



Nesting ecology of *Chelodina longicollis* in stormwater ponds, Australian Capital Territory, Australia

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ABSTRACT

Despite urbanisation threatening many species worldwide, the eastern long-necked turtle (*Chelodina longicollis*) inhabits urban ponds and wetlands across Australia. However, little is known about its nesting habits in these environments, information that would help to understand and support its urban resilience. This study examines the nesting ecology of *C. longicollis* in two urbanised drainages in Canberra, south-eastern Australia, over two nesting seasons, and correlates nesting parameters and behaviour with physical and climatic conditions. Females nested in a range of locations, with many nests successfully established at the edge of urban structures (e.g. fences, drains). There was no difference between nest attempts and nests completed to egg-laying in weather or habitat parameters, except for slope. Overnight decreases in barometric pressure and relative humidity were both correlated with *C. longicollis* nesting activity. Additionally, minimum and maximum daily temperatures predicted nest emergence and pre-emergence behaviour in *C. longicollis*. Finally, we observed that invasive and native grasses can interfere with incubation and cause embryo mortalities. These findings shed some light on the reproductive ecology of *C. longicollis* inhabiting stormwater ponds, and help us understand their persistence and survival in an urban context.

Keywords: freshwater turtle, grass root intrusion, hatchling, incubation, nest attempt, overwintering, pre-emergence behaviour, reproduction, stormwater pond, urban ecology.

Introduction

Urbanisation is one of the main threats to wildlife inhabiting cities around the world (McKinney 2002; Riley *et al.* 2003; Xu *et al.* 2018). Despite many species suffering declines from urbanisation and associated mortality, some species benefit from the increased productivity of urban ecosystems, including some species of birds, mammals and reptiles (Souza and Abe 2000; McKinney 2002; Shochat *et al.* 2006; McKinney 2008). For aquatic ecosystems, urbanisation brings changes such as damming of rivers, road crossings and wetlands draining (McCauley *et al.* 2013; Fuller *et al.* 2015; Gido *et al.* 2015), which cause fragmentation, habitat destruction, and dispersal and migration disruption for several aquatic species (McCauley *et al.* 2013; Gido *et al.* 2015). However, with urban development and growth, several countries have legislation mandating stormwater management and the creation of stormwater ponds, including all states and territories in Australia (Roy *et al.* 2008; Radcliffe 2019). The design of these ponds is guided by Water Sensitive Urban Design principles with the aim of treating polluted stormwater from urban impervious surfaces (Wong and Brown 2009). Stormwater ponds not only provide water quality improvements, but also benefit aquatic ecosystem health, increasing the diversity of macroinvertebrates, and the provision of habitat for aquatic species in urban areas (Greenway 2010; Hassall and Anderson 2015).

Several species of freshwater turtles benefit from urbanisation through increased food availability (Souza and Abe 2000; El Hassani *et al.* 2019), and the provision of additional habitat, such as man-made ponds (Winchell and Gibbs 2016; Dupuis-Desormeaux *et al.* 2018). In Australia, the eastern long-necked turtle (*Chelodina longicollis*) inhabits ponds,

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lakes, and urban wetlands (Atlas of Living Australia 2026), and is believed to be resilient to urbanisation, based on population studies in Canberra and the Melbourne region (Kennett *et al.* 2009; Roe *et al.* 2011; Stokeld *et al.* 2014). *Chelodina longicollis* appears to succeed in urban ponds partly because of its migratory ability: individuals can move overland for long distances and use a range of aquatic habitats (Kennett *et al.* 2009; Roe *et al.* 2011; de Oliveira Ferronato *et al.* 2024). Nevertheless, habitat connectivity within urban areas remains important to their persistence (de Oliveira Ferronato *et al.* 2024).

Despite the ability of *C. longicollis* to colonise and establish in new ponds (Roe *et al.* 2011; Stokeld *et al.* 2014; de Oliveira Ferronato *et al.* 2024), less is known about where females nest in the urban landscape and which environmental factors influence nest placement. In this study, we describe the physical characteristics associated with *C. longicollis* nests in the surroundings of stormwater ponds, describe their nesting behaviour and correlate it with climatic and environmental factors. We also examine incubation, hatchling survival and nest emergence over two nesting seasons in stormwater ponds in the Canberra region, south-eastern Australia.

Materials and methods

Study species and sites

Chelodina longicollis is known to leave the water during the nesting season in November and December and search for nesting sites, generally during, or just after, rainfall (Vestjens 1969). Females prefer a crest or ridge at the top of a slope (Kennett *et al.* 2009), usually within sparse vegetation (Vestjens 1969; Chessman 1978; Ferronato *et al.* 2015), and nesting between 2 and 2.5 m above the waterline (Vestjens 1969). Where there is a gentle slope from the water's edge, females tend to nest further from the water (up to 70 m: Ferronato *et al.* 2015), and occasionally nest as far as 500 m (Kennett *et al.* 2009). Conversely, if the slope is steeper, females may climb only a short distance and nest where the terrain is flat, sometimes only 2 m from the water's edge (Ferronato *et al.* 2015).

From November 2020 to October 2022, we monitored *C. longicollis* nests in stormwater ponds in two drainages in the Australian Capital Territory (ACT), south-eastern Australia. In the first season (November 2020 to September 2021), searches were conducted at two stormwater ponds in the Ginninderra Creek drainage (Jarramlee Pond and Fassifern Pond). In the second season (November 2021 to October 2022), we expanded the searches to eight stormwater ponds (Ginninderra Creek drainage: Jarramlee Pond, Fassifern Pond, Refshauge Crescent Pond, and Hollows Circuit Pond. Sullivans Creek drainage: Dickson Wetland, Lyneham Wetland, David Street Wetland, Banksia Street Wetland; the 'wetlands' are stormwater ponds, despite their label). These ponds were

similar in size and age (size: 1115 m²–12,046 m²; 8–28 years since construction) and the majority were surrounded by manicured gardens and lawns. They were located within the suburbs of Dunlop, MacGregor, Dickson, Lyneham and O'Connor, and were bordered by housing and urban infrastructure (e.g. roads, bike paths and residential areas). Stormwater ponds in the Ginninderra Creek drainage have greater habitat connectivity (sparser road network and an unmodified creek), with moderate to low use of the area by members of the public as they are periurban. The study sites in the Sullivans Creek drainage have lower habitat connectivity (denser road network and stormwater drains), with higher pedestrian use, as they are highly urbanised. For further details on the stormwater ponds and drainages, see de Oliveira Ferronato *et al.* (2024).

Climate

The ACT has a temperate climate, with an average annual rainfall of 616 mm and mean monthly maximum air temperature ranging from 11.4°C in July to 28.0°C in January, and mean minimum air temperature from −0.1°C in July to 13.2°C in January (1939–2010: Australian Bureau of Meteorology 2024). The region is characterised by droughts, punctuated by periods of elevated rainfall, and influenced by meteorological phenomena such as El Niño, La Niña, and the Indian Ocean Dipole. During the study period, there was a higher-than-average rainfall recorded for the area (2020: 790 mm; 2021: 912 mm; 2022: 892 mm; Canberra Airport weather station), reflecting the influence of La Niña and a negative Indian Ocean Dipole (Australian Bureau of Meteorology 2024; de Oliveira Ferronato *et al.* 2024).

Nest searches and data collection

We located nests by walking along the edges of the stormwater ponds during late spring and early summer (November and December), which covers *C. longicollis* nesting season in this region (Vestjens 1969; Ferronato *et al.* 2017). Searches for nesting females, nest attempts (where a female dug the cavity but did not lay eggs), and intact nests (where a female dug a cavity, laid eggs and plugged the nest: Ferronato *et al.* 2015) were done two mornings a week throughout the nesting season. If rainfall was predicted, sites were checked daily for at least three consecutive days, in the mornings or afternoons. When a nesting female was found, searchers remained at least 15 m away until she had finished nesting. Once a nest was found (attempt or intact), we recorded several physical parameters of the nesting site, and protected intact nests from fox predation using plastic mesh pegged down over the nest (plastic trellis, 5 × 5 cm aperture, 50 × 50 cm mesh size). We also recorded the physical parameters of any nests that were found depredated. Intact and depredated nests are combined under the term 'nests completed to egg-laying' for some analyses.

We recorded geographic coordinates, distance from water, slope from water to the nest, orientation of the slope, slope at the nest, estimated vegetation height (average) at the nesting site, estimated vegetation height (average) within 2 m from the nesting site, whether a man-made structure was present within 2 m of the nesting site, and whether the nest was at the edge of tall vegetation. Distances and vegetation heights were measured with a tape measure and slope was measured with a Haglöf ECII-D electronic clinometer (ASICS Crop., Sweden). Weather data were retrieved from the Canberra Airport weather station (Australian Bureau of Meteorology 2024) for the estimated nesting date of each nest attempt and intact nest, including daily maximum and minimum temperature (°C), rainfall (mm) (2400 hours to 0900 hours), relative humidity at 0900 hours and 1500 hours (%), and barometric pressure at 0900 hours and 1500 hours (hPa).

We monitored the nests throughout incubation to emergence in April, or, in the case of overwintering nests, emergence in the following spring (September/October). Pre-emergence behaviour (signs of hatchlings digging from the nest), nest emergence (opening dug on the top of the nest) and number of hatchlings emerging were recorded. For each emergence date, we retrieved the same weather variables described above.

Statistical analysis

Analyses were performed in R (R Core Team 2023). To evaluate the differences between nest attempts and nests completed to egg-laying, we used linear models for continuous nest site parameters and binomial models for the presence of nearby man-made structures and whether the nest was located at the edge of tall vegetation. We also compared minimum and maximum daily temperature, daily rainfall and relative humidity and barometric pressure at 0900 hours on the nesting date. We similarly compared the nest site parameters between successful intact nests (eggs developed) and unsuccessful intact nests (eggs were laid but did not develop).

To investigate if daily weather variables were associated with the number of nests dug (all nest attempts, and nests completed to egg-laying only) on a given day during the nesting season (November–December), we fitted generalised linear models with a negative binomial error distribution. Predictor variables included rainfall, daily maximum and minimum temperature, relative humidity at 0900 hours, barometric pressure at 0900 hours and change in relative humidity and barometric pressure since 1500 hours the previous day. All predictors were centred before analysis. We used the same approach to examine whether daily weather variables were associated with the number of nest-emergence or pre-emergence events recorded on a given day during autumn (March–May) and spring emergence periods (nest overwintering, August–October).

Ethics approval

Our project was conducted with approvals and permits from the ACT Licensing and Compliance (LT202011) and University of Canberra Animal Ethics Committee (no. 3379).

Results

Nests and nesting attempts

We found 16 intact nests, four depredated nests, and 16 nest attempts during the study. Foxes were probably responsible for the observed nest predation, as they are common in the area and known to heavily prey upon turtle eggs and adult females (Kennett *et al.* 2009; Ferronato *et al.* 2015). In the first season (2020), nests were laid over a 10-day period in November (Table 1), with additional nesting attempts observed over 27 days from November to December (Table 2). In the second season (2021), nests were laid over a 20-day period in December (Table 1), with additional nesting attempts observed over 10 days in early December (Table 2). Most nests and attempts occurred at the Fassifern Pond site (Tables 1 and 2, Figs 1 and 2).

Of the 16 intact nests found, 11 completed incubation and showed evidence of nest emergence (Table 1, Fig. 3). One nest was apparently poached and four did not develop. The poached nest was laid in gravel. Of the four that did not develop, grass root intrusion occurred in three nests, at three different sites in 2021 (Table 1, Fig. 4). A mix of perennial exotic and native grasses were observed at the top of the affected nests. At Lyneham Wetland, these included *Paspalum dilatatum*, exotic), goose grass (*Eleusine tristachya*, exotic) and windmill grass (*Chloris truncata*, native); at Hollows Circuit Pond: *Paspalum*, couch grass (*Cynodon dactylon*, exotic), slender rat's tail grass (*Sporobolus creber*, native), Brown's love grass (*Eragrostis brownii*, native), and red leg grass (*Bothriochloa macra*, native); and at Fassifern Pond: couch, goose, and windmill grass. No grass root intrusion was observed into nests at the other sites, despite the presence of these species.

On average, the 36 nests and nest attempts located during this study were 11.7 ± 11.1 m from the stormwater ponds (summary statistics reported as mean $\pm$ one standard deviation; range: 4.1–46 m) (Tables 1 and 2). The mean slope at the nest was $11.4 \pm 5.9^\circ$ (0.8–19.9), mean estimated vegetation height at the nest was 15.2 ± 9.9 cm (3.0–35.0 cm), and mean estimated vegetation height within 2 m from the nest was 115.7 ± 81.8 cm (3.0–250.0 cm). Seventeen nests or attempts were located at the edge of tall vegetation, and six were located within 2 m of a man-made structure (e.g. fence, concrete drain or footpath: Tables 1 and 2). Most nest and nest attempt sites faced south-east (61%; Fig. 2). Of the measured site variables, only slope from water to nest location differed between nests completed to egg-laying (14.5 ± 3.9 , range: 6–19.3, $n = 20$) and nest attempts

Table 1. Habitat parameters associated with intact and depredated nests of *Chelodina longicollis* in the Canberra region, ACT, Australia (2020–2022).

Site	Nesting date	Distance (m)	Slo 1 (°)	Slo Or	Slo 2 (°)	Veg 1 (cm)	Veg 2 (cm)	Structure (Y/N)	Tall Veg (Y/N)	Pre-Emerg	Emergence date	Overw	Incub. Per. (days)	Obs
Jarramlee	13/11/2020	4.1	18	SW	15	15	45	N	N		4/09/2021	Y	296	
Jarramlee	13/11/2020	31.15	6	SE	5	5	3	Y	N		24/03/2021	N	133	Fence
Fassifern	23/11/2020	8.4	16	SE	17	10	150	N	Y	24/03/2021	4/05/2021	N	164	
Fassifern	23/11/2020	7	14	SE	18	10	150	N	Y		24/03/2021	N	123	
Fassifern	23/11/2020	6.6	16	SE	16	10	200	N	Y		24/03/2021	N	123	
Fassifern	23/11/2020	6.6	16	SE	16	15	200	N	Y		24/03/2021	N	123	
Fassifern	3/12/2021	8.4	16.7	SSE	17.7	15	200	N	Y		7/10/2022	Y	310	
Jarramlee	3/12/2021	46	6.8	SE	10	5	—	Y	N	05/08/2022	9/09/2022	Y	282	Fence
Fassifern	4/12/2021	7.7	17.3	SSE	18.3	15	200	N	Y	05/08/2022	9/09/2022	Y	281	
Fassifern	4/12/2021	7.5	13.5	SW	2.1	10	10	N	N		—	—		Grass infiltration
Lyneham	6/12/2021	11	10.4	NW	6.7	5	25	N	N		—	—		Grass infiltration
Fassifern	7/12/2021	6.4	19.3	SE	18.5	30	250	N	Y		—	—		Depredated
Hollows	7/12/2021	8.5	13.4	SE	9.1	25	30	N	N		—	—		Grass infiltration
Hollows	7/12/2021	5.4	12.6	SE	8.4	25	25	N	N		9/09/2022	Y	278	
Fassifern	9/12/2021	5.8	18	SE	19.9	35	200	N	Y		—	—		Depredated
Fassifern	9/12/2021	7.1	16.4	SSE	14.4	30	200	N	Y		—	—		Depredated
Fassifern	9/12/2021	8.3	15.9	SSE	16.8	35	150	N	Y		—	—		Depredated
Fassifern	11/12/2021	4.4	16.1	SE	17.8	25	150	N	Y		23/09/2022	Y	288	
Dickson	14/12/2021	10	18.7	NW	4.4	—	8	Y	N		—	—		Gravel nesting, footpath, poached
Jarramlee	23/12/2021	42	8.5	NE	1.7	3	—	Y	N		—	—		Fence, eggs not developed

Distance, distance of nest from water; Slo 1, slope from water to the nest; Slo Or, slope orientation; Slo 2, slope at the nest; Veg 1, estimated vegetation height at nesting site; Veg 2, estimated vegetation height within 2 m from nest site; Structure, man-made structure within 2 m from the nest site; Tall Veg, nest at the edge of tall vegetation; Pre-Emerg, date of pre-emergence behaviour; Overw, overwintered; Incub. Per., incubation period; Obs, observation.

(11.8 ± 3.8 , range: 4.4–16.8, $n = 16$). The slope was steeper for completed nests than attempts ($\beta \pm \text{s.e.} = 2.71 \pm 1.28$, $t = 2.1$, $P = 0.04$).

Comparing successful intact nests (eggs developed) with unsuccessful intact nests (eggs were laid but did not develop), the slope at the nest site was steeper for successful nests ($\beta \pm \text{s.e.} = 9.67 \pm 2.26$, $t = 4.3$, $P < 0.001$), and vegetation within 2 m of the nest site was taller for successful nests ($\beta \pm \text{s.e.} = 114.05 \pm 40.23$, $t = 2.8$, $P = 0.02$). No other habitat variables differed significantly between successful and unsuccessful nests.

Weather variables on the day of digging did not differ between completed nests and nest attempts. On average, digging occurred on days with a minimum temperature of $12.1 \pm 2.5^\circ\text{C}$ (range: 5.9 – 16.8°C) and maximum temperature of $24.1 \pm 4.2^\circ\text{C}$ (14.1 – 30.2°C), with 6.5 ± 11.6 mm of rainfall (0 – 34 mm). Relative humidity at 0900 hours was $75.8 \pm 14.7\%$ (34 – 99%) and barometric pressure at 0900 hours was 1012.4 ± 4.6 hPa (1001.6 – 1025.5 hPa).

During the studied nesting seasons, barometric pressure increased on average by 2.5 ± 4.0 hPa between 1500 and 0900 hours each night and relative humidity increased on

average by 21.2 ± 18.9 percentage points. Nights when these increases were smaller than usual, including those when pressure or humidity fell overnight, were associated with an increase in the expected number of nesting or nesting attempts (Fig. 5). For every unit increase in the magnitude of overnight pressure drop, the expected number of nest or nest attempt events increased by 23% (log odds: 0.20 ± 0.10 , $z = 2.1$, $P = 0.04$). For every unit increase in the magnitude of overnight drop in relative humidity, the expected number of nest or nest attempt events increased by 4% (log odds: 0.04 ± 0.02 , $z = 2.0$, $P = 0.05$). None of the other weather variables were significantly associated with nesting or attempts. When only the 20 completed nests were considered, none of the weather variables were significantly related to the number of nests dug on a given day.

Incubation and nest emergence

Six nests completed incubation during the first season (2020), of which only one overwintered before hatchlings attempted to emerge. By contrast, during the second season (2021), five

Table 2. Habitat parameters associated with nest attempts of *Chelodina longicollis* in the Canberra region, ACT, Australia (2020–2022).

Site	Date found	Distance (m)	Slo 1 (°)	Slo Or	Slo 2 (°)	Veg 1 (cm)	Veg 2 (cm)	Structure (Y/N)	Tall Veg (Y/N)	Obs
Fassifern	16/11/2020	6.3	15	SE	13	10	150	N	Y	
Fassifern	22/11/2020	6.6	15	SE	16	15	150	N	N	
Fassifern	22/11/2020	7.3	13	SE	11	10	200	N	Y	
Fassifern	22/11/2020	9.3	11	SE	11	15	150	N	Y	
Fassifern	29/11/2020	8.9	12	S	1	5	10	N	N	
Fassifern	13/12/2020	8.4	15	SE	17	10	150	N	Y	
Fassifern	1/12/2021	8.2	16.8	SSE	19	30	200	N	Y	
Fassifern	2/12/2021	6.5	16.4	SSE	16.1	25	150	N	Y	
Jarramlee	3/12/2021	46	6.8	SE	10	5	—	Y	N	Fence
Fassifern	7/12/2021	7.9	10.9	SE	7.4	15	150	N	N	
Fassifern	7/12/2021	8.3	12.2	SE	6.7	15	45	N	N	
Fassifern	7/12/2021	7.3	12.2	SE	6.7	10	20	N	N	
David St.	10/12/2021	15	4.5	NE	5.2	5	5	N	N	
David St.	10/12/2021	17	4.4	NE	0.8	3	3	N	N	
Fassifern	11/12/2021	8.6	11	SE	9.5	20	200	Y	N	Concrete drain
Fassifern	11/12/2021	8.3	12.2	SE	6.7	30	40	N	N	

Distance, distance of nest attempt from water; Slo 1, slope from water to the nest attempt; Slo Or, slope orientation; Slo 2, slope at the nest attempt; Veg 1, estimated vegetation height at nest attempt site; Veg 2, estimated vegetation height within 2 m from nest attempt site; Structure, man-made structure within 2 m of the nest attempt; Tall Veg, nest attempt at the edge of tall vegetation; Obs, observation.

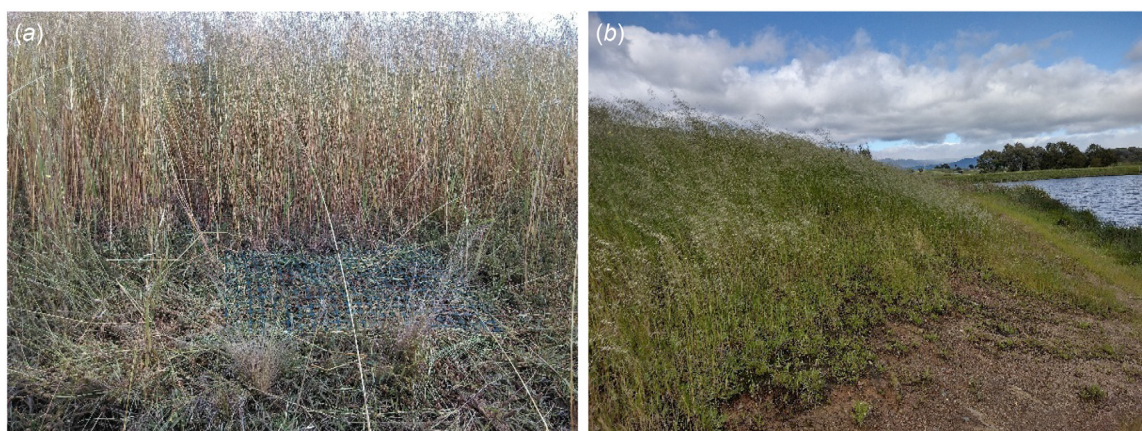


Fig. 1. Nesting site in Fassifern Pond (Canberra, Australian Capital Territory, Australia), where several *Chelodina longicollis* nests were found. (a) Front view of nesting site along the tall invasive grass Wild oat (*Avena fatua*). Nest protected with a mesh. (b) Lateral view of the nesting site.

nests completed incubation and all of them overwintered before emergence (Table 1).

For nests that did not overwinter, the incubation period was 133 ± 17 days ($n = 5$, range = 123–164 days), with the longest one (164 days) emerging in early May (Table 1). For nests that overwintered, the incubation period was 289 ± 12 days ($n = 6$, range: 278–310 days). We observed pre-emergence behaviour in one nest that did not overwinter and two that did. This behaviour consisted of signs of digging by the hatchlings, which produced a small opening at the top of

the nest, smaller than the usual nest opening length of 3 cm (Ferronato, pers. obs.). In two nests, the opening was approximately 1.5 cm long and no hatchlings appeared to have emerged. In one overwintering nest, the opening was only slightly smaller than 3 cm and may have allowed some hatchlings to emerge (Fig. 6). This opening was seen on 5 August 2022, and we were able to observe the behaviour of the hatchlings within the nest using a mobile phone camera with in-built LED flash for illumination. The camera was aimed through the opening from the outside of the nest,

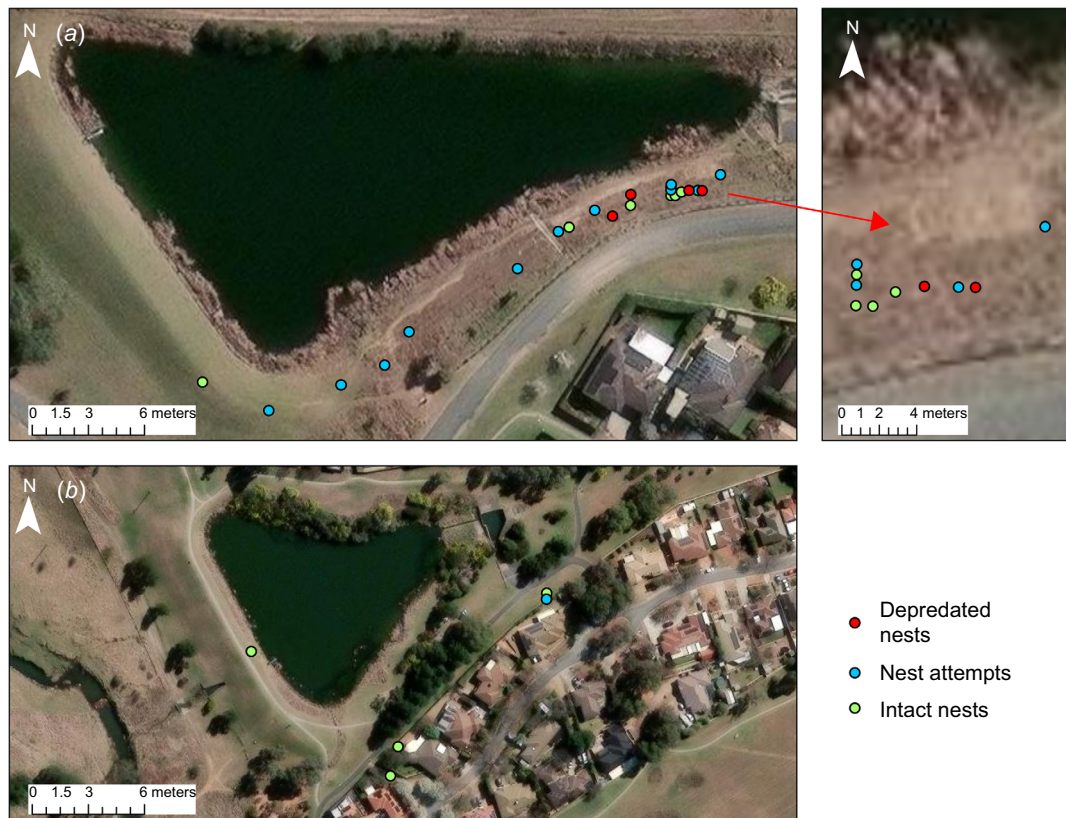


Fig. 2. Depredated nests, nest attempts and intact nests at Fassifern (a) and Jarramlee Ponds (b), Canberra, Australian Capital Territory, Australia. These two sites had the most nest observations in our study areas.



Fig. 3. Two intact nests (a, b) and a nest attempt (c) of the *Chelodina longicollis* in Canberra, Australian Capital Territory, Australia. Note the dried-up plug (a) and the fresh nest plug (b).

and zoomed in to allow a closer view of the five hatchlings. We checked the nest every three days, using the camera to look through the opening into the nest. The hatchlings changed position regularly within the nest (Fig. 6), but we observed no further sign of emergence for another 35 days. The hatchlings finally emerged from the nest on 9 September 2022. We observed and filmed one hatchling that remained inside the nest on that date (Fig. 6); it was active, nodding its head, and was eventually removed from the nest, assisted by the researchers.

We could not calculate hatching success, as the nests had a mesh and were not disturbed during incubation. The mesh prevented predation, but the mesh grid size allowed hatchlings to leave the nest. After the nests showed signs of emergence, the number of hatchlings found inside was 6.5 ± 4.1 (range: 2–15, $n = 10$ nests), although some hatchlings may have already emerged before counting. In one nest we found only empty eggshells at the bottom of the nest chamber, indicating that the hatchlings had all emerged. Hatchlings emerged at different



Fig. 4. Grass root intrusion on *Chelodina longicollis* nests in Canberra, Australian Capital Territory, Australia. (a) Example of roots infiltrating the egg laterally. (b) Roots completely infiltrated this egg.

times of the day, and, in some cases, we observed hatchlings both inside and outside the nest.

The average minimum daily temperature across the spring and autumn emergence periods in our study was $5.6 \pm 5.2^\circ\text{C}$

(-6.3 to 17.2°C) and the average maximum daily temperature was $18.3 \pm 4.2^\circ\text{C}$ (6.8 – 30.1°C). Nest emergence and pre-emergence behaviour occurred on days with an average minimum temperature of $11.1 \pm 3.7^\circ\text{C}$ (range: 6.6 – 15.6°C) and average maximum temperature of $16.8 \pm 2.8^\circ\text{C}$ (12.8 – 19.9°C). Minimum and maximum daily temperatures were associated with emergence and pre-emergence events on a given day, with emergence events more likely on days with warmer minimum temperatures and cooler maximum temperatures. For every unit increase in the minimum daily temperature, the expected number of emergence or pre-emergence events increased by 62.6% (log odds = 0.49 ± 0.20 , $z = 2.5$, $P = 0.01$). For every unit increase in the maximum daily temperature, the expected number of emergence or pre-emergence events decreased by 35.0% (log odds = -0.43 ± 0.21 , $z = -2.09$, $P = 0.04$). Rainfall, relative humidity and barometric pressure were not significantly associated with emergence or pre-emergence events. On average, emergence and pre-emergence events occurred on days with 20.5 ± 13.0 mm rainfall (range: 0.4 – 43.8 mm), $88.5 \pm 9.5\%$ relative humidity (79 – 100%), and barometric pressure of 1008.3 ± 8.3 hPa (998.7 – 1019.6 hPa).

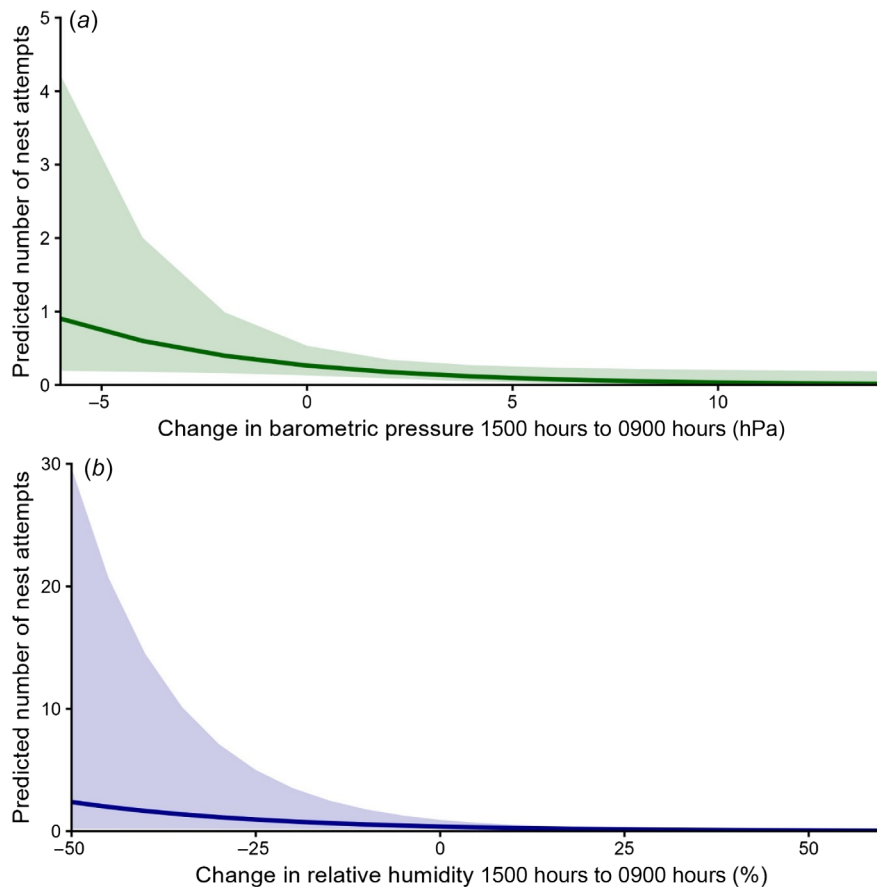


Fig. 5. Model predictions for the number of nesting attempts in relation to the overnight change in barometric pressure (a) or relative humidity (b). Note the large increase in confidence intervals (shaded ribbons) as the predicted value increases.

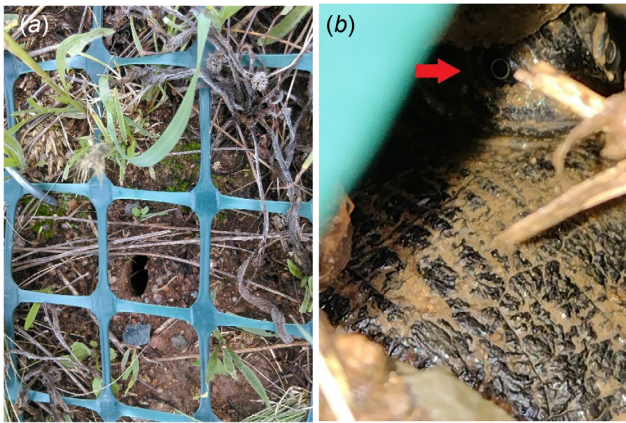


Fig. 6. Examples of opening for nest emergence by *Chelodina longicollis* in Canberra, Australian Capital Territory, Australia. (a) Protective mesh with 5 × 5 cm aperture, and hole that hatchlings dug to emerge from the nest. (b) View inside of the nest cavity in a different nest, taken with a mobile phone camera. Note the carapace of one hatchling covering most of the bottom part of the picture, and the head and eyes of another hatchling (red arrow) at the top.

Discussion

Our study highlights the nesting behaviour and ecology of the *C. longicollis* in stormwater ponds in Canberra, south-eastern Australia. Some findings are specific to nesting in modified habitats, whereas others concern the influence of climatic conditions on nest timing and emergence. We found that *C. longicollis* nests across a range of urbanised sites and conditions, but favoured one of our study areas, and we found no difference between completed and attempted nests in regard to climatic conditions and habitat parameters, except for slope. More specifically, we identified that overnight drops in barometric pressure or relative humidity were associated with nesting activity. We identified a risk factor affecting recruitment: invasive and native grasses can disrupt turtle egg incubation and kill *C. longicollis* embryos. And finally, we described pre-emergence behaviour in hatchlings, and found that minimum and maximum daily temperatures were associated with nest emergence and pre-emergence behaviour.

In this study, female *C. longicollis* nested in a wider range of sites and conditions within urban environments than has been described for natural and rural areas (Vestjens 1969; Chessman 1978; Ferronato et al. 2015). Although some habitat parameters, such as distance of nest from water, vegetation height at nest site, nests within sparse vegetation and no canopy cover at nest site, were similar to those reported previously (Vestjens 1969; Ferronato et al. 2015), 47% of nesting activity occurred at the edge of tall grass and 17% at the edge of man-made structures such as fences and concrete drains (Fig. 7). In Jarramlee Pond, for example, nests and attempts were concentrated along fences (Fig. 2), possibly because the surrounding



Fig. 7. Example of a concrete drain in northern Canberra, close to Lyneham Wetland, Australian Capital Territory, Australia.

houses limited access to more distant nesting habitat. Females might have moved further for nesting but encountered barriers and nested where their path was blocked. A similar pattern has been observed in Jerrabomberra Wetlands (Canberra, ACT), where turtles moving up-slope from Kellys Swamp nested along a chicken wire fence separating the swamp from a flat grassy area (Ferronato, pers. obs.). Comparative observations have been reported elsewhere. Houses and fences can obstruct nesting snapping turtles (*Chelydra serpentina*), thus reducing nest success (Kolbe and Janzen 2002).

At Fassifern Pond, where most nesting was recorded, most females nested at the edge of tall invasive vegetation (*Avena fatua*) (Figs 1, 2). Again, females appeared to move up-slope and stop when they reached dense vegetation; the mean slope at the nesting site there was 17.2° (Table 1). Even so, six of the seven nests laid along tall vegetation completed incubation and hatchlings emerged. Although *C. longicollis* shows a preference for nesting on flat surfaces near the top of slopes (Kennett et al. 2009; Ferronato et al. 2015), sites with higher slope did not appear to affect embryo development and survival in the present study. Similarly, in marine turtles (*Caretta caretta*), experimental barriers placed along the path of nesting females did not reduce the rate of nest completion or egg survival relative to controls (Witherington et al. 2011). In the present study, tall grass at Fassifern Pond may even have buffered females against nearby road mortality, given the proximity of the road (Fig. 2).

We also observed a female *C. longicollis* nesting in gravel at Dickson Wetland, where the other nests were found within natural substrate. Although gravel-road nesting has been reported previously for this species (Kennett et al. 2009), the context here is noteworthy. The nest was placed at the edge of a gravel surface only 20 cm from an open manicured grass

area 5 m from a footpath (Fig. 8). The female nested behind a medium-sized boulder, which was positioned between the gravel area and the manicured grass. Dickson Wetland is heavily used by pedestrians, dog walkers and cyclists throughout the day and evening, so the female may have nested in this less suitable site to keep some distance from passers-by. Unfortunately, the nest was removed or poached, so we could not follow it through incubation. Human disturbance is known to alter turtle nesting behaviour in North America (Bowen and Janzen 2008), and turtles may alter their nesting behaviour in response to recreation (Moore and Seigel 2006). If females perceive humans as a predation risk, they could alter their nesting behaviour, with potential consequences for nesting success and offspring fitness (Bowen and Janzen 2008).

We found no differences in nest-site or daily weather variables between intact nests and incomplete nest attempts, except for slope from the water to the nest. Previous studies have suggested that weather conditions differ between completed and abandoned nesting attempts (Muell *et al.* 2021), but that did not seem to be the case for *C. longicollis*. Many local factors could cause freshwater turtles to start nesting but not finish egg laying, including loose or dry soil (Congdon *et al.* 2000), inappropriate substrate such as gravel roadbeds (Holley 2021), rocks or roots encountered while digging (Booth 2010), predators (Moore and Seigel 2006; Baxter 2015) or human disturbance (Moore and Seigel 2006; Booth 2010; Holley 2021; Durkin *et al.* 2022). Turtles may also abandon nests

without any obvious external cause (Moore and Seigel 2006; Baxter 2015; Thompson and Ligon 2023). Most of the intact nests and nest attempts in our study were found around Fassifern Pond, a site with nearby roads but relatively little pedestrian traffic. Open abandoned nests have been reported previously in Canberra (Vestjens 1969), as have trial nests in Gippsland, Victoria (Chessman 1978). We cannot yet determine whether predators, humans or other disturbances caused females to abandon nesting, or whether nest attempts represent a normal exploratory phase before egg-laying. However, the pattern appears common enough in *C. longicollis* to warrant further study.

Three of the four nests that failed during incubation were affected by grass root intrusion, which to the best of our knowledge, is reported here for the first time for an Australian freshwater turtle. Although female *C. longicollis* nested within sparse vegetation or excavated the nest within mowed grass (Fig. 3), we observed in some instances that during summer ground vegetation had grown on the top of the nest plug. Root intrusion has been reported in freshwater turtle nests in North America (*Emydoidea blandingii*: Congdon *et al.* 2000; *Malaclemys terrapin*: Wnek *et al.* 2013; *Clemmys guttata*: Garrison *et al.* 2023; *Glyptemys insculpta*: Garber and Burger 1995, Wantman 2024), and in marine turtles elsewhere (*Dermochelys coriacea*: Conrad *et al.* 2011; *Caretta caretta*: Read *et al.* 2020, Redding *et al.* 2024). Nesting in anthropogenic areas may increase exposure to invasive plant roots (Garber and Burger 1995). Root intrusion by grasses may therefore be an



Fig. 8. *Chelodina longicollis* nest at Dickson Wetland, Canberra, Australian Capital Territory, Australia. Note nest at the edge of gravel (a, b), the proximity of manicured grass and footpath (b), and location behind a boulder (c).

additional cause of nest failure in suburban *C. longicollis* and further work is needed to determine whether it is also common in less modified sites.

Support in the literature is variable on whether weather conditions provide cues for freshwater turtle nesting (Bowen *et al.* 2005; Espinoza *et al.* 2018; Geller *et al.* 2022). A drop in barometric pressure, often associated with rainfall, has been linked to nesting in *Chelodina oblonga* in Western Australia (Santoro *et al.* 2023a) and in *Chrysemys picta* in North America (Muell *et al.* 2021). In contrast, a drop in barometric pressure is not required for nesting by *Graptemys ouachitensis* and other freshwater turtles (reviewed by Geller *et al.* 2022). Marine turtles respond to either falling or rising barometric pressure (Pike 2008; Palomino-González *et al.* 2020). In *C. longicollis*, females are known to nest after rain, but previous evidence for an association with falling barometric pressure has been weak (reviewed by Geller *et al.* 2022). In our study, overnight drops in barometric pressure or relative humidity were associated with increased nesting activity, although the effects were modest. Low barometric pressure is often linked to rainfall, and we observed turtles nesting on rainy days. However, *C. longicollis* also nested on sunny conditions with no rainfall on the day of nesting or on the preceding day. Our analysis found that an overnight drop in relative humidity – associated with a lower chance of rain – was also related to an increased likelihood of nesting or nest searches. In summary, a change in weather conditions can be associated with nesting in *C. longicollis*, possibly indicating that females are fine-tuned to sense changes in environmental conditions.

Most parameters related to incubation and hatching in this study are similar to those reported previously, including nest emergence months, incubation period of nests that did and did not overwinter, and number of hatchlings found in nests (Vestjens 1969; Chessman 1978; Kennett *et al.* 2009; Ferronato *et al.* 2015, 2017). As in Ferronato *et al.* (2015), we observed *C. longicollis* hatchlings overwintering in two seasons, especially in 2021–2022. Chessman (2018) argued that overwintering by *C. longicollis* in Gippsland, Victoria, is less likely to be adaptive, and instead reflects nest imprisonment caused by hard soil. That may occur during drought years in the Canberra region, as we observed nest imprisonment and hatchling mortality in overwintering nests during the 2018–2019 drought (Ferronato, pers. obs.). However, in cooler, wetter years, as observed in 2020–2022, overwintering was common despite softer and easier to dig soils, making nest imprisonment a less likely explanation, leaving open the possibility that overwintering is adaptive, perhaps allowing emergence to coincide with greater resource availability (Gibbons and Nelson 1978; Costanzo *et al.* 2008). Above average rainfall also occurred when hatchling overwintering in the nest was first documented in this species (Ferronato *et al.* 2015, 2017). The recent record of an adult female *C. longicollis* overwintering under ice in a creek pool in the New England region of New South Wales, further highlights

this species' tolerance of extreme conditions (Dowling *et al.* 2024). A fuller understanding of the dichotomous hatchling overwintering strategy in *C. longicollis* will require additional study.

We also observed pre-emergence behaviour of *C. longicollis*, which to our knowledge has not previously been described for this species. Embryonic development, prehatching behaviour and synchronous hatching have been well documented under laboratory studies (Spencer 2012; McGlashan *et al.* 2015), and pre-emergence sound production has been documented in the North American freshwater turtle *Apalone spinifera* (Geller and Casper 2023). We observed incomplete nest openings, indicating that *C. longicollis* hatchlings had begun to dig towards the surface, on three occasions, including one overwintering nest in August. We were able to document hatchling behaviour inside the nest cavity, including frequent repositioning and head movement on the day of emergence. We also observed that *C. longicollis* hatchlings do not emerge from the nest simultaneously, based on six monitored nests, but over an extended period, which may reduce the chance of detection by predators (Spencer 2012).

Minimum and maximum daily temperatures were associated with pre-emergence behaviour and nest emergence in *C. longicollis*, with emergence events more frequent on days with relatively warm minima and cool maxima for the season. A similar pattern has been reported for *C. oblonga* in Western Australia, where warmer temperatures during the week of emergence increased the chance of nest emergence in both autumn and spring (Santoro *et al.* 2023b). Santoro *et al.* (2023b) also found that rainfall during the week of emergence increased the probability of autumn emergence but not spring emergence. In our study, rainfall was not significantly associated with the number of emergence or pre-emergence events, although such events occurred across a rainfall range of 0.4–43.8 mm. Some soil moisture is probably needed to facilitate hatchling digging (Kennett *et al.* 2009; Chessman 2018; Santoro *et al.* 2023b), and wetter years associated with La Niña events may therefore promote emergence when temperatures are also conducive to hatchling metabolism (Santoro *et al.* 2023b). One limitation of this study was that we did not measure substrate compaction, substrate temperature and substrate moisture content within the nests. These additional variables would provide microclimate information and would increase our understanding of additional factors influencing incubation and nest emergence.

Despite relatively high numbers of potentially reproductive females (carapace length > 16.5 cm, $n = 87$) at the study sites, especially Fassifern and Jarramlee Pond (de Oliveira Ferronato *et al.* 2024), we found only 20 clutches (intact plus depredated nests) across eight study areas and two breeding seasons. We may not have detected all the nests laid during the breeding season, and some females may have moved well beyond the study areas to nest. However, a previous study in the Canberra region found a low proportion of gravid females by X-ray examination (Ferronato *et al.* 2017), which suggests

lower reproductive output than in warmer, lower altitude parts of the species' range (Kennett *et al.* 2009). Whatever the cause, the lower number of nests recorded highlights the importance of continued monitoring to determine whether recruitment is sufficient to maintain these urban populations, continued use of protective mesh over the nests, and the inclusion of artificial floating islands in stormwater ponds to increase nesting opportunities for females (Hunter *et al.* 2025).

From a management perspective, our results suggest that mowing regimes within stormwater pond fringes should consider impacts on the reproductive success of *C. longicollis*. For example, pond margins should be mown before the nesting season begins (October in the Canberra region) to improve access to potential nesting sites, and mowing should be avoided during the nesting season to prevent potential injury to nest-searching females (Erb and Jones 2011). Mowing should also occur before hatchling emergence begins (Canberra region: February for non-overwintering nests, and August for overwintering nests). Additionally, our observation that tall, thick vegetation appeared to limit females' travel in search of nesting sites suggests that plantings of this type could be used to create protective barriers – e.g. preventing turtles from accessing roads to reduce a common source of urban mortality. Management of vegetation around stormwater ponds to avoid root intrusion should be considered, and further studies conducted to increase knowledge on grass species impacting turtle nests.

As urbanisation continues in Australia and elsewhere (Garden *et al.* 2006; Simkin *et al.* 2022), understanding the ecological requirements of species in modified landscapes becomes increasingly important (Baldwin *et al.* 2004; Kirk *et al.* 2021; Santoro *et al.* 2024). Here, we have described the spatial and temporal conditions associated with nesting behaviour of *C. longicollis* in stormwater ponds in Canberra, south-eastern Australia. Turtles nested across a range of conditions, often at the edge of urban structures (e.g. fences, drains), and many nests completed incubation and showed evidence of emergence. Within the urban setting, invasive grasses and some native grasses interfered with incubation and caused embryo mortality. These findings extend earlier work on the resilience of *C. longicollis* in urbanised areas based on movement ecology and demography (Roe *et al.* 2011; Stokeld *et al.* 2014; Ferronato *et al.* 2016), by clarifying the nesting ecology in early developmental stages of the species in stormwater ponds.

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Data availability. Underlying data are available by request to the corresponding author.

Conflicts of interest. The authors declare that they have no conflicts of interest.

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