

Additional observations of nesting behaviour in the Johnstone River Snapping Turtle *Elseya* sp.

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Abstract

I report data on clutch size, nest size, the times taken to complete nesting stages and a description of nesting behaviours of 17 wild Johnstone River Snapping Turtles *Elseya* sp. based on observations spanning ten years. Clutch size ranged from 3 to 15 eggs, the nest opening was essentially circular (60 mm diameter), vertical nest depths ranged from 100 to 210 mm, egg laying times from 3 to 17 minutes, and nest filling-in times from 13 to 48 minutes. Excavation times were always the longest stage of the nesting process (> 1 hr), although few complete times were obtained. There was no relationship between clutch size and either egg-laying times nor nest filling-in times. A few nesting females used their knees (as well as the feet) to compact soil (n = 4) and also the plastron to flatten the soil surface during the filling in of nests (n = 3). Eggs with impact fractures were uncommon (6% of clutches) and in nearly all instances fractures were due to embedded stones in the wall of the egg chamber. I observed two instances where the entire nesting process was completed, including back-filling the nest, yet no eggs were laid.

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Introduction

The Johnstone River Snapping Turtle *Elseya* sp. is a relatively large freshwater turtle confined to the Johnstone River catchment of the Wet Tropics region of north Queensland where it is common but patchy in its distribution (Cann 1998; Turner 2006; O'Malley 2007; Freeman 2018). It is closely related to Irwin's Turtle *Elseya irwini* and regarded by some authors as conspecific (e.g. Georges & Thompson 2010; Cogger 2014) while others consider it a separate species (e.g. Cann & Sadlier (2017) as *Elseya stirlingi*); I refer to it hereafter as simply Johnstone River *Elseya* sp. I have described the nesting behaviour of *Elseya* sp. previously (Turner 2004), based on the observation of seven females. The nesting process comprised six stages: emergence from the water, selection of a nest site, excavation of the nest, egg deposition, filling-in the nest and returning to the water, behaviours that are typical of other Australian freshwater turtles

and freshwater turtles generally (Ehrenfeld 1979; Cann 1998; Booth 2010). This study contains quantitative data from an additional 17 nesting events, an elaboration of the behaviours exhibited during some nesting stages, and a description of several novel nesting behaviours.

Methods

The nesting events described below were recorded between 2004-2010 inclusive. Nest sites were located on small islands, the banks of anabranches, the main flow and several tributaries of the North Johnstone River approximately 12 km west of Innisfail (146°01'E, 17°32'S). The main flow consisted of large pools separated by riffle zones and rapids. Nesting is triggered by rain (typical of many Australian chelids; Cann 1998; including the Gulf Snapping Turtle *Elseya lavarackorum* – Freeman 2010) and occurred on wet evenings

from late May through to July any time after nightfall (> 7 pm) through to the early hours of the morning. A 55 Watt quartz-halogen spotlight connected to a 12 V battery was used to locate turtles initially and then a switch was made to a LED headlamp. Observation of females while nesting was from the rear (at a distance of about 0.5 m) where a clear view of the nesting process was possible. Flash photography was used to capture some stages of nesting in three of the females (to minimise the possibility of disturbance) and this did not appear to disrupt nesting. The following measurements of nest dimensions were made (to the nearest 5 mm) where possible: nest opening, which was nearly circular (see below) and so two diameters (at right-angles to each other) were measured at ground level, the slanted nest depth (from the surface opening to the bottom of the egg chamber) and vertical nest depth (from the surface directly above the nest chamber to the bottom of the chamber). The dimensions of the nest opening were carefully made as the turtle nested (usually during pauses when excavating the egg chamber) by placing a small stainless steel ruler on the ground close to the opening. The slanted nest depth was measured at the completion of nest excavation when possible, by inserting a straight length of thin dowel to the bottom of the egg chamber and marking the point where it was level with the ground. The vertical nest depth was often unable to be measured while turtles' nested but was measured from partially depredated nests (i.e. nests with some eggs still in situ). Clutch size was recorded by counting eggs as they were deposited into the nest by the female. The following times were recorded during the nesting process: (i) time taken to excavate the nest, (ii) time between the laying of the first and last egg, and (iii) time taken to cover-up the nest (from the time soil was first deposited into the nest to when the turtle left the nest). Relatively few excavation times were recorded because I was not usually present at the start of the process. Care was taken to minimise disturbance of nesting females and of completed nests and for this reason data collection was often incomplete. On evenings when turtles were nesting, several 'sweeps' were made of the nest site and the various activities of all observed females were recorded using the following categories: moving-up stream, in shallows with

snout/head out of water, active out of water, excavating the nest, egg-laying, filling-in the nest and returning to the water. Given the randomness of observer arrival times to the nesting sites, and the variation of localised weather conditions effecting the movement of females, the cumulative frequencies obtained by pooling this frequency data over all nesting evenings was used as an independent measure of the relative duration of each activity. Follow-up observations of some nests were made with predated and partially predated nests commonly seen in the days following nesting events and these provided additional information about the nest structure and clutch size.

Observations

While my reported data relates primarily to the observations of 17 nesting events (Table 1), a total of 30 females were observed to complete nesting and were part of more than 70 females observed in various stages of nest construction, albeit, only in part.

Sensitivity to disturbance

Females were observed to abandon nesting attempts at any stage prior to the commencement of egg-laying due to disturbance, though this rarely occurred once excavation was well advanced (i.e. nests were more than half the maximum depth) and never during egg-laying or covering-up ($n = 36$). Females were most prone to disturbance when searching for a nest site and during the early stages of excavation of the nest and their usual reaction was to return to the water ($n = 8$), although in several instances the females moved less than 10 m away and nested. When approached during either of these stages, females would typically cease moving and remain absolutely still ($n \approx 40$). Those females that had commenced excavation would typically sit motionless with one rear limb in the nest and the other on the surface. If females did not resume nesting activity within 10 minutes, then they would invariably abandon the attempt and leave the nest soon after the perceived danger had passed ($n = 11$). As well as depending on the nesting stage, sensitivity to disturbance seemed to depend to some extent on the weather conditions, with disturbance much less likely during very wet conditions that stimulated large numbers of females to nest. Females who laid eggs were observed to depart nest sites by walking slowly in a

Table 1. Data on clutch size and duration of nesting stages in the Johnstone River Snapping Turtle *Elseya* sp. The date, clutch size, and duration of nesting stages of 17 female *Elseya* sp. observed nesting on the banks of the North Johnstone River over the period 2004-2010 (inclusive). Mean values are given in the last row.

Female #	Date	Clutch size	Excavation time (min)	Egg-laying time (min)	Filling-in time (min)
1	23/6/04	10	66	14	28
2	15/6/04	9	> 30	9	24
3	1/7/04	13	–	5	23
4	22/7/04	14	64	16	30
5	23/7/04	5	–	<10	32
6	1/6/05	5	–	12	13
7	1/6/05	12	> 30	10	26
8	4/7/05	5	–	4	48
9	5/7/05	5	–	15	24
10	18/6/06	10	–	12	13
11	18/6/06	10	–	10	18
12	17/6/07	9	> 20	8	16
13	17/6/07	7	> 30	3	30
14	7/7/08	15	–	17	35
15	15/7/08	8	–	–	31
16	26/5/09	4	–	<10	26
17	22/6/10	5	> 65	4	–
Mean		8.6	65.0	9.9	26.1

more or less direct line towards the water (instead of scurrying which is employed when fleeing over land) indicating that the presence of an observer did not unduly affect the behaviour of the female during or at the completion of nesting.

The nesting stages

From direct observations of turtles nesting, excavation times generally exceeded one hour and were the longest stage of the nesting process, followed by the covering-up of the nest and then egg-laying which was always the shortest (see Table 1; also Turner 2004). The proportion of time spent during the three nesting stages from Table 2 were in close agreement with the proportions obtained by direct observations (using the average times) in Table 1: excavating (70% vs 64%), egg-laying (7% vs 10%) and covering-up (24% vs 26%). The transition from one nesting stage to another was in all instances very brief (< 3 mins), with the cessation of egg-laying and commencement of

filling-in being less than a minute in some instances (n = 8; see Booth (2010) for similar comments).

Nest excavation & substrate type

Nest excavation in *Elseya* sp. is a repetitive and stereotypical nesting stage in which the rear limbs are used alternately to remove soil by cupping the feet and in the process two small mounds of soil are created on the ground at the rear of the carapace as is typical for freshwater turtles (Turner 2004; Booth 2010). The rate at which the female digs is not constant but rather steadily declines as the nest depth increases and as the female presumably becomes more fatigued, resulting in pauses of up to 2 minutes towards the end of that nesting stage (n > 9). Substrates used for nesting were essentially either sand or clay (or mixtures thereof; see Table 3) with a small number females nesting in flood debris (a mixture of decaying vegetation and silt). There was no evidence to indicate a preference by females for particular

Table 2. Number of female Johnstone River Snapping Turtles *Elseya* sp. engaged in each nesting stage.

Total number of female *Elseya* sp. engaged in each nesting stage from the North Johnstone River during 2001-2010 seasons. Frequencies represent the cumulative number of females engaged in each activity over all nesting evenings.

Activity	Moving upstream	In shallows	Active out of water	Excavating nest	Egg-laying	Filling-in nest	Returning to water
Frequency	19	73	89	53	5	18	9

Table 3. Nest size, clutch size, and substrate types for nests of the Johnstone River Snapping Turtle *Elseya* sp. Nest dimensions, clutch size, and substrate type of nests made by 19 *Elseya* sp. from the North Johnstone River during 2001-2010 seasons. Slanted nest depth was measured from the surface opening to the bottom of the egg chamber.

Female #	Nest entrance size (both in mm)	Clutch size	Slanted nest depth (mm)	Vertical nest depth (mm)	Substrate type
1	60 × 75	10	150	–	Sandy loam
2	–	9	–	–	Sandy loam
3	–	13	160	–	Sandy loam
4	–	14	210	170	Sandy loam
5	–	5	–	150	Clay
-	65 × 65	5	180	130	Clay
-	55 × 65	12	170	–	Sandy loam
8	65 × 65	5	–	130	Sandy loam
9	55 × 55	5	160	145	Sandy loam
10	–	10	200	–	Sand
11	45 × 55	4	130	–	Sandy loam
12	75 × 80	4	175	–	Sand
13	–	7	–	140	Sand
-	–	12	–	210	Sand
-	65 × 55	4	110	–	Clay
-	55 × 50	8	–	160	Clay-loam
-	–	5	–	170	Loam
-	55 × 60	9	120	–	Loam
-	65 × 60	4	125	–	Clay-loam
-	65 × 70	6	–	130	Flood debris
-	–	6	–	170	Sand
-	65 × 70	11	210	160	Sand
-	50 × 50	8	170	150	Sand
-	55 × 45	6	170	–	Sand
-	70 × 55	3	120	100	Sandy loam
-	65 × 60	4	125	–	Clay-loam
-	–	11	170	135	Sand
-	70 × 55	3	120	100	Sandy-loam
-	60 × 50	5	200	–	Sandy-loam
Mean	61 × 60	7.2	159	147	
N	19	28	20	16	
max.	80	15	210	210	
min.	45	3	110	100	

substrate types (and this is generally true of turtles; Ehrenfeld 1979; Booth 2010). There was insufficient data to compare excavation times in different substrates, although the few excavations observed of females nesting in clay (rather than clay loam) were of longer duration (> 70 mins; $n = 2$) compared to sandy substrates. Substrate hardness affects excavation times in other turtle species (see Booth 2010).

Females would abandon nest excavation on encountering imbedded stones ($n = 6$) but typically moved only a short distance before immediately excavating a second nest (Fig. 1). They did not fill-in the incomplete nests. In one instance, a female that was observed to abandon a nest due to the presence of a large embedded stone, walked around behind the observer (< 1 m), and immediately started excavating a new nest which it completed. Stones were present in $< 5\%$ of all nests observed, including numerous predated nests, but were invariably present in abandoned nests (see below).

The poorer drainage of clay soils sometimes resulted in nests filling with rainwater during excavation; this was not observed in sand or sand-loam soil. One female that nested during persistent heavy rain in clay soil, deposited eggs into a nest that had completely filled with rainwater and then proceeded to fill-in the flooded nest. Upon removal of the nest 'plug' at the completion of nesting, the water in the egg chamber had been absorbed by the surrounding soil.

Clutch size

Clutch size varied from 3 to 15 eggs with an average of 7.3 eggs (Table 1 & 3; cf. mean 9 eggs, $n = 7$; Turner 2004). A positive correlation between egg-laying times and clutch sizes was expected and while this was confirmed, the relationship was weak and not statistically significant ($r = 0.36$, $df = 11$, $P(1\text{-tailed}) = 0.117$). There was no relationship between the time taken to fill in the nest and clutch size ($r = -0.05$, $df = 10$, $P(2\text{-tailed}) = 0.885$).



Figure 1. Abandoned nests of the Johnstone River Snapping Turtle *Elseya* sp.

In the photo are three partially completed and subsequently abandoned *Elseya* sp. nests from a mid-stream island of the North Johnstone River on which a shallow layer of sand overlays stony ground. Large imbedded stones were present in all three nests.

Nest shape and air pockets within the nest

The nest entrance (= shaft) at ground level was essentially circular with mean dimensions 61 × 60 mm (Table 2) and the values of both dimensions combined varied from 45 to 80 mm. The slanted nest depth was always slightly greater than the vertical nest depth because the shaft of the nest was invariably slanted approximately 10 to 40° to the vertical (relative to the ground surface), even if nesting occurred on flat ground. This resulted from females reaching forwards with their rear limbs when excavating the shaft and to an even greater extent when excavating the egg chamber. The reach of the female's rear limbs was achieved by fully extending the front and rear limbs, resulting in the shell tilting down and the rear marginal scutes protruding into the nest opening. As a result, the egg chamber did not lie directly above the shaft but instead was anterior to it (when viewed above from the rear of carapace). Consequently, the filling-in of nests generally resulted in relatively little soil (compared to that excavated) being deposited on top of the eggs, leaving an air pocket between them and the top of the chamber and also air pockets in between adjacent eggs (n = 15).

The manipulation of eggs

The manipulation of eggs by the rear limbs of the female mainly involved the eggs being pushed forward into the egg chamber to make room for additional eggs immediately before they were deposited. Both rear limbs, alternating one at a time, were used to manoeuvre eggs and this occurred up to six times during a nesting event. The manoeuvring of eggs did not occur each time an egg was laid but typically after two or three eggs were laid (n = 14). During egg-laying there was always one rear limb hanging down into the nest until egg-laying was completed. In one instance eggs were not manipulated by the female and the nest was very shallow with a poorly developed egg chamber (despite it being in sand and free from obstructions) with one egg only 4 cm below the ground surface.

Impact fractures and indents occurred during the deposition and manipulation of eggs, but were uncommon (5 of 83 observations; 6%). Damage to eggs during deposition occurred when eggs dropped from the cloaca directly onto imbedded stones (n = 2), while damage to eggs by manipulation occurred when eggs in direct contact with

the wall of the chamber were pushed against imbedded stones or else were pushed against other eggs (n = 3). The damage caused ranged from small, single, indents to large areas of extensive cracking (up to approx. 40% of surface area) but in no instances was the underlying membrane perforated (n = 18). The largest number of eggs with fractured shells recorded in a single clutch was three (in a clutch of seven) and was apparently the result of the eggs being crammed into a small egg chamber lined with stones embedded in firm clay. In all other affected clutches just one or two eggs were damaged. All of the damaged eggs appeared to be viable and were otherwise similar in appearance to other eggs of the same clutch (e.g. had developed opaque patches).

Covering up the nest

Soil was initially scrapped from the walls of the shaft and this fell onto eggs directly below. Soil was then scrapped from the mounds of excavated soil at the rear of the carapace and raked over the eggs by gently pushing with curled toes and without downward pressure being applied. Once several centimetres of soil covered the eggs, pressure was applied by the hind feet in order to compact it. The inner-most part of the rear foot and 'heel' were commonly used to apply pressure to the soil in the shaft (Turner 2004). This 'pressure stand' occurred prior to the soil being levelled-off with the surface and was observed in all instances of nest filling-in (n = 17). On some occasions the pressure stand involved just one foot at a time, while the other foot fanned out to drag both soil and debris over the nest both; at other times both feet were used together and were overlapping, applying pressure to just a small area. Some females stood on the tips of their toes (n = 4) while others were observed to use their knees to compact the substrate (n = 4). Once the soil in the nest was near level with the surrounding ground, females would sweep and drag excavated soil and debris in towards the nest and this sweeping extended further outwards (Fig. 2) as the filling-in progressed, covering an area that in all instances exceeded that which was covered by the excavated soil. In several instances debris was dragged from up to 0.4 m from the nest opening. This was achieved by swivelling the entire carapace to the right and left about a pivot point (at the anterior carapace) thereby extending the reach of the rear limbs to ground where no soil had been deposited.



Figure 2. A nesting Johnstone River Snapping Turtle *Elseya* sp. This female *Elseya* sp. from the North Johnstone River is reaching out with its left rear limb to drag more sand and surface debris over the nest during the filling-in stage.

The angle of the swivel was at least double that when excavating the nest (see Turner 2004). As the rear limbs were stretched-out to gather soil and surface debris, they would 'feel' for material by clenching the toes and sometimes fail to gather anything but nonetheless still completed the same sweeping action.

Plastron 'tapping'

Three females were observed to tap the soil surface repeatedly during the covering-up stage of

nesting. It occurred when the nest had been filled-in and the excavated soil was levelled with the ground. The plastron was quickly lowered flat against the ground six to eight times though not in succession. This was achieved by bending all four legs but was never executed with great force and the contact was not audible; for this reason, it is most accurately described as plastron 'tapping'. In some instances, the plastron was lowered but not quite to ground level ($n > 5$).

Appearance of completed nests

While nests were generally inconspicuous, it was often possible to detect undisturbed nests by visual means within days of nesting having occurred. This was easiest when turtles nested on smooth sandy beaches during light rain with no or little follow-up rain. Under these circumstances, disturbed sand and claw marks from females having 'raked' excavated soil (and other material) over the nest were obvious (Fig. 3). Heavy rain invariably made the visual detection of nests in any substrate more difficult because it smoothed out irregularities on surface, obliterated claw marks, and washed clean the ground vegetation such as grasses that were muddied during the excavation process. Nonetheless there was typically some indication of the ground having been disturbed, such as partially buried leaves and grass stems. After about a week, surface traces of nesting activity typically disappeared due to rain or soil disturbance by other animals, making intact nests difficult to locate (at least by visual means). By this time nests were also severely reduced in number due to predation (Turner, in prep.).

False nests

Two instances of false nesting were recorded, one of which was directly observed.

1. A female (CCL = 245 mm) was observed nesting at 6:50 pm (twilight) on 12/7/04 approx. 1.5 m from the water's edge on a sandy, inclined, bank. It had only just started excavating a nest (< 5 cm depth) and was observed briefly because of the risk of disturbance. When I returned at 7:25 pm she was well advanced in covering-up the nest, with the rear limbs fanning outwards, scrapping sand and a small amount of debris over the nest. It was noted at the time that this nesting had been unusually fast. At 8:07 pm the female left the nest and was intercepted and examined. Palpation of the inguinal pocket indicated the female was still gravid. The nest was excavated only to find that it was shallow (depth 0.10 m) and had no egg chamber or eggs.

2. A second false nest was located on 8/8/04 on a small mound of sand rising just above the flow and 0.5 m from the bank. The surface markings were entirely consistent with other successful nesting attempts and claw marks were clearly visible. The



Figure 3. Completed nest of a Johnstone River Snapping Turtle *Elseya* sp.

A completed *Elseya* sp. nest from the North Johnstone River made the previous evening on a sandy beach. Note the distinctive claw marks towards the edges of the disturbed ground.

nest was shallow (0.10 m depth) with no egg chamber nor eggs. The location of this nest meant there was seepage of water in to it and inundation would have certainly occurred even after moderate rainfall.

Discussion

The observations reported here broaden the behavioural repertoire previously described for nesting in Johnstone River *Elseya* sp. (Turner 2004). The alternating sequence of rear limb use during next excavation is a highly stereotypical behaviour exhibited turtles (Ehrenfield 1979) and seen in all Australian chelids for which nesting has so far been observed (Booth 2010), with one exception (where front legs are used and not always alternately; Kuchling 1993). The presence of one leg in the nest while egg-laying occurs as observed in *Elseya* sp. has been reported in two other species of Australian chelids (Broad-shell River Turtle *Chelodina expansa* and Brisbane River Turtle *Emydura signata*; Booth 2010) and in some instances the leg is used to position the recently deposited eggs, typically moving them forward into the egg chamber. Several species accounts state that the leg is inserted after (or during?) one or several eggs are deposited and then used to position them (e.g. Macquarie River Turtle *Emydura macquari* – Goode 1965; Eastern Long-necked Turtle *Chelodina longicollis* – Curtis 1928; Beck 1991; Green 1997). There was no indication in *Elseya* sp. that the rear limb was used purposefully to cushion the fall of eggs (cf. South-western Snake-necked Turtle *Chelodina colliei* – Russ 1970), though this did occur incidentally on a number of occasions (see also Turner 2004). The reduced tendency for females to abandon a nest as excavation progresses has also been noted in *E. signata* (Booth 2010). Excavation requires a considerable effort by females, as is indicated by their obvious fatigue nearing the end of this stage, and so this may explain why there is reluctance by females to abandon the nesting attempt once this stage is substantially complete or complete. Nests were never abandoned by female *Elseya* sp. during subsequent stages of nesting, presumably because of the effort they have already invested in nest construction. Plastron tapping, patting, stamping or slamming the substrate during the latter stages of filling-in the nest has been observed in other species of Australian turtles (*Emydura macquari* – Goode 1965; *C. longicollis* – Kennerson 1969;

Vestjens 1969; Cann 1978; Hill 1979; Beck 1991; Green 1997; *C. expansa* – Booth 2010; *C. colliei* (as *C. oblonga*) – Russ 1970; Nicholson 1975; Clay 1981) but had not been previously recorded in *Elseya* sp. In contrast to previous reports, plastron tapping in Johnstone River *Elseya* sp. is a gentle process, (the force not exceeding the weight of the female) and certainly could not be described as ‘stamping’ or ‘slamming’ as in other species accounts. Plastron tapping behaviour was observed in relatively few females, so it is not a stereotypical feature of nesting in *Elseya* sp. as it appears to be in *C. longicollis* (Kennerson 1969; Vestjens 1969; Cann 1978; Hill 1979; Beck 1991; Green 1997). In female Johnston River *Elseya* sp. the purpose of plastron tapping appears to be flattening or smoothing the soil surface rather than to compact it. The ‘pressure stand’ described previously in this species (Turner 2004) during the filling-in stage of nesting was observed in all instances and its purpose was clearly to compact the soil in the upper part of the shaft creating a soil ‘plug’.

The length and width of the nest openings recorded in the present study were considerably smaller than the average recorded previously for this species (cf. 99 × 81 mm, n = 8; Turner 2004). The reason for this difference is due to measurements being made during nesting while those in Turner (2004) were the dimensions of the nest after either partial or complete excavation of the nest by predators which tended to enlarge the opening. The slanted nest depths recorded previously for this species (n = 7; Turner 2004) fall within the range of depths reported here. One might expect the slant depth to reflect rear limb length (e.g. Harrington 1933) and hence the female size (i.e., carapace length) but limited data suggests a weak relationship (if any at all) in both instances (G. Turner, unpublished data). Other factors such as clutch size, weather conditions at the time of nesting, and soil characteristics might also influence the slanted nest depth.

The two observations of false nesting are significant because in all other instances that *Elseya* sp. females abandoned a nesting attempt, abandonment was caused by outside disturbance or impediments to digging (i.e. imbedded stones), and there was never any attempt to fill-in the nest. The failure to fill-in abandoned nests is common in Australian chelid turtles (*C. longicollis* – Vestjens 1969; *C. expansa* and *E. signata* – Booth 2010) and

the behaviour makes sense in that the female does not expend extra energy filling in a nest which contains no eggs. From this perspective, false nesting in which the nest is filled-in and the entrance concealed, makes no sense. This behaviour by the female *Elseya* sp. was likely caused by it being aware of my presence but does not explain it. Both instances of false nesting occurred within days of major nesting events and the large size of the females observed indicate that this was not their first nesting season. I am not aware of any other accounts of false nesting in Australian chelids, but this behaviour has been reported in other turtle species. For example, a female Common Snapping Turtle *Chelydra serpentina* nested a second time within a week, on the first occasion depositing eggs but on the second occasion depositing no eggs, but she back-filled the nest as if it contained eggs (Corichi *et al.* 2014).

Observations of eggs being damaged by nesting females, similar to that observed in *Elseya* sp., have also been reported in *C. longicollis* (Vestjens 1969). Vestjens (1969) recorded viable dented eggs, presumably the result of either impacts when deposited or repositioning by the female, and also significant egg mortality with claw punctures in eggs from 60% of nests examined, resulting in egg losses between 8 and 25% per clutch. Claw punctures were not seen in any eggs of *Elseya* sp. which was not surprising given the relatively blunt rear claws of females and the quite thick durable egg shell (pers. obs.).

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