 ± 1 (33% ±7%)	1 ± 0 (6% ±2%)	1 ± 0 (8% ±2%)	1 ± 0 (10% ±3%)	3 ± 1 (32% ±6%)	1 ± 1 (8% ±6%)	0 ± 0 (3% ±1%)
	Artificial	Hope Rd	16 (12 + 4)	1 (6%)	0	2 (13%)	1 (6%)	12 (75%)	0	0
		South Play Art	10	0 (0%)	0	1 (10%)	0	8 (80%)	0	1 (10%)
		Mean ± SE	13 ± 3	1 ± 1 (3% ±3%)	0 ± 0 (0% ±0%)	2 ± 1 (12% ±2%)	1 ± 1 (3% ±3%)	10 ± 2 (78% ±3%)	0 ± 0 (0% ±0%)	1 ± 1 (5% ±5%)
	Total	17	189	52	10	16	18	72	14	7
Total		25	278	88 (32%)	12 (4%)	25 (9%)	26 (9%)	104 (37%)	14 (5%)	9 (3%)

[a] Nest was destroyed on 5/6/19 – 2 hatchlings missing, 2 released.

[b] Recovered from semi-predated nest.

Bureau of Meteorology Jandakot station (~5 km from the study site). Specifically, daily temperature (minimum, maximum and readings at 900 and 1500 h) and total rainfall data were obtained. As nests were monitored weekly, the daily readings were then used to calculate the average weekly temperature (i.e. the average of all of the minimum, maximum, 0900 and 1500 readings) and total rainfall.

Statistical analyses

As hatchling emergence occurred in both autumn and spring, the data were split into two groups: autumn (earliest emergence–July 15th) and spring (July 16th–latest emergence). This allowed us to assess if the hatchlings were responding to different weather variables during the different emergence periods. Possible collinearity between the total rainfall and average temperature within each emergence period was initially checked by undertaking pairwise correlation analyses (Tables S1, S2). Maximum pairwise correlations were <0.45 (autumn) and <0.12 (spring) (Tables S1, S2). All analyses were performed in R (Studio Version 1.4.1106) (RStudio Team, 2022).

To assess whether hatchling emergence from the nest was triggered by temperature or rainfall, a global generalized linear mixed model (GLMM) was built with a beta-binomial distribution for each of the autumn and spring emergence periods using the 'glmmTMB' package (v 1.1.3) (Brooks et al., 2022). The response variable was the proportion of total hatchlings emerging from each nest, each week of the monitoring period. Possible temporal autocorrelation of the response variable was assessed using the Autocorrelation Function in R, and most values were <0.2 (Figures S1, S2). To account for variation in the number of hatchlings in each nest, the number of hatchlings present within each nest, each week was used as a weighting term in the model (i.e. this number declined each time hatchlings emerged from each nest). This positively weighted emergence proportions of nests with higher numbers of hatchlings present each week. Nest was included as a random effect. Each model included average temperature and total rainfall as predictor variables.

For the selection of the most parsimonious GLMM for each emergence period, models containing all possible combinations of predictors were ranked based on the Akaike Information Criterion corrected for small sample size (AICc) using the MuMIn package (Barton, 2023) (Table S3). The best-fitting model for the autumn emergence period included average temperature and total rainfall as predictors, while the best model for the spring emergence period included only average temperature as a predictor (Table S3). To visualize the fixed effects of the best model for each emergence period, predictors were plotted using the "effects" package in R. Model assumptions were checked using the diagnostic plots in the "performance" package in R (Figures S3, S4).

RESULTS

A total of 278 eggs were monitored over the 2 years of the study (Table 2). Clutch size ranged from 9 to 14 eggs (10 ± 1 Mean ± SE) in 2018/2019 and from 7 to 17 eggs (11 ± 1 Mean ± SE) in 2019/2020 (Table 2). In 2018/2019, one nest was found in a semi-predated state and two eggs remained intact (Table 2). In each year, one artificial nest included clutches from two females (10 and 12 eggs in 2018/2019, and four and 12 eggs in 2019/2020) (Table 2).

Incubation duration

Hatching of eggs within the 2018 nests began prior to the 8th of May 2019, when the nests were first checked, and all eggs were hatched by the 18th of June 2019 (Table 1). In comparison, the 2019 nests were first checked on the 27th of March 2020, and hatching had already occurred for 14 (7%) eggs, with hatching complete by the 8th of June 2020 (Table 1). Incubation duration ranged from 162 to 257 days for 2018/2019 nests and 168–251 days for 2019/2020 nests (Table 1).The mean incubation duration was slightly longer in 2018/2019 (200 ± 3 days) compared to 2019/2020 (195 ± 2 days) (Table 1), but the difference was not significant ($t = 0.506$, $p = 0.629$). However, in both years, the incubation time for some eggs was shorter than recorded due to hatching occurring before the first nest check.

Hatching and emergence of success

Eighty-eight eggs (32% overall and 31% ±5 Nest Mean ± SE) hatched, and hatchlings emerged successfully, with an additional 12 eggs (4% overall and 4% ±2 Nest Mean ± SE) hatching and the hatchlings subsequently released into the wetland by the researcher (Table 2). Twenty-five eggs (9% overall and 9% ±2 Nest Mean ± SE) hatched, and the hatchlings subsequently died before emerging (Table 2). Twenty-six eggs (9% overall and 8% ±2 Nest Mean ± SE) contained undeveloped hatchlings, while 104 eggs (37% overall and 39% ±6 Nest Mean ± SE) were infertile/failed to develop (Table 2). Fourteen eggs (5% overall and 2% ±1 Nest Mean ± SE) were predated during hatching, and the fate of the remaining nine eggs (3% overall and 3% ±1 Nest Mean ± SE) is unknown (Table 2). Three natural nests (15%) failed completely, while two artificial nests (33%) failed completely (Table 2).

Artificial nests had more eggs that did not hatch, undeveloped hatchlings and hatchlings that died before emerging in 2018/2019 compared to 2019/2020 (Table 2). Two nests were predated during the hatching and emergence time periods of 2019/2020 resulting in 36% and 88% of eggs being lost from those nests (Table 2). One 2018/2019 nest cage was damaged by an unauthorized vehicle, and two hatchlings were unaccounted for (Table 2). It is assumed they emerged in the time between the nest cage being damaged and the next time the nest was checked. The fate of a total of seven eggs from nests in 2019/2020 could not be determined (Table 2). Presumably, these eggs hatched, hatchlings emerged between nest checks and the remains of the shells were misidentified as belonging to other eggs.

Emergence timing

Hatchling emergence from nests began earlier in 2020 compared to 2019 (before 27th March and on the 21st of May, respectively) (Table 1, Figure 2). The final hatchling to emerge from a nest occurred at a similar time in each year (early September) (Table 1). The mean emergence period per nest was briefer in 2019 than 2020 (41 ± 6 and 54 ± 9 days, respectively (Table 1)), though the difference was not significant ($W = 568.5$, $p = 0.420$). The range of emergence period was less in 2019 than 2020 (0–118 days and 0–140 days, respectively) (Table 1). However, mean percentage emergence was higher in 2018/2019 compared to 2019/2020 (Table 2). In both years, the percentage emergence was generally greater from natural nests (50%–100%) than from artificial nests (33%–91%) (Table 2).

The timing of hatchling emergence from nests varied between the years. In both years, larger proportions of hatchlings emerged in the autumn period than the spring period (i.e. they did not overwinter in the nest) (Figure 2). In 2019, larger proportions of hatchlings emerged during the winter months than in 2020 (Figure 2). However, in 2019, all but two hatchlings (5%) emerged either before or on the 7th of June and on or after the 11th of August. In 2020, 84% of hatchlings emerged outside the winter months (70% before winter and 14% after winter) (Figure 2).

Environmental predictors of emergence

The best fitting GLMM explaining the probability of turtle hatchlings emerging from the nest in the autumn emergence period included average temperature as a significant predictor, while total rainfall was almost significant (Table 3). Average temperature was a significant predictor in the best-fitting GLMM, explaining the probability of turtle hatchlings emerging from the nest in the spring emergence period (Table 3). The probability of hatchling emergence from nests increased as the average temperature and total rainfall increased in the week of emergence for the

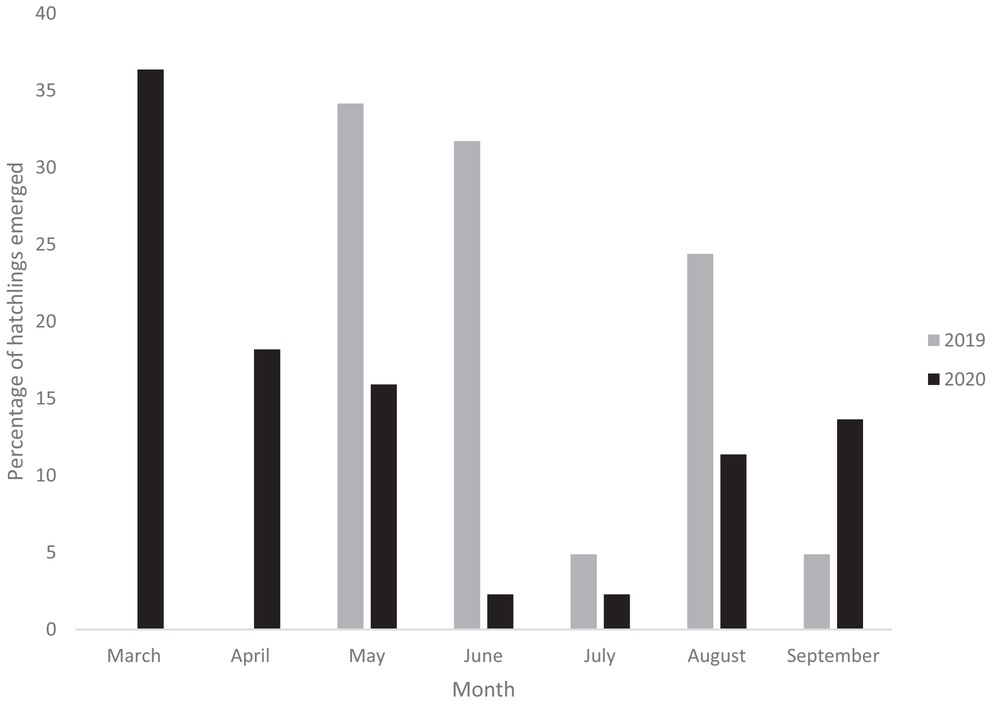

FIGURE 2 Percentage of *Chelodina oblonga* hatchlings emerging from nests each month in 2019 and 2020. $n = 41$ (2019) and 44 (2020).

TABLE 3 Results for the best generalized linear mixed model for the effects of temperature and rainfall on *Chelodina oblonga* hatchling emergence from nests in autumn and spring. * = significant effect (<0.05) and *** = highly significant effect (<0.001).

Emergence period	Effect	Estimate	Std.Error	Z	*p*
Autumn	Intercept	−5.49	1.45	−3.78	<0.001***
	Average Temperature	0.15	0.07	2.06	0.040*
	Total Rainfall	0.02	0.01	1.91	0.056
Spring	Intercept	−9.73	4.02	−2.42	0.015*
	Average Temperature	0.60	0.29	2.11	0.035*

autumn emergence period and as the average temperature increased in the week of emergence for the spring emergence period (Figures 3, 4, Table 3).

DISCUSSION

This study assessed the early life-history of *C. oblonga* and found that hatchling emergence is associated with temperature and rainfall. It has also revealed a shorter duration of incubation and earlier hatchling emergence compared with historic observations (Burbidge, 1967; Clay, 1981) that were made at a time that approximated the beginning of an ongoing period of considerable rainfall decline and increased rate of warming in this region (Hope et al., 2015). While additional studies are needed, the findings suggest that past and future projected increases in temperatures may cause shortened incubation periods for the species. Similarly, the ongoing reductions in rainfall in the region are likely to alter the timing of hatchling emergence from nests. The study thus provides some insight into how freshwater turtle hatching and emergence may be impacted by climate change in warming and drying regions.

Incubation duration

Chelodina oblonga incubation duration ranged from 162 to 257 days, with an average of ~200 days. This is a much wider range than reported by Clay (1981) and Burbidge (1967) (210–222 days and 200–230 days, respectively).

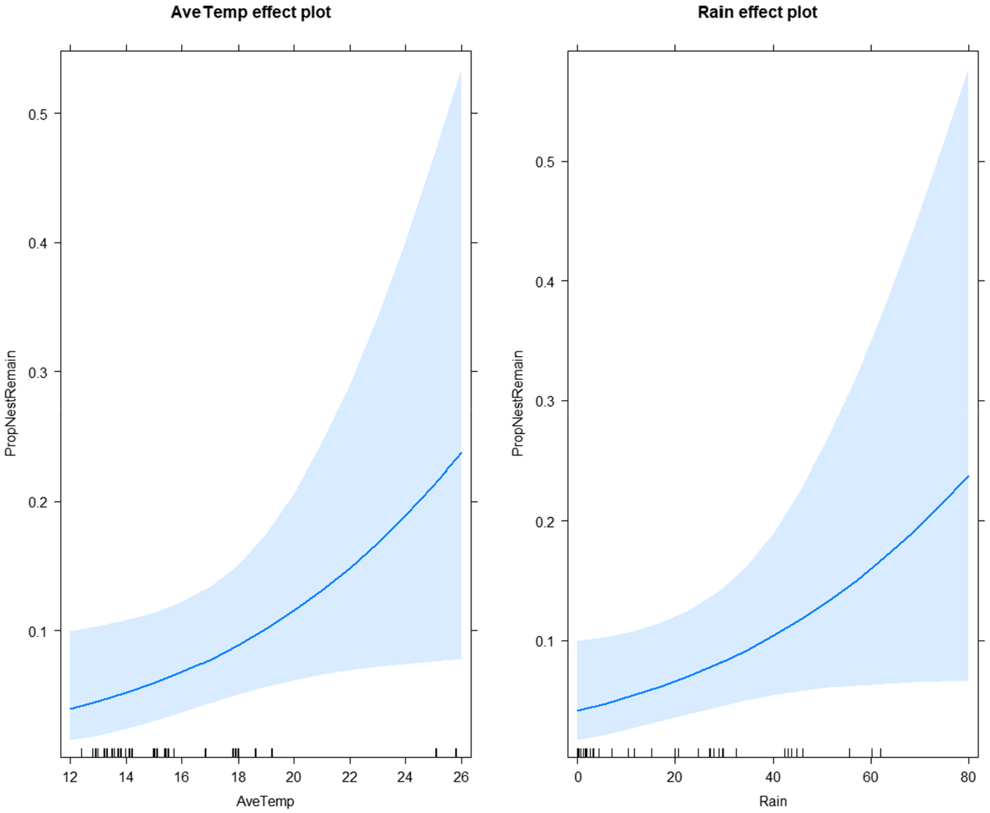

FIGURE 3 The predicted effects of temperature and rainfall on the proportion of *Chelodina oblonga* hatchlings emerging from nests in autumn from the best AICc-ranked generalized linear mixed model. The effect of temperature was significant ($p = 0.040$), while rainfall was almost significant ($p = 0.056$).

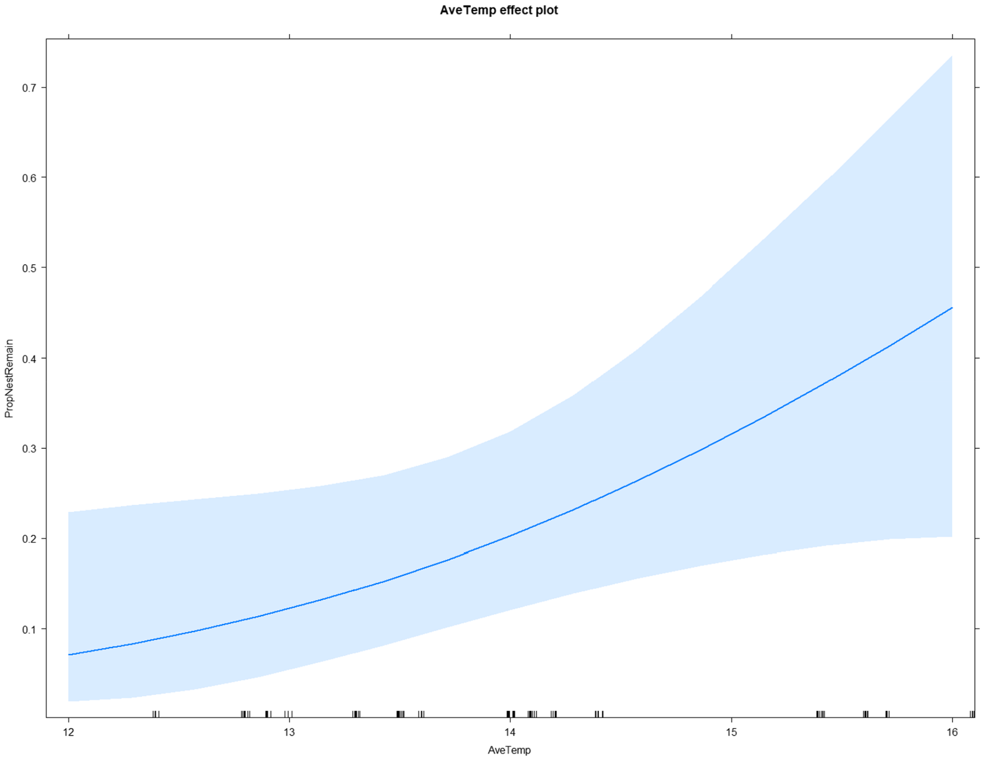

FIGURE 4 The predicted effect of temperature on the proportion of *Chelodina oblonga* hatchlings emerging from nests in spring from the best AICc ranked generalized linear mixed model. The effect was significant ($p = 0.035$).

Incubation duration was less than the minimum observed by Clay (1981) for 80% of eggs and over Clay's maximum for 11% of eggs that hatched. Comparison with Burbidge (1967) was not feasible as the incubation range reported was based on general months of laying and hatching, rather than dates for specific eggs as in the current study. In general, incubation duration appeared to decline, concurrent with an increase in average maximum temperature in Perth by >1°C over this time period (Bureau of Meteorology, 2021). Natural temperature variance among study sites is likely to be minimal between the current study and Clay (1981) and Burbidge (1967), as they are within 5 and 15 km of each other, respectively. As freshwater turtle nests are generally relatively shallow, they provide minimal thermal buffering against temperature variations at the surface (Refsnider et al., 2013), making nests highly sensitive to ambient temperature changes of this magnitude. Restoration or creation of nesting areas with increased canopy cover may be needed to prevent further declines in incubation duration.

Furthermore, urbanization is altering the availability of nesting habitat, leading to some *C.oblonga* females choosing nest-sites in anthropogenic environments (Santoro, 2022) that potentially have warmer thermal regimes than natural environments (Francis et al., 2019). Warmer nest temperatures have been shown to reduce the duration of incubation (Deeming & Ferguson, 1991; Ewert, 1979, 1985). Briefer incubation durations may lead to hatchlings either emerging earlier or spending increased time overwintering in the nest, the implications of which are discussed below.

Hatching success

Hatching success varied among nests and is known to vary both within and among species of freshwater turtle, with hatching rates between 28% and

95% commonly reported, as well as complete success or failure of individual nests (Baker et al., 2013; Burger, 1976; Christens & Bider, 1987; Congdon et al., 1983, 1987; Escalona et al., 2009; Geller et al., 2020; Knoerr, Graeter, et al., 2021; Tryon, 2009; Whitlock, 2002; Zappalorti et al., 2017). Egg infertility, insufficient nest temperatures to complete incubation, heat stress and/or death of embryos are common reasons for egg failure in freshwater turtles (Christens & Bider, 1987; Congdon et al., 1983, 1987; Escalona, 2003; Knoerr, Graeter, et al., 2021; Warner et al., 2010; Zappalorti et al., 2017). Egg failure in the current study was a combination of egg infertility and the death of embryos. However, as the cause of death was not assessed, it is possible that heat stress from increased ambient temperatures contributed to the egg failure. Further research into in-situ incubation conditions may shed light on reasons for failure, and ex-situ trials could be used to identify ideal incubation conditions for *C. oblonga*.

Hatching strategy

Hatching synchrony was not exhibited by *C. oblonga*. While hatching synchrony has been observed in several species of freshwater turtles (Burger, 1976; Doody et al., 2001; Lacroix et al., 2022; McGlashan et al., 2012; Spencer et al., 2001), reports of asynchronous hatching were found in only one other species (Riley et al., 2020). Synchronous hatching is suggested to facilitate synchronous emergence from the nest (Spencer et al., 2001; Tucker et al., 2008) and likely occurs when an environmental cue signals favourable conditions for hatching and emergence (Doody, 2011; Doody et al., 2012). However, synchronous hatching comes with the cost of reducing some individuals' incubation time, which can lead to diminished fitness (Andrews, 2004; Colbert et al., 2010; Peterson & Kruegl, 2005). Riley et al. (2020) proposed that the lack of synchronous hatching in *Graptemys geographica* may be because the hatchlings overwinter before emergence, reducing the need to hatch synchronously. *Chelodina oblonga* did not exhibit synchronous emergence, further reducing the need for hatching synchrony.

Emergence success

Emergence success following hatching varied in natural nests. High rates of hatchling mortality and variance in emergence success among nests are common among freshwater turtles (Burger, 1976; Congdon et al., 1983; Escalona et al., 2009; Gibbons, 1968; Wilbur, 1975). Common causes of hatchling mortality include dehydration, energy depletion and cold/heat stress (Baker et al., 2006; Finkler, 1999; Finkler et al., 2002; Nagle et al., 2004). While the cause of hatchling mortality prior to emergence was not assessed in the current study, elevated temperature and low moisture may have contributed through heat stress and dehydration. Determining the cause of emergence failure would aid in assessing whether conservation management is necessary to improve recruitment in stressed populations and should be a focus of future research.

Emergence strategy

Hatchling emergence synchrony was not exhibited by *C. oblonga*. Both synchronous and asynchronous emergence has been observed in freshwater turtles, with some species exhibiting both (Baker et al., 2010, 2013;

Burger, 1976; Congdon et al., 1983, 1987; Geller et al., 2020). However, asynchronous emergence is reported to occur over a briefer time period than was observed in the current study (2018: 41 ± 6 and 2019: 54 ± 9 days), often ranging from 2 to 11 days (Burger, 1976; Castellano et al., 2008; Congdon et al., 1983, 1987).

Group emergence has been suggested to have evolved as a method of predator avoidance, through either swamping predators or reducing exposure to generalist predators that prey switch (Arnold & Wassersug, 1978; Bradbury et al., 2004; Dehn, 1990; Martins et al., 2021; Santos et al., 2016; Tucker et al., 2008). However, asynchronous emergence may be favoured when high densities and large groups of hatchlings attract predators (Glen et al., 2005). It is possible that *C. oblonga* did not evolve synchronous emergence as historic nesting habitats provided enough vegetative cover and/or natural predators were sparsely distributed. With European settlement has come the introduction of novel predators (fox), subsidized native predators such as ravens (Boarman, 2003; Kristan & Boarman, 2003; Segura et al., 2020) and landscape change (e.g., vegetation clearing) that has almost certainly shifted predator–prey dynamics involving turtle hatchling success. *Chelodina oblonga* may have shifted to a greater reliance on asynchronous emergence following this shift in the predator–prey dynamic.

Emergence timing

Chelodina oblonga hatchlings emerged from nests up to 2 months earlier than historic observations (Burbidge, 1967; Clay, 1981). Early emergence in the current study could be due to early hatching caused by the increased ambient temperatures of the current climate. As highlighted by Gibbons (2013), the timing of emergence has significant implications with regard to the hospitability of the environment. For example, ambient temperatures in Australia are warmer in March than May, increasing the risk of desiccation (Paterson et al., 2012), and wetlands will be drier and thus smaller, increasing the distance between nest and water. Thus, the survival of hatchlings emerging months earlier than usual may be severely diminished and should be a focus of future research.

Proportionately, more hatchlings emerged shortly after hatching compared to overwintering in the nest. Similar observations were made by Burbidge (1967); however, this contrasts with Clay's (1981) observations that all hatchlings emerged in August (i.e. late winter, early spring). This also contrasts with the suggestion by Gibbons (2013) that delayed emergence is the default for freshwater turtle hatchlings, as emergence will then coordinate with favourable environmental conditions such as increasing spring temperatures, wet-season rains and productive wetlands. *Chelodina oblonga* hatchlings may now prefer autumn emergence, as emerging soon after hatching provides hatchlings with the benefit of energy reserves that have not depleted while overwintering (Tucker et al., 1998; Tucker & Paukstis, 1999), which can limit locomotor performance while migrating from nest to wetland (Willette et al., 2005). Reduced locomotor performance may increase the predation and dehydration of hatchling turtles when migrating overland to water due to their reduced ability to 'right themselves' when tipped upside down (Burger, 1976; Finkler, 1999; Kolbe & Janzen, 2002).

Some hatchlings also overwintered in the nest, delaying emergence until spring. Given the Mediterranean climate of Perth, winter temperatures rarely reach 0°C (Bureau of Meteorology, 2022), thus hatchlings may not need to overwinter within the nest to avoid thermal minima.

Delayed emergence in *C. oblonga*'s case may be a strategy to avoid the potential of wetlands being dry prior to refilling by winter and spring rains (Jackson, 1994). Tracking *C. oblonga* individuals after emergence from the nest in autumn and spring presents an interesting next step in research that could highlight variation in hatchling behaviours and survival in different seasons in a shifting climate.

To some extent, the range in emergence period observed in the current study of *C. oblonga* is comparable to that from studies of the eastern Australian snake-necked turtle (*Chelodina longicollis*). However, variation in *C. longicollis* emergence has only been observed at the among-nest level (Chessman, 2018; Ferronato et al., 2015). In comparison, while both autumn and spring emergence have been observed collectively across northern hemisphere turtles, many species appear only to emerge in one season of the year [autumn: (Burger, 1976; Congdon et al., 1983, 1987; Diaz-Paniagua et al., 1997; Lovich et al., 2014); spring: (Lovich et al., 2014; Tinkle et al., 1981)]. However, there are a few species that have been observed exhibiting both autumn and spring emergence (Baker et al., 2013; Carroll & Ultsch, 2007; Nagle et al., 2004; Riley et al., 2014), typically in populations situated in warm climates (Aresco, 2004; Jackson, 1994). The expression of autumn and spring emergence in *C. oblonga*, both within and between nests, demonstrates a dynamic strategy operating at the level of the individual hatchling, which may provide some resilience against the unpredictable and variable environmental conditions of climate change. Future research could assess the basis for this behaviour, including individual characteristics such as position in the nest, body size or personality (boldness).

Comparable studies on freshwater turtle hatchling emergence patterns encompassing climate alterations over a >40-year period were not found in the literature. As aligns with observations of others, long-term data are invaluable in ecology for following trends (Edge et al., 2017; Hughes et al., 2017; Lindenmayer et al., 2012). The capacity to compare and contrast findings with historical studies has been shown in this study to be imperative to identifying the likely impacts of climate change and presents an important aspect of future research in the conservation of freshwater turtles globally.

Emergence trigger

Effects of temperature

In the current study, the proportion of hatchlings emerging increased with the average temperature during the week of emergence in both the relevant autumn and spring periods. This contrasts with the other southwest Australian turtle (*P. umbrina*) and six American species whose trigger for autumn emergence is reported to be decreasing temperature (Baker et al., 2013; Burbidge, 1981). It is likely that while temperatures were generally decreasing during autumn in the current study, the hatchlings may have been responding to the warmer weeks that increased their metabolism when making the migration from nest to water. Increasing spring temperatures have been found to trigger the emergence of some species of freshwater turtle hatchlings after overwintering in the nest (Christens & Bider, 1987; Tucker, 1999). The emergence of hatchlings being associated with increasing temperatures in spring may also be due to metabolism or an environmental signal that aquatic environments are entering a highly productive state suitable for growth and survival (Gibbons, 2013).

Effects of rainfall

The emergence of *C.oblonga* hatchlings was enhanced by rainfall (in the week of emergence) during the autumn period, though this was not quite a significant relationship. Similarly, the autumn emergence of other Australian freshwater turtles' hatchlings (*P.umbrina* and *Carettochelys insculpta*) has been found to be triggered by rainfall, with the authors contending that the onset of the wet season increases feeding opportunities (Burbidge, 1981; Doody et al., 2001). A relationship between autumn emergence and rainfall could have negative ramifications for *C.oblonga* recruitment given the projected continued decline of rainfall in the southwestern Australian region (Hope et al., 2015; Intergovernmental Panel on Climate Change, 2023; Silberstein et al., 2012). Furthermore, the reduction in total rainfall combined with increased groundwater extraction from urbanization (McFarlane et al., 2012) means hatchlings emerging in autumn would be less likely to find an inundated wetland, diminishing prospects for survival and growth (Gibbons & Nelson, 1978).

Rainfall was not a significant predictor of *C. oblonga* hatchling emergence during the spring period. Similarly, the spring emergence of three species of American freshwater turtles was not correlated with rainfall (Baker et al., 2013). Surface waters of wetlands are more abundant in spring than autumn, and the soil above the nest has been softened throughout winter, potentially explaining the reduced influence of rainfall as a spring emergence trigger during the current study.

A considerable proportion of *C.oblonga* hatchlings emerged from nests in September, a month later than historic observations (Burbidge, 1967; Clay, 1981). This delayed emergence may have been caused by the shift in the timing of rainfall in southwest WA; winter rainfall has significantly reduced while summer rainfall has increased (McFarlane et al., 2020). While rainfall is not triggering spring emergence, the hatchlings emerging may be reliant on spring rainfall, as winter rainfall may no longer adequately soften substrates and/or indicate inundated wetlands. This may be reducing emergence success as hatchlings may be trapped in nests due to hardened soils (Chessman, 2018). Furthermore, late emergence could increase hatchling mortality through desiccation due to warmer temperatures (Paterson et al., 2012). All these factors would likely lead to reduced recruitment.

Continued drying in southwestern Australia may also reduce recruitment through impacts related to drought. For example, low rainfall in 2010 (504 mm (Bureau of Meteorology, 2011)) resulted in some Beeliar wetlands not reflooding in winter and remaining dry throughout the consecutive year (authors pers. observation). Chessman (2011) found that the presence of juvenile *Chelodina longicollis* and *Emydura macquarii* significantly declined after a decade of drought in Eastern Australia, with the declines attributed to reduced success of recruitment. Drought has adverse effects on incubation and hatchlings, with one study finding that drier nests resulted in shorter incubation, reduced hatching success and produced smaller hatchlings than moister nests (Cagle et al., 1993). Moist nests are cooler than dry nests, and thus, the impacts of drought may incorporate those of warmer temperatures (Bodensteiner et al., 2015) (detailed above). Furthermore, as rainfall reductions are projected for Mediterranean climates globally (Cramer et al., 2018; García-Ruiz et al., 2011; Giorgi & Lionello, 2008; Seager et al., 2019), freshwater turtles in these regions may experience similar effects.

Caveats

Nests were excavated to check on eggs and hatchlings on a weekly basis. Any less invasive means than this established method (Nagle et al., 2004;

Pignati et al., 2013) were not found in the literature. While the greatest care was taken when excavating nests and handling eggs and hatchlings, it is possible that this method led to some observer effects, including embryo mortality, alterations to the length of incubation, time from hatching to emergence and hatchling survival. Developing a novel, less invasive method of monitoring underground egg and hatchling ecology is encouraged, as it has far-reaching potential to improve the study of all freshwater turtles and many other terrestrial and semi-aquatic taxa.

CONCLUSIONS

Temperature and rainfall were found to be important triggers for freshwater turtle hatchling emergence from the nest. The climate in southwestern Australia is both drying and warming on an interdecadal scale, and this is the first study to provide some evidence that severely reduced rainfall is likely to impact a temperate freshwater turtle's reproductive cycle through altered and potentially reduced emergence in the hatchling phase. Increased average temperatures will likely continue to shorten incubation time, altering the timing of emergence and potentially impacting hatchling survival. As the southwest of Western Australia is recognized as a climate change hotspot with extremely pronounced warming and drying (Intergovernmental Panel on Climate Change, 2023), the findings of the current study also serve as an indication for what is to come in other warming and drying regions and thus have implications for freshwater turtles globally.

AUTHOR CONTRIBUTIONS

Anthony Santoro: Conceptualization (lead); data curation (lead); formal analysis (equal); investigation (lead); methodology (lead); writing – original draft (lead); writing – review and editing (lead). **Jane M. Chambers:** Conceptualization (supporting); formal analysis (supporting); methodology (supporting); supervision (lead); writing – review and editing (supporting). **Brendan Ebner:** Conceptualization (supporting); formal analysis (supporting); methodology (supporting); supervision (supporting); writing – review and editing (supporting). **Steve J. Beatty:** Conceptualization (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); supervision (supporting); writing – review and editing (supporting).

ACKNOWLEDGEMENTS

The authors would like to acknowledge the Noongar people, who are the traditional custodians of the land on which this research took place. We would like to thank all the ‘Turtle Trackers' who contributed time to help the Oblong turtle. This research was undertaken in compliance with the following permits: Murdoch University's Animal Ethics Committee permit no. R3053/18, Department of Primary Industries and Regional Development’s, Western Australia exemption no. 3137 and Department of Biodiversity, Conservation and Attractions Regulation 25 licence no. FO25000094-4. This project was supported by Murdoch University, the City of Cockburn, the Department of Biodiversity, Conservation and Attractions Parks and Wildlife, WA Wildlfe and the Wetlands Centre Cockburn. Open access publishing facilitated by Murdoch University, as part of the Wiley - Murdoch University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Anthony Santoro https://orcid.org/0000-0003-4606-6294

REFERENCES

Andrews, R.M. (2004) Patterns of embryonic development. In: Deeming, D.C. (Ed.) *Reptilian incubation; environment, evolution, and behaviour*. Nottingham, UK: Nottingham University Press, pp. 75–102.

Aresco, M.J. (2004) Reproductive ecology of *Pseudemys floridana* and *Trachemys scripta* (testudines: Emydidae) in northwestern Florida. *Journal of Herpetology*, 38, 249–256.

Arnold, S.J. & Wassersug, R.J. (1978) Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. *Ecology*, 59, 1010–1022.

Baker, P.J., Costanzo, J.P., Herlands, R., Wood, R.C. & Lee, R.E.J. (2006) Inoculative freezing promotes winter survival in hatchling diamondback terrapin, Malaclemys terrapin. *Canadian Journal of Zoology*, 84(1), 116–124. Available from: https://doi.org/10.1139/Z05-183

Baker, P.J., Costanzo, J.P., Iverson, J.B. & Lee, R.E., Jr. (2003) Adaptations to terrestrial overwintering of hatchling northern map turtles, *Graptemys geographica*. *Journal of Comparative Physiology*, 173, 643–651.

Baker, P.J., Costanzo, J.P., Iverson, J.B. & Lee, R.E.J. (2013) Seasonality and interspecific and intraspecific asynchrony in emergence from the nest by hatchling freshwater turtles. *Canadian Journal of Zoology*, 91, 451–461. Available from: https://doi.org/10.1139/cjz-2012-0335

Baker, P.J., Iverson, J.B., Lee, R.E., Jr. & Costanzo, J.P. (2010) Winter severity and phenology of spring emergence from the nest in freshwater turtles. *Naturwissenschaften*, 97, 607–615. Available from: https://doi.org/10.1007/200114-010-0675-x

Barton, K. (2023) *Package* '*MuMIn*' *Multi-Model Inference*. Comprehensive R Archive Network. Available online: https://cran.r-project.org/web/packages/MuMIn/index.html [Accessed 22nd March 2022].

Boarman, W.I. (2003) Managing a subsidized predator population: reducing common raven predation on desert tortoises. *Environmental Management*, 32(2), 205–217. Available from: https://doi.org/10.1007/s00267-003-2982-x

Bodensteiner, B.L., Mitchell, T.S., Strickland, J.T., Janzen, F.J. & Herrel, A. (2015) Hydric conditions during incubation influence phenotypes of neonatal reptiles in the field. *Functional Ecology*, 29(5), 710–717. Available from: https://doi.org/10.1111/1365-2435.12382

Booth, D.T., Burgess, E., McCosker, J. & Lanyon, J.M. (2004) The influence of incubation temperature on post-hatching fitness characteristics of turtles. *International Congress Series*, 1275, 226–233. Available from: https://doi.org/10.1016/j.ics.2004.08.057

Bradbury, I.R., Campana, S.E., Bentzen, P. & Snelgrove, P.V.R. (2004) Synchronized hatch and its ecological significance in rainbow smelt *Osmerus mordax* in St. Mary's bay, Newfoundland. *Limnology and Oceanography*, 49(6), 2310–2315.

Breitenbach, G.L., Congdon, J.D. & Van Loben Sels, R.C. (1984) Winter temperature of *Chrysemys picta* nests in Michigan: effects on hatchling survival. *Herpetologica*, 40, 76–81.

Brooks, M., Bolker, B., Kristensen, K., Maechler, M., Magnusson, A., McGillycuddy, M. et al. (2022) *Package* '*glmmTMB*'. Generalized linear mixed models using template model builder. Available online: https://cran.r-project.org/web/packages/glmmTMB [Accessed 1st December 2022].

Burbidge, A.A. (1967) The biology of south-western Australian tortoises. PhD The University of Western Australia.

Burbidge, A.A. (1981) The ecology of the western swamp tortoise *Pseudemydura umbrina* (Testudines: Chelidae). *Australian Wildlife Research*, 8, 203–223. Available from: https://doi.org/10.1071/WR9810203

Bureau of Meteorology. (2011) *Perth in 2010: one of the hottest and driest years on record*. Australia: Available online: http://www.bom.gov.au/climate/current/annual/wa/archive/2010.perth.shtml#:~:text=Perth%20Metro%20recorded%20503.8%20mm,the%20466.8%20mm%20in%202006.

Bureau of Meteorology. (2021) *Climate data online*. 21st September 2021. Bureau of Meteorology: Australian Government. Available online: http://www.bom.gov.au/climate/data/

Bureau of Meteorology. (2022) *Climate statistics for Australian locations*. Australia: Australian Government. Available online: http://www.bom.gov.au/climate/averages/tables/cw_009225.shtml [Accessed 3rd March 2023].

Burger, J. (1976) Behavior of hatchling diamondback terrapins (*Malaclemys terrapin*) in the field. *Copeia*, 1976, 742–748.

Burke, R.L. & Capitano, W. (2011) Eastern box turtle, *Terrapene carolina*, neonate overwintering ecology on Long Island, New York. *Chelonian Conservation and Biology*, 10(2), 256–259. Available from: https://doi.org/10.2744/ccb-0855.1

Butler, C.J. (2019) A review of the effects of climate change on chelonians. *Diversity*, 11(8), 138. Available from: https://doi.org/10.3390/d11080138

Cagle, K.D., Packard, G.C., Miller, K. & Packard, M.J. (1993) Effects of the microclimate in natural nests on development of embryonic painted turtles, Chrysemys picta. *Functional Ecology*, 7(6), 653–660.

Carr, A.F. & Hirth, H. (1961) Social facilitation in green turte siblings. *Animal Behaviour*, 9, 68–70. Available from: https://doi.org/10.1016/0003-3472(61)90051-3

Carranco, A.S., Gillingham, M.A.F., Wilhelm, K., Torres, M.L., Sommer, S. & Romo, D. (2022) Transcending Sea turtles: first report of hatching failure in eggs of an Amazonian freshwater turtle with symptoms of the fungal emerging disease fusariosis. *Transboundary and Emerging Diseases*, 69(5), e3282–e3288. Available from: https://doi.org/10.1111/tbed.14596

Carroll, D.M. & Ultsch, G.R. (2007) Emergence season and survival in the nest of hatchling turtles in southcentral New Hampshire. *Northeastern Naturalist*, 14(2), 307–310. Available from: https://doi.org/10.1656/1092-6194(2007)14[307:Esasit]2.0.Co;2

Carstairs, S., Paterson, J.E., Jager, K.L., Gasbarrini, D., Mui, A.B. & Davy, C.M. (2019) Population reinforcement accelerates subadult recruitment rates in an endangered freshwater turtle. *Animal Conservation*, 22, 589–599. Available from: https://doi.org/10.1111/acv.12503

Castellano, C.M., Behler, J.L. & Ultsch, G.R. (2008) Terrestrial movements of hatchling wood turtles (*Glyptemys insculpta*) in agricultural fields in New Jersey. *Chelonian Conservation and Biology*, 7(1), 113–118.

Chessman, B.C. (2011) Declines of freshwater turtles associated with climatic drying in Australia's Murray-Darling basin. *Wildlife Research*, 38(8), 664–671. Available from: https://doi.org/10.1071/wr11108

Chessman, B.C. (2018) Freshwater turtle hatchlings that stay in the nest: strategists or prisoners? *Australian Journal of Zoology*, 66(1), 34. Available from: https://doi.org/10.1071/zo17054

Christens, E. & Bider, J.R. (1987) Nesting activity and hatching success of the painted turtle (*Chrysemys picta marginata*) in southwestern Quebec. *Herpetologica*, 43(1), 55–65.

Clay, B.T. (1981) Observations on the breeding biology and behaviour of the long-necked tortoise. *Journal of the Royal Society of Western Australia*, 4(1), 27–32.

Colbert, P.L., Spencer, R.J. & Janzen, F.J. (2010) Mechanism and cost of synchronous hatching. *Functional Ecology*, 24(1), 112–121. Available from: https://doi.org/10.1111/j.1365-2435.2009.01602.x

Congdon, J.D., Breitenbach, G.L., van Loben Sels, R.C. & Tinkle, D.W. (1987) Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in southeastern Michigan. *Herpetologica*, 43(1), 39–54.

Congdon, J.D., Tinkle, D.W., Breitenbach, G.L. & Richard, C.v.L.S. (1983) Nesting ecology and hatching success in the turtle *Emydoidea blandingi*. *Herpetologica*, 39(4), 417–429.

Costanzo, J.P., Iverson, J.B., Wright, M.F. & Lee, R.E., Jr. (1995) Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. *Ecology*, 76(6), 1772–1785.

Costanzo, J.P., Lee, R.E., Jr. & Ultsch, G.R. (2008) Physiological ecology of overwintering in hatchling turtles. *Journal of Experimental Zoology. Part A, Ecological Genetics and Physiology*, 309(6), 297–379. Available from: https://doi.org/10.1002/jez.460

Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J.-P., Iglesias, A. et al. (2018) Climate change and interconnected risks to sustainable development in the Mediterranean. *Nature Climate Change*, 7, 972–980.

Davis, J.A. & Froend, R. (1999) Loss and degradation of wetlands in southwestern Australia: underlying causes, consequences and solutions. *Wetlands Ecology and Management*, 7, 13–23. Available from: https://doi.org/10.1023/A:1008400404021

Dawes, W., Ali, R., Varma, S., Emelyanova, I., Hodgson, G. & McFarlane, D. (2012) Modelling the effects of climate and land cover change on groundwater recharge in south-West Western Australia. *Hydrology and Earth System Sciences*, 16(8), 2709–2722. Available from: https://doi.org/10.5194/hess-16-2709-2012

Deeming, D.C. & Ferguson, M.W.J. (1991) Physiological effects of incubation temperature on embryonic development in reptiles and birds. In: Deeming, D.C. & Ferguson, M.W.J.

(Eds.) *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge: Cambridge University Press, pp. 147–171.

Dehn, M.M. (1990) Vigilance for predators: detection and dilution effects. *Behavioral Ecology and Sociobiology*, 26, 337–342.

DePari, J.A. (1996) Overwintering in the nest chamber by hatchling painted turtles, *Chrysemys picta*, in northern New Jersey. *Chelonian Conservation and Biology*, 2, 5–12.

Diaz-Paniagua, C., Keller, C. & Andreu, A.C. (1997) Hatching success, delay of emergence and hatchling biometry of the spur-thighed tortoise, *Testudo graeca*, in South-Western Spain. *Journal of Zoological Society of London*, 243, 543–553.

Doody, J.S. (2011) Environmentally cued hatching in reptiles. *Integrative and Comparative Biology*, 51, 49–61.

Doody, J.S., Georges, A., Young, J.E., Pauza, M.D., Pepper, A.L., Alderman, R.L. et al. (2001) Embryonic aestivation and emergence behaviour in the pig-nosed turtle, Carettochelys insculpta. *Canadian Journal of Zoology*, 79(6), 1062–1072. Available from: https://doi.org/10.1139/cjz-79-6-1062

Doody, J.S., Stewart, B., Camacho, C. & Christian, K. (2012) Good vibrations? Sibling embryos expedite hatching in a turtle. *Animal Behaviour*, 83(3), 645–651. Available from: https://doi.org/10.1016/j.anbehav.2011.12.006

Draud, M., Bossert, M. & Zimnavoda, S. (2004) Predation on hatchling and juvenile diamondback terrapins (*Malaclemys terrapin*) by the Norway rat (*Rattus norvegicus*). *Journal of Herpetology*, 38(3), 467–470.

Edge, C.B., Rollinson, N., Brooks, R.J., Congdon, J.D., Iverson, J.B., Janzen, F.J. et al. (2017) Phenotypic plasticity of nest timing in a post-glacial landscape: how do reptiles adapt to seasonal time constraints? *Ecology*, 98(2), 512–524.

Escalona, T. (2003) *Maternal effects on reproductive success in a river turtle (Podocnemis unifilis) in southern Venezuela*. PhD. University of Missouri.

Escalona, T., Valenzuela, N. & Adams, D.C. (2009) Nesting ecology in the freshwater turtle *Podocnemis unifilis*: spatiotemporal patterns and inferred explanations. *Functional Ecology*, 23(4), 826–835. Available from: https://doi.org/10.1111/j.1365-2435.2009.01562.x

Ewert, M.A. (1979) The embryo and its egg: development and natural history. In: Harless, M. & Morlock, H. (Eds.) *Turtles: perspectives and research*. New York, USA: John Wiley and Sons, pp. 333–413.

Ewert, M.A. (1985) Embryology of turtles. In: Gans, C., Maderson, P.F.A. & Billett, F. (Eds.) *Biology of the Reptilia*. New York: Wiley-Interscience, pp. 75–267.

Ferronato, B.O., Roe, J.H. & Georges, A. (2015) First record of hatchling overwintering inside the natal nest of a chelid turtle. *Australian Journal of Zoology*, 63(4), 287. Available from: https://doi.org/10.1071/zo15044

Finkler, M.S. (1999) Influence of water availability during incubation on hatchling size, body composition, desiccation tolerance, and terrestrial locomotor performance in the snapping turtle *Chelydra serpentina*. *Physiological and Biochemical Zoology*, 72, 714–722.

Finkler, M.S., Bowen, J.T., Christman, T.M. & Renshaw, A.D. (2002) Effects of hydric conditions during incubation on body size and triglyceride reserves of overwintering hatchling snapping turtles (*Chelydra serpentina*). *Copeia*, 2002, 504–510.

Francis, E.A., Moldowan, P.D., Greischar, M.A. & Rollinson, N. (2019) Anthropogenic nest sites provide warmer incubation environments than natural nest sites in a population of oviparous reptiles near their northern range limit. *Oecologia*, 190(3), 511–522. Available from: https://doi.org/10.1007/s00442-019-04383-3

García-Ruiz, J.M., López-Moreno, I.I., Vicente-Serrano, S.M., Lasanta-Martínez, T. & Beguería, S. (2011) Mediterranean water resources in a global change scenario. *Earth Science Reviews*, 105, 121–139.

Geller, G.A., Casper, G.S. & Halstead, B.J. (2020) Hatchling emergence ecology of Ouachita map turtles (*Graptemys ouachitensis*) on the lower Wisconsin River, Wisconsin. *Chelonian Conservation and Biology*, 19(2), 217–235. Available from: https://doi.org/10.2744/ccb-1415.1

Gibbons, J.W. (1968) Reproductive potential, activity, and cycles in the painted turtle *Chrysemys picta*. *Ecology*, 49, 399–409.

Gibbons, J.W. (2013) A long-term perspective of delayed emergence (aka overwintering) in hatchling turtles: some they do and some they don't, and some you just can't tell. *Journal of Herpetology*, 47(2), 203–214.

Gibbons, J.W. & Nelson, D.H. (1978) The evolutionary significance of delayed emergence from the nest by hatchling turtles. *Evolution*, 32(2), 297–303.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S. et al. (2000) The global decline of reptiles, deja vu amphibians. *Bioscience*, 50(8), 653–666. Available from: https://doi.org/10.1641/0006-3568(2000)050[0653:TGDORD]2.0.CO;2

Giorgi, F. & Lionello, P. (2008) Climate change projections for the Mediterranean region. *Global and Planetary Change*, 63, 90–104.

Glen, F., Broderick, A.C., Godley, B.J. & Hays, G.C. (2005) Patterns in the emergence of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtle hatchlings from their nests. *Marine Biology*, 146(5), 1039–1049. Available from: https://doi.org/10.1007/s00227-004-1492-6

Hill, J.E., Paladino, F.V., Spotila, J.R. & Tomillo, P.S. (2015) Shading and watering as a tool to mitigate the impacts of climate change in sea turtle nests. *PLoS ONE*, 10(6), e0129528. Available from: https://doi.org/10.1371/journal.pone.0129528

Hope, P., Abbs, D., Bhend, J., Chiew, F., Church, J., Ekström, M. et al. (2015) *Southern and South-Western flatlands cluster report*. Australia: CSIRO and Bureau of Meteorology.

Houghton, J.D. & Hays, G.C. (2001) Asynchronous emergence by loggerhead turtle (*Caretta caretta*) hatchlings. *Naturwissenschaften*, 88(3), 133–136. Available from: https://doi.org/10.1007/s001140100212

Hughes, B.B., Beas-Luna, R., Barner, A.K., Brewitt, K., Brumbaugh, D.R., Cerny-Chipman, E.B. et al. (2017) Long-term studies contribute disproportionately to ecology and policy. *Bioscience*, 67(3), 271–281. Available from: https://doi.org/10.1093/biosci/biw185

Ims, R.A. (1990) On the adaptive value of reproductive synchrony as a predator-swamping strategy. *American Naturalist*, 136, 485–498. Available from: https://doi.org/10.1086/285109

Intergovernmental Panel on Climate Change. (2023) Climate Change 2023: Synthesis Report. In: Core Writing Team, Lee, H. & Romero, J. (Eds.) *Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, Geneva, Switzerland: IPCC, pp. 35–115. Available from: https://doi.org/10.59327/IPCC/AR6-9789291691647

Iverson, J.B. (1991) Patterns of survivorship in turtles (order testudines). *Canadian Journal of Zoology*, 69(2), 385–391. Available from: https://doi.org/10.1139/z91-060

Jackson, D.R. (1994) Overwintering of hatchling turtles in northern Florida. *Journal of Herpetology*, 28, 401–402.

Janzen, F.J., Tucker, J.K. & Paukstis, G.L. (2000) Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. *Journal of Evolutionary Biology*, 13, 947–954.

Janzen, F.J., Tucker, J.K. & Paukstis, G.L. (2007) Experimental analysis of an early life-history stage: direct or indirect selection on body size of hatchling turtles? *Functional Ecology*, 21(1), 162–170. Available from: https://doi.org/10.1111/j.1365-2435.2006.01220.x

Klemens, M.W. (2000) *Turtle conservation.* Washington DC: Smithsonian Institute Press.

Knoerr, M.D., Graeter, G.J. & Barrett, K. (2021) Hatch success and recruitment patterns of the bog turtle. *Journal of Wildlife Management*, 85(2), 293–302. Available from: https://doi.org/10.1002/jwmg.21989

Knoerr, M.D., Tutterow, A.M., Graeter, G.J., Pittman, S.E. & Barrett, K. (2021) Population models reveal the importance of early life-stages for population stability of an imperiled turtle species. *Animal Conservation*, 25(1), 53–64. Available from: https://doi.org/10.1111/acv.12718

Kolbe, J.J. & Janzen, F.J. (2002) Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology*, 83(1), 269–281. Available from: https://doi.org/10.1890/0012-9658(2002)083[0269:IONSSO]2.0.CO;2

Kristan, W.B. & Boarman, W.I. (2003) Spatial pattern of risk of common raven predation on desert tortoises. *Ecology*, 84, 2432–2443.

Lacroix, C., Davy, C.M. & Rollinson, N. (2022) Hatchling vocalizations and beneficial social interactions in subterranean nests of a widespread reptile. *Animal Behaviour*, 187, 233–244. Available from: https://doi.org/10.1016/j.anbehav.2022.03.006

Laloë, J.O., Tedeschi, J.N., Booth, D.T., Bell, I., Dunstan, A., Reina, R.D. et al. (2021) Extreme rainfall events and cooling of sea turtle clutches: implications in the face of climate warming. *Ecology and Evolution*, 11(1), 560–565. Available from: https://doi.org/10.1002/ece3.7076

Lindeman, P.V. (1991) Survivorship of overwintering hatchling painted turtles, *Chrysemys picta*, in northern Idaho. *Canadian Field-Naturalist*, 105, 263–266.

Lindenmayer, D.B., Likens, G.E., Andersen, A., Bowman, D., Bull, C.M., Burns, E. et al. (2012) Value of long-term ecological studies. *Austral Ecology*, 37(7), 745–757. Available from: https://doi.org/10.1111/j.1442-9993.2011.02351.x

Lovich, J.E., Ennen, J.R., Agha, M. & Gibbons, J.W. (2018) Where have all the turtles gone, and why does it matter? *Bioscience*, 68(10), 771–781. Available from: https://doi.org/10.1093/biosci/biy095

Lovich, J.E., Ernst, C.H., Ernst, E.M. & Riley, J.L. (2014) A 21-year study of seasonal and interspecific variation of hatchling emergence in a nearctic freshwater turtle community: to overwinter or not to overwinter. *Herpetological Monographs*, 28, 93–109.

Martins, S., Sierra, L., Rodrigues, E., Oñate-Casado, J., Torres Galán, I., Clarke, L.J. et al. (2021) Ecological drivers of the high predation of sea turtle hatchlings during emergence. *Marine Ecology Progress Series*, 668, 97–106. Available from: https://doi.org/10.3354/meps13751

McFarlane, D., George, R., Ruprecht, J., Charles, S. & Hodgson, G. (2020) Runoff and groundwater responses to climate change in south West Australia. *Journal of the Royal Society of Western Australia*, 103, 9–27.

McFarlane, D., Strawbridge, M., Stone, R. & Paton, A. (2012) Managing groudwater levels in the face of uncertainty and change: a case study from Gnangara. *Water Supply*, 12(3), 321–328. Available from: https://doi.org/10.2166/ws.2011.137

McGlashan, J.K., Spencer, R.J. & Old, J.M. (2012) Embryonic communication in the nest: metabolic responses of reptilian embryos to developmental rates of siblings. *Proceedings: Biological Sciences*, 279(1734), 1709–1715. Available from: https://doi.org/10.1098/rspb.201

Micheli-Campbell, M.A., Campbell, H.A., Cramp, R.L., Booth, D.T. & Franklin, C.E. (2011) Staying cool, keeping strong: incubation temperature affects performance in a freshwater turtle. *Journal of Zoology*, 285(4), 266–273. Available from: https://doi.org/10.1111/j.1469-7998.2011.00840.x

Moll, E.O. & Legler, J.M. (1971) *Life history of a neotropical slider turtle, Pseudemys scripta (Schoepff), in Panama*, 1st edition. Los Angeles: County Museum of Natural History.

Moran, K.L., Bjorndal, K.A. & Bolten, A.B. (1999) Effects of the thermal environment on the temporal pattern of emergence of hatchling loggerhead turtles *Caretta caretta*. *Marine Ecology Progress Series*, 189, 251–261.

Muldoon, K.A. & Burke, R.L. (2012) Movements, overwintering, and mortality of hatchling diamond-back terrapins (*Malaclemys terrapin*) at Jamaica Bay, New York. *Canadian Journal of Zoology*, 90, 651–662. Available from: https://doi.org/10.1139/Z2012-032

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. Available from: https://doi.org/10.1038/35002501

Nagle, R.D., Lutz, C.L. & Pyle, A.L. (2004) Overwintering in the nest by hatchling map turtles (*Graptemys geographica*). *Canadian Journal of Zoology*, 82, 1211–1218.

Packard, G.C., Packard, M.J., McDaniel, P.L. & McDaniel, L.L. (1989) Tolerance of hatchling painted turtles to subzero temperatures. *Canadian Journal of Zoology*, 67, 828–830.

Pappas, M.J., Brecke, B.J. & Congdon, J.D. (2000) The blanding's turtles (*Emydoidea blandingii*) of weaver dunes, Minnesota. *Chelonian Conservation and Biology*, 3, 557–568.

Paterson, J.E., Steinberg, B.D. & Litzgus, J.D. (2012) Revealing a cryptic life-history stage: differences in habitat selection and survivorship between hatchlings of two turtle species at risk (*Glyptemys insculpta* and *Emydoidea blandingii*). *Wildlife Research*, 39(5), 408. Available from: https://doi.org/10.1071/wr12039

Paterson, J.E., Steinberg, B.D. & Litzgus, J.D. (2014) Effects of body size, habitat selection and exposure on hatchling turtle survival. *Journal of Zoology*, 294(4), 278–285. Available from: https://doi.org/10.1111/jzo.12176

Peterson, C.C. & Kruegl, A. (2005) Peaked temporal pattern of embryonic metabolism in an emydid turtle (*Chrysemys picta*). *Journal of Herpetology*, 39, 678–681.

Pignati, M.T., Fernandes, L.F., Miorando, P.S. & Pezzuti, J.C.B. (2013) Hatching and emergence patterns in the yellow-spotted river turtle, *Podocnemis unifilis* (Testudines: Podocnemididae), in the Várzea floodplains of the lower Amazon River in Santarém, Brazil. *Chelonian Conservation and Biology*, 12(1), 127–133. Available from: https://doi.org/10.2744/ccb-0953.1

Refsnider, J.M., Bodensteiner, B.L., Reneker, J.L. & Janzen, F.J. (2013) Nest depth may not compensate for sex ratio skews caused by climate change in turtles. *Animal Conservation*, 16(5), 481–490. Available from: https://doi.org/10.1111/acv.12034

Riley, J.L., Hudson, S., Frenette-Ling, C. & Davy, C.M. (2020) All together now! Hatching synchrony in freshwater turtles. *Behavioral Ecology and Sociobiology*, 74(58), 1–15. Available from: https://doi.org/10.1007/s00265-020-2800-y

Riley, J.L. & Litzgus, J.D. (2014) Cues used by predators to detect freshwater turtle nests may persist late into incubation. *The Canadian Field-Naturalist*, 128(2), 179–188.

Riley, J.L., Tattersall, G.J. & Litzgus, J.D. (2014) Potential sources of intra-population variation in the overwintering strategy of painted turtle (*Chrysemys picta*) hatchlings. *Journal of Experimental Biology*, 217, 4174–4183. Available from: https://doi.org/10.1242/jeb.111120

RStudio Team. (2022) *RStudio: integrated development for R*. Boston, MA: Posit Software, PBC. Available online: http://www.rstudio.com/ [Accessed 23rd March 2021].

Rusli, M.U., Booth, D.T. & Joseph, J. (2016) Synchronous activity lowers the energetic cost of nest escape for sea turtle hatchlings. *Journal of Experimental Biology*, 219, 1505–1513.

Santidrián Tomillo, P., Saba, V.S., Lombard, C.D., Valiulis, J.M., Robinson, N.J., Paladino, F.V. et al. (2015) Global analysis of the effect of local climate on the hatchling output of leatherback turtles. *Scientific Reports*, 5, 16789.

Santoro, A. (2022) *The implications of climate change and urbanisation throughout the life-cycle of a freshwater turtle*. PhD. Murdoch University.

Santoro, A., Chambers, J.M., Robson, B.J. & Beatty, S.J. (2020) Land use surrounding wetlands influences urban populations of a freshwater turtle. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(5), 1050–1060. Available from: https://doi.org/10.1002/aqc.3324

Santos, R.G., Pinheiro, H.T., Martins, A.S., Riul, P., Bruno, S.C., Janzen, F.J. et al. (2016) The anti-predator role of within-nest emergence synchrony in sea turtle hatchlings. *Proceedings. Biological sciences*, 283(20160697), 1–7. Available from: https://doi.org/10.1098/rspb.2016.0697

Seager, R., Osborn, T.J., Kushnir, Y., Simpson, I.R., Nakamura, J. & Liu, H. (2019) Climate variability and change of Mediterranean-type climates. *Journal of Climate*, 32, 2887–2915.

Segura, A., Jimenez, J. & Acevedo, P. (2020) Predation of young tortoises by ravens: the effect of habitat structure on tortoise detectability and abundance. *Scientific Reports*, 10(1), 1874. Available from: https://doi.org/10.1038/s41598-020-58851-5

Silberstein, R.P., Aryal, S.K., Durrant, J., Pearcey, M., Braccia, M., Charles, S.P. et al. (2012) Climate change and runoff in South-Western Australia. *Journal of Hydrology*, 475, 441–455. Available from: https://doi.org/10.1016/j.jhydrol.2012.02.009

Sim, L.L., Davis, J.A., Strehlow, K., McGuire, M., Trayler, K.M., Wild, S. et al. (2013) The influence of changing hydroregime on the invertebrate communities of temporary seasonal wetlands. *Freshwater Science*, 32(1), 327–342. Available from: https://doi.org/10.1899/12-024.1

Spencer, R.J., Thompson, M.B. & Banks, P.B. (2001) Hatch or wait? A dilemma in reptilian incubation. *Oikos*, 93, 401–406.

Stanford, C.B., Iverson, J.B., Rhodin, A.G.J., Paul van Dijk, P., Mittermeier, R.A., Kuchling, G. et al. (2020) Turtles and tortoises are in trouble. *Current Biology*, 30(12), R721–R735. Available from: https://doi.org/10.1016/j.cub.2020.04.088

Storey, K.B., Storey, J.M., Brooks, S.P.J., Churchill, T.A. & Brooks, R.J. (1988) Hatchling turtles survive freezing during winter hibernation. *Proceedings of the National Academy of Sciences of the United States of America*, 85, 8350–8354.

Sturman, A. & Tapper, N. (1996) *The weather and climate of Australia and New Zealand*, 1st edition. New York: Oxford University Press, Melbourne, Australia.

Tinkle, D.W., Congdon, J.D. & Rosen, P.C. (1981) Nesting frequency and success: implications for the demography of painted turtles. *Ecology*, 62, 1426–1432.

Tryon, B. (2009) Egg-harvesting, hatching and release: a population augmentation tool for bog turtles in Tennessee. *Turtle Survival*, 2009, 44–45.

Tucker, J.K. (1999) Environmental correlates of hatchling emergence in the red-eared turtle, *Trachemys scripta elegans*, in Illinois. *Chelonian Conservation and Biology*, 3, 401–406.

Tucker, J.K., Filoramo, N.I., Paukstis, G.L. & Janzen, F.J. (1998) Residual yolk in captive and wild-caught hatchlings of the red-eared slider turtle (*Trachemys scripta elegans*). *Copeia*, 1998, 488–492. Available from: https://doi.org/10.2307/1447448

Tucker, J.K. & Paukstis, G.L. (1999) Post-hatching substrate moisture and overwintering hatchling turtles. *Journal of Herpetology*, 33(4), 608–615.

Tucker, J.K., Paukstis, G.L. & Janzen, F.J. (2008) Does predator swamping promote synchronous emergence of turtle hatchlings among nests? *Behavioral Ecology*, 19(1), 35–40. Available from: https://doi.org/10.1093/beheco/arm097

Valenzuela, N. (2001) Constant, shift, and natural temperature effects on sex determination in Podocnemis expansa turtles. *Ecology*, 82(11), 3010. Available from: https://doi.org/10.2307/2679831

Warner, D.A., Jorgensen, C.F. & Janzen, F.J. (2010) Maternal and abiotic effects on egg mortality and hatchling size of turtles: temporal variation in selection over seven years. *Functional Ecology*, 24, 857–866.

Water Corporation. (2021) Rainfall. Created online: https://www.watercorporation.com.au/Our-water/Rainfall-and-dams/Rainfall

Whitlock, A. (2002) *Ecology and status of the bog turtle (Clemmys muhlenbergii) in New England*. PhD. University of Massachusetts, Amherst.

Wilbur, H.M. (1975) The evolutionary and mathematical demography of the turtle *Chrysemys picta*. *Ecology*, 56, 64–77.

Willette, D.A.S., Tucker, J.K. & Janzen, F.J. (2005) Linking climate and physiology at the population level for a key life-history stage of turtles. *Canadian Journal of Zoology*, 83, 845–850. Available from: https://doi.org/10.1139/z05-078

Zappalorti, R.T., Tutterow, A.M., Pittman, S.E. & Lovich, J.E. (2017) Hatching success and predation of bog turtle (*Glyptemys muhlenbergii*) eggs in New Jersey and Pennsylvania. *Chelonian Conservation and Biology*, 16(2), 194–202. Available from: https://doi.org/10.2744/ccb-1237.1

Zhu, X.-P., Wei, C.-Q., Zhao, W.-H., Du, H.-J., Chen, Y.-L. & Gui, J.-F. (2006) Effects of incubation temperatures on embryonic development in the Asian yellow pond turtle. *Aquaculture*, 259(1–4), 243–248. Available from: https://doi.org/10.1016/j.aquaculture.2006.05.025

SUPPORTING INFORMATION

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

How to cite this article:
Santoro, A., Chambers, J.M., Ebner, B. & Beatty, S.J. (2023) Climate change affects the early-life history of a freshwater turtle in a severely drying region. *Austral Ecology*, 48, 2205–2229. Available from: https://doi.org/10.1111/aec.13456