

First record of hatchling overwintering inside the natal nest of a chelid turtle

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Abstract. Hatchling overwintering inside the natal nest is a strategy used by several Northern Hemisphere species of freshwater turtles. We recorded hatchling overwintering in the nest by *Chelodina longicollis* (Chelidae) in south-eastern Australia, during three reproductive seasons. Hatchlings spent, on average, 320 days inside the nest from the date eggs were laid until emergence. Some nests were carefully opened adjacent to the nest plug, one during winter and one in spring, to confirm that eggs had hatched and were not in diapause, although we could not precisely confirm hatching dates. Despite our small sample size, we observed a dichotomous overwintering strategy, with hatchlings from one nest emerging in autumn and spending their first winter in the aquatic environment, and hatchlings from three nests overwintering in the nest and emerging in spring. These findings expand the phylogenetic range of turtles exhibiting hatchling overwintering behaviour. Future research should evaluate whether this strategy is widespread among other long-necked turtles in temperate regions and examine physiological mechanisms involved in coping with winter temperatures.

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Introduction

Time of emergence from the nest has profound ecological and evolutionary implications for egg-laying species, including freshwater turtles (Gibbons and Nelson 1978; Costanzo *et al.* 2008; Gibbons 2013). Delayed emergence has been hypothesised as one of the strategies used by turtles to better coincide emergence with resource availability (Gibbons and Nelson 1978; Mitchell 1988; Costanzo *et al.* 2008; Buhlmann *et al.* 2009). The delay can be of a few days to several months after hatching (Wilson *et al.* 1999; Gibbons 2013; Lovich *et al.* 2014; Riley *et al.* 2014). Hatchling overwintering in the nest, also known as terrestrial aestivation, is one type of delayed emergence in temperate areas (Gibbons 2013), where hatchlings spend winter inside the natal nest and emerge the following spring (Costanzo *et al.* 2008; Gibbons 2013). Another strategy used by some species is to emerge from the nest in the autumn, but hatchlings overwinter on land in refuges before reaching the wetland in spring (Muldoon and Burke 2012; Paterson *et al.* 2012).

Overwintering in the nest has costs and benefits. Direct costs include nest mortality from freezing, flooding, predation, dehydration and energy depletion arising from extended duration of nest occupancy (Gibbons and Nelson 1978; Packard 1997; Costanzo *et al.* 2008). Benefits include accelerated growth by timing emergence with an environment in which thermal and food resources are increasing rather than decreasing (Gibbons and Nelson 1978; Costanzo *et al.* 1995, 2008). Hatchling overwintering in the nest has been mainly observed in turtle species in the

Northern Hemisphere, especially in the family Emydidae (reviewed by Gibbons 2013), with only one record of an emydid turtle living in the Southern Hemisphere (Bager *et al.* 2007).

Long-necked turtles belong to the family Chelidae, which occurs in Australia, South America, New Guinea, Timor Leste and the Indonesian island of Roti (Georges and Adams 1992; Seddon *et al.* 1997). *Chelodina longicollis* is a common long-necked turtle with a broad geographic distribution in south-eastern Australia, occurring in a wide range of permanent and ephemeral freshwater habitats (Kennett *et al.* 2009). *C. longicollis* mates in the austral autumn (April) and early spring (September), lays eggs in late spring and early summer (October–January), and emerges from nests in autumn (April–May) (Vestjens 1969; Parmenter 1985). Delayed emergence has been reported for some turtle species in Australia (Goode and Russell 1968; Kennett *et al.* 1993a, 1993b; Doody *et al.* 2001), but this adjusted timing of emergence arises through early or late embryonic aestivation in the egg. Delayed emergence via hatchling overwintering inside the nest has been suggested (Chessman 1978; Kennerson 1980; Dalem and Burgin 1996), but not documented. Here, we report, for the first time, hatchling overwintering inside the natal nest by *C. longicollis*, with temperature data for the entire incubation period and nest emergence.

Methods

We monitored *C. longicollis* nests in the Gungahlin region, Australian Capital Territory (ACT), south-eastern Australia, from

November 2011 to October 2014. The ACT climate is temperate, with mean monthly maximum air temperature ranging from 11°C in July to a peak 28°C in January and February, and a mean monthly minimum air temperature ranging from 0°C to 13°C in the same months. Mean annual rainfall is 633 mm (1974–88, Australian Bureau of Meteorology). Nests were located around ponds in three locations. The Ginninderra Experiment Station operated by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) consists of areas with native grasses and eucalypts, in addition to areas with crops and pastures (Webster and Butler 1976). The Gungahlin suburb is an industrial and residential area with high road densities and managed suburban green spaces such as golf courses, suburban parks, gardens and sport ovals (see Rees et al. 2009; Roe et al. 2011). The 791-ha Mulligans Flat Nature Reserve comprises woodlands, grasslands, several ponds and the upper tributaries of Ginninderra Creek (Rees et al. 2009; Roe et al. 2011).

We monitored 10 natural nests from 2011 to 2014, and in five of them we observed nest emergence. Nests were located by walking along the perimeter of the ponds during late spring and early summer (November–December), which corresponds to the nesting season in this region (Vestjens 1969). Once a nest was found, usually by visually locating the nest plug, we measured the distance from the water and removed the nest plug to access the nest and take measurements of the length and the width of the eggs (cm), in addition to the depth of the nest cavity and the width of the nest mouth (cm). We then returned eggs to the nests, inserting an iButton® (Maxim Integrated, 160 Rio Robles, San Jose, CA 95134, USA) that recorded temperature every 2 h in the core of the nest. The nest plug was replaced and covered with wire mesh to protect it from fox predation and to capture emerging hatchlings to allow us to record dates of hatchling emergence. Nests were visually monitored during the incubation period, and monitored every other day during the expected time of emergence in autumn (March–April) (Vestjens 1969). We chose two nests from which the hatchlings did not emerge by autumn and carefully opened them adjacent to the nest plug, one during winter and the other at the beginning of spring, to confirm whether eggs were in diapause or had hatched, although we were not able to precisely detect hatching dates. Nests were monitored in the following spring every other day (September–November). Whenever there were signs of nest emergence, the mesh cover was removed and the nest accessed. We then recorded hatchling success, carapace and plastron length (cm), and body mass (g).

Results

In four of the 10 monitored nests, hatchlings overwintered inside the nest and emerged in spring, and in one nest the hatchlings did not overwinter and emerged in autumn (Table 1). The other five nests showed no signs of nest emergence after 16 months. They were opened and contained unhatched eggs or hatchlings that had pipped but were dead within the shell (Table 1). We confirmed that in at least two overwintering nests (one checked in winter and one in early spring), eggs had hatched and hatchlings were in torpor, had no yolk sac, and umbilical scars were closed. Hatching possibly occurred before winter, as winter temperatures induce inactivity in turtles (Ultsch 2006), but we were not able to document the precise time of hatching. We assumed that hatching should have occurred before winter in the other two unchecked overwintering nests.

Overwintering by hatchlings inside the nest was observed in each of the three years, and emergence from the nest occurred after 320 ± 31 (mean \pm s.d.) days ($n = 4$, range = 284–356 days), with hatching success ranging from 36 to 100% (Table 1). Incubation period of the nest that did not overwinter was 125 days, with a 92% hatching success (Table 1). Nests were 25.6 ± 24.9 m ($n = 10$, range = 2–70 m) away from the ponds, nest depth and nest mouth width were 8.9 ± 1.4 cm ($n = 10$, range = 6.8–11 cm) and 5.9 ± 1.0 cm ($n = 10$, range = 4.5–7.5 cm), respectively. Egg length and width were 3.17 ± 0.10 cm ($n = 111$, range = 2.94–3.42 cm) and 1.99 ± 0.05 cm ($n = 111$, range = 1.84–2.19 cm), respectively, and hatchling carapace length, plastron length and mass were 2.80 ± 0.12 cm ($n = 48$, range = 2.4–3.0 cm), 2.16 ± 0.07 cm ($n = 48$, range = 1.93–2.36 cm), and 4.28 ± 0.39 g ($n = 48$, range = 3.0–4.9 g), respectively.

Owing to iButton failure, we were able to record nest temperatures for the entire incubation period in only two nests in the 2013–14 season, representing a clutch that did not overwinter and one that did from the same population (Table 1, Fig. 1). Temperatures inside of the nest that did not overwinter were $24.4 \pm 4.3^\circ\text{C}$ ($n = 1$, range = 14.1–36.0°C). For the overwintering nest, temperature for the first 125 days of incubation (up to the date of hatching for the non-overwintering nests) was $26.5 \pm 6.1^\circ\text{C}$ ($n = 1$, range = 13.2–44.7°C), and $11.9 \pm 4.1^\circ\text{C}$ ($n = 1$, range = 3.7–23.9°C) through the overwintering period until the time of emergence (Fig. 1). We were able to recover partial temperature data for two nests that successfully overwintered and emerged in spring, for which the recorded

Table 1. *Chelodina longicollis* nests monitored during three reproductive seasons in Gungahlin, Australian Capital Territory, Australia

Season	Area	Found	Emergence	Overwintered	Eggs (n)	Hatching success
2011–12	Csiro_4	29 November 2011	19 November 2012	Yes	13	100%
	Csiro_5	29 November 2011	03 October 2012	Yes	11	82%
	Csiro_14	07 December 2011	–	–	14	0%
	Csiro_19	13 December 2011	–	–	12	0%
	Reserve_1	08 December 2011	–	–	9	0%
	Reserve_4	03 January 2012	–	–	10	0%
	Suburb_1	05 January 2012	–	–	11	0%
2012–13	Suburb_8	07 December 2012	17 September 2013	Yes	10	100%
2013–14	Csiro_21	26 November 2013	24 October 2014	Yes	11	36%
	Csiro_22	26 November 2013	31 March 2014	No	13	92%

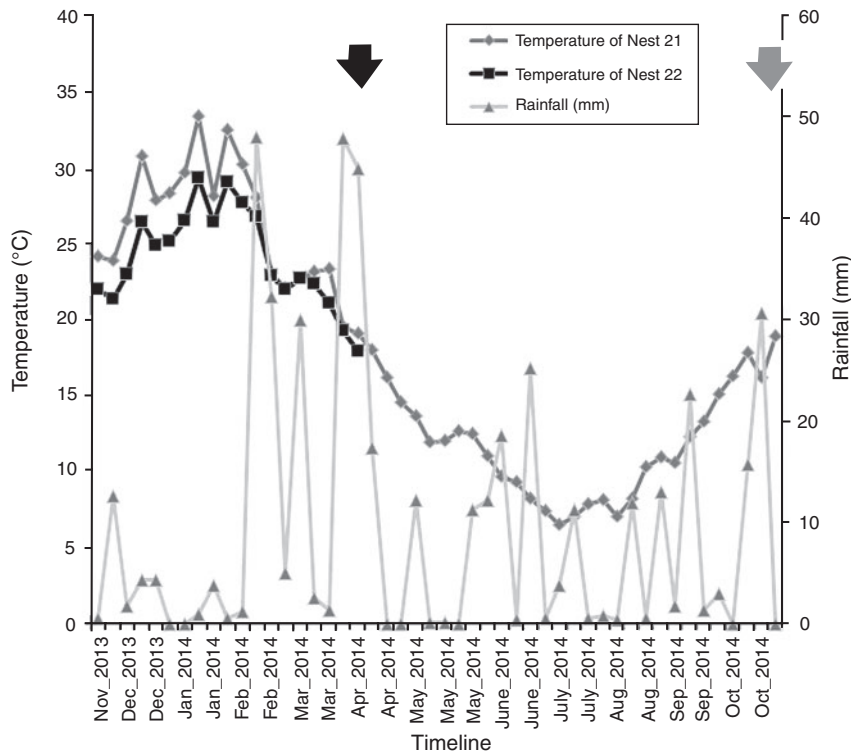


Fig. 1. Incubation period and nest emergence of *Chelodina longicollis* from Gungahlin, Australian Capital Territory, Australia, during the 2013–14 nesting season. Nest 22 did not overwinter and hatchling emergence is depicted with a black arrow. Nest 21 overwintered and hatchling emergence is depicted with a grey arrow (nest temperature values are represented by mean weekly records and rainfall is characterised by the accumulated amount during weekly periods).

winter temperatures were as low as 1.3°C and 2.3°C during the 2011–12 season (Table 1).

Discussion

To our knowledge, this is the first study to document hatchling overwintering inside the nest by a chelid turtle and only the second report for turtles of the Southern Hemisphere. The implications of this behaviour relate to evolutionary aspects of nest emergence in long-necked turtles, in addition to the physiology and conservation of this species. Although previous studies have suspected delayed emergence by *C. longicollis* hatchlings on finding freshly emerged hatchlings in wetlands at the beginning of spring (Chessman 1978; Kennerson 1980; Dalem and Burgin 1996), definitive evidence has been lacking. Favourable environmental conditions are needed for females to nest and hatchlings to emerge from the nest, with sometimes a considerable time gap between the two events. This gap can be bridged in Australian turtles by either early embryonic diapause such as in *Chelodina expansa* (Goode and Russell 1968; Booth 2002) and *Chelodina rugosa* (Kennett *et al.* 1993a, 1993b), late embryonic aestivation, as described in *Carettochelys insculpta* (Doody *et al.* 2001), or by delayed hatchling emergence from the nest in *C. longicollis* over the winter (this study).

Current research indicates that overwintering of hatchlings inside the nest can be quite variable among and within populations

(Costanzo *et al.* 2008; Gibbons 2013; Lovich *et al.* 2014; Riley *et al.* 2014), even including differences in timing of nest emergence among siblings sharing the same nest (see Costanzo *et al.* 2008). Research attempting to elucidate mechanisms and environmental cues responsible for intrapopulation variation in hatchling overwintering inside the natal nest are scarce (Riley *et al.* 2014). Some evidence suggests that environmental factors such as nest temperature, nest slope, percentage of bare ground surrounding the nest, and risk of predation by sarcophagid fly larvae may influence overwintering strategy in painted turtle hatchlings (Riley *et al.* 2014). Despite our limited sample size, we have evidence that *C. longicollis* can exhibit a dichotomous hatchling overwintering strategy within the same population, though we have no conclusive information on possible triggers and environmental conditions that affect these variable responses. For example, temperatures inside overwintering nests tend to be cooler than in non-overwintering nests (Riley *et al.* 2014), but we found an opposite result, with mean temperatures higher for the overwintering nest up to the time of emergence in the non-overwintering nest. We also observed hatchling overwintering in the nest in each year of the study (2011–14) but, interestingly, such behaviour was not reported in a previous investigation in the same region, where only autumn emergence was documented (Vestjens 1969). Such findings suggest that hatchling overwintering in *C. longicollis* may vary among years, as reported for other species (Lovich *et al.* 2014). In addition, further research

is needed to evaluate whether the effect of drought–flood cycles in the Australian environment could influence responses of hatchling overwintering in chelid turtles, as there is evidence that rainfall and cool temperatures play a role in delayed emergence by hatchling turtles (Lovich *et al.* 2014).

The incubation period of 125 days for *C. longicollis* that did not overwinter was in the range reported by others (Vestjens 1969; Parmenter 1985). The extended period inside the nest by *C. longicollis* hatchlings that overwintered (incubation plus overwintering = 320 days, on average) is similar to the period experienced by species in the Northern Hemisphere (Gibbons and Nelson 1978; Costanzo *et al.* 1995; Wilson *et al.* 1999; Gibbons 2013), but temperatures experienced inside the nest during winter in our study were milder than those in the USA and Canada (Packard 1997; Costanzo *et al.* 2000a; Riley *et al.* 2014). North American turtle hatchlings use physiological mechanisms, such as supercooling, to tolerate freezing temperatures (Costanzo *et al.* 2000b; Packard and Packard 2005), though further investigation would be necessary to investigate whether *C. longicollis* performs such physiological mechanisms. While our nests did not experience freezing temperatures, *C. longicollis* populations elsewhere in more southerly locations, higher elevations and colder climates would likely have to cope with freezing (e.g. winter temperatures as low as -13.9°C at the Cooma Airport Weather Station, Australian Bureau of Meteorology: Dunsmore 1966).

Previous studies have detailed the importance of terrestrial habitats for numerous aspects of the behaviour and population dynamics of *C. longicollis* (Roe and Georges 2008a, 2008b; Rees *et al.* 2009). Hatchling overwintering is yet another critical aspect of ecology that occurs in terrestrial environments. Consequently, hatchlings may be vulnerable while in the nest to terrestrial disturbances outside of typical activity periods, such as changes in soil management practices, in addition to increased risk of predation by invasive predators, such as foxes (*Vulpes vulpes*) (Thompson 1983; Spencer *et al.* 2006) and fire ants (*Solenopsis invicta*) (Gibbons 2013).

Overwintering in the nest was once thought to be an unusual phenomenon observed in only a few North American turtle species, but after extensive research it is now believed to be a much more common behaviour in many species worldwide (Gibbons 2013). Our findings of a chelid species engaging in this behaviour increases our knowledge of the phylogenetic range of turtles exhibiting hatchling overwintering behaviour, and we suspect that this should also occur in other chelid species inhabiting temperate regions of South America and Australia. Further studies are needed to investigate whether hatchling overwintering in the nest is more widespread in *C. longicollis* (Chessman 1978; Kennerson 1980; Dalem and Burgin 1996) and other species of long-necked turtles, in addition to the environmental context in which it occurs.

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References

- Bager, A., Fagundes, C. K., and Piedras, S. R. N. (2007). *Trachemys dorbignyi* (Brazilian slider). Hatchling overwintering. *Herpetological Review* **38**, 335–336.
- Booth, D. T. (2002). The breaking of diapause in embryonic broad-shell river turtles (*Chelodina expansa*). *Journal of Herpetology* **36**, 304–307. doi:10.1670/0022-1511(2002)036[0304:TBODIE]2.0.CO;2
- Buhlmann, K. A., Congdon, J. D., Gibbons, J. W., and Greene, J. L. (2009). Ecology of chicken turtles (*Deirochelys reticularia*) in a seasonal wetland ecosystem: exploiting resource and refuge environments. *Herpetologica* **65**, 39–53. doi:10.1655/08-028R1.1
- Chessman, B. C. (1978). Ecological studies of freshwater turtles in southeastern Australia. Ph.D. Thesis, Monash University, Melbourne.
- Costanzo, J. P., Iverson, J. B., Wright, M. F., and Lee, R. E. Jr (1995). Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. *Ecology* **76**, 1772–1785. doi:10.2307/1940709
- Costanzo, J. P., Litzgus, J. D., Iverson, J. B., and Lee, R. E. Jr (2000a). Ice nuclei in soil compromise cold hardiness of hatchling painted turtles (*Chrysemys picta*). *Ecology* **81**, 346–360. doi:10.1890/0012-9658(2000)081[0346:INISCC]2.0.CO;2
- Costanzo, J. P., Litzgus, J. D., Iverson, J. B., and Lee, R. E. Jr (2000b). Seasonal changes in physiology and development of cold hardiness in the hatchling painted turtle *Chrysemys picta*. *The Journal of Experimental Biology* **203**, 3459–3470.
- Costanzo, J. P., Lee, R. E. Jr, and Ultsch, G. R. (2008). Physiological ecology of overwintering in hatchling turtles. *The Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* **309A**, 297–379. doi:10.1002/jez.460
- Dalem, A. A. G., and Burgin, S. (1996). Possible overwintering on land by hatchling *Chelodina longicollis*. *Herpetofauna* **26**, 14–15.
- Doody, J. S., Georges, A., Young, J. E., Pauza, M. D., Pepper, A. L., Alderman, R. L., and Welsh, M. A. (2001). Embryonic aestivation and emergence behaviour in the pig-nosed turtle, *Carettochelys insculpta*. *Canadian Journal of Zoology* **79**, 1062–1072. doi:10.1139/z01-061
- Dunsmore, J. D. (1966). Nematode parasites of free-living rabbits, *Oryctolagus cuniculus* (L.), in eastern Australia. I. Variation in the number of *Thichostrongylus retortaeformis* (Zeder). *Australian Journal of Zoology* **14**, 185–199. doi:10.1071/ZO9660185
- Georges, A., and Adams, M. (1992). A phylogeny for Australian chelid turtles based on allozyme electrophoresis. *Australian Journal of Zoology* **40**, 453–476. doi:10.1071/ZO9920453
- 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**, 203–214. doi:10.1670/12-122
- Gibbons, J. W., and Nelson, D. H. (1978). The evolutionary significance of delayed emergence from the nest by hatchling turtles. *Evolution* **32**, 297–303. doi:10.2307/2407597
- Goode, J., and Russell, J. (1968). Incubation of eggs of three species of chelid tortoises, and notes on their embryological development. *Australian Journal of Zoology* **16**, 749–761. doi:10.1071/ZO9680749
- Kennerson, K. J. (1980). Notes on hatchling *Chelodina longicollis* (Shaw). *Herpetofauna* **11**, 27–28.
- Kennett, R., Christian, K., and Pritchard, D. (1993a). Underwater nesting by the tropical freshwater turtle, *Chelodina rugosa* (Testudinata: Chelidae). *Australian Journal of Zoology* **41**, 47–52. doi:10.1071/ZO9930047
- Kennett, R., Georges, A., and Palmer-Allen, M. (1993b). Early developmental arrest during immersion of eggs of a tropical freshwater turtle, *Chelodina*

- rugosa* (Testudinata: Chelidae), from northern Australia. *Australian Journal of Zoology* **41**, 37–45. doi:10.1071/ZO9930037
- Kennett, R., Roe, J., Hodges, K., and Georges, A. (2009). *Chelodina longicollis* (Shaw 1784) – eastern long-necked turtle, common long-necked turtle, common snake-necked turtle. In 'Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group'. Chelonian Research Monographs No. 5. (Eds A. G. J. Rhodin, P. C. H. Pritchard, P. P. Van Dijk, R. A. Saumure, K. A. Buhlmann, J. B. Iverson, and R. A. Mittermeier.) pp. 031.1–031.8. (Chelonian Research Foundation: Lunenburg, MA.)
- Lovich, J. E., Ernst, C. H., Ernst, E. M., and 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 Monograph* **28**, 93–109. doi:10.1655/HERPMONOGRAPHS-D-14-00001
- Mitchell, J. C. (1988). Population ecology and life histories of the freshwater turtles *Chrysemys picta* and *Sternotherus odoratus* in an urban lake. *Herpetological Monograph* **2**, 40–61. doi:10.2307/1467026
- Muldoon, K. A., and Burke, R. L. (2012). Movements, overwintering, and mortality of hatchling diamond-backed terrapins (*Malaclemys terrapin*) at Jamaica Bay, New York. *Canadian Journal of Zoology* **90**, 651–662. doi:10.1139/z2012-032
- Packard, G. C. (1997). Temperatures during winter in nests with hatchling painted turtles (*Chrysemys picta*). *Herpetologica* **53**, 89–95.
- Packard, M. J., and Packard, G. C. (2005). Patterns of variation in glycogen, free glucose and lactate in organs of supercooled hatchling painted turtles (*Chrysemys picta*). *The Journal of Experimental Biology* **208**, 3169–3176. doi:10.1242/jeb.01743
- Parmenter, C. J. (1985). Reproduction and survivorship of *Chelodina longicollis* (Testudinata: Chelidae). In 'Biology of Australasian Frogs and Reptiles'. (Eds G. Grigg, R. Shine, and H. Ehmman) pp. 53–61. (Royal Society of New South Wales: Sydney.)
- Paterson, J. E., Steinberg, B. D., and 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**, 408–418. doi:10.1071/WR12039
- Rees, M., Roe, J. H., and Georges, A. (2009). Life in the suburbs: behavior and survival of a freshwater turtle in response to drought and urbanization. *Biological Conservation* **142**, 3172–3181. doi:10.1016/j.biocon.2009.08.019
- Riley, J. L., Tattersall, G. J., and Litzgus, J. D. (2014). Potential sources of intra-population variation in the overwintering strategy of painted turtle (*Chrysemys picta*) hatchling. *The Journal of Experimental Biology* **217**, 4174–4183. doi:10.1242/jeb.111120
- Roe, J. H., and Georges, A. (2008a). Maintenance of variable responses for coping with wetland drying in freshwater turtles. *Ecology* **89**, 485–494. doi:10.1890/07-0093.1
- Roe, J. H., and Georges, A. (2008b). Terrestrial activity, movements and spatial ecology of an Australian freshwater turtle, *Chelodina longicollis*, in a temporally dynamic wetland system. *Austral Ecology* **33**, 1045–1056. doi:10.1111/j.1442-9993.2008.01877.x
- Roe, J. H., Rees, M., and Georges, A. (2011). Suburbs: dangers or drought refugia for freshwater turtle populations? *Journal of Wildlife Management* **75**, 1544–1552. doi:10.1002/jwmg.219
- Seddon, J. M., Georges, A., Baverstock, P. R., and McCord, W. (1997). Phylogenetic relationships of chelid turtles (Pleurodira: Chelidae) based on mitochondrial 12S rRNA gene sequence variation. *Molecular Phylogenetics and Evolution* **7**, 55–61. doi:10.1006/mpev.1996.0372
- Spencer, R. J., Janzen, F. J., and Thompson, M. B. (2006). Counterintuitive density-dependent growth in a long-lived vertebrate after removal of nest predators. *Ecology* **87**, 3109–3118. doi:10.1890/0012-9658(2006)87[3109:CDGIAL]2.0.CO;2
- Thompson, M. B. (1983). Populations of the Murray River tortoise, *Emydura (Chelodina)*: the effect of egg predation by the red fox, *Vulpes vulpes*. *Australian Wildlife Research* **10**, 363–371. doi:10.1071/WR9830363
- Ultsch, G. R. (2006). The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biological Reviews of the Cambridge Philosophical Society* **81**, 339–367. doi:10.1017/S1464793106007032
- Vestjens, W. J. M. (1969). Nesting, egg-laying and hatching of the snake-necked tortoise at Canberra, ACT. *Australian Zoologist* **15**, 141–149.
- Webster, R., and Butler, B. E. (1976). Soil classification and survey studies at Ginninderra. *Australian Journal of Soil Research* **14**, 1–24. doi:10.1071/SR9760001
- Wilson, D. S., Mushinsky, H. R., and McCoy, E. D. (1999). Nesting behaviour of the striped mud turtle, *Kinosternon baurii* (Testudines: Kinosternidae). *Copeia* **1999**, 958–968. doi:10.2307/1447971

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