Feeding behaviour, aggregations, and interactions between Johnstone River Snapping Turtles *Elseya* sp.

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Abstract

Field observations of feeding behaviour, aggregations, and individual interactions in adult Johnstone River Snapping Turtles *Elseya* sp. are described. Turtles fed by day on windfall plant debris (leaves, flowers, fruits) at the water's surface especially during the driest months and on filamentous algae and other vegetation on the substrate by day and night year-round. Turtles were recorded feeding on 17 different plant species but were very selective in what they consumed. Significantly more adult females were observed surface feeding compared to males; subadults and juveniles rarely engaged in surface feeding. Some turtles partially or completely emerged from water to seize food items. The nocturnal movement of adult turtles from the river into anabranches during the driest months to feed on algae growing on stones was recorded with some displacements exceeding 150 m in a single night. Adult female aggregations were recorded: (i) feeding beneath flowering and fruiting trees, (ii) in pools adjacent to nesting sites within days or weeks of nesting, (iii) as daytime 'processions' with all females heading in the same direction along the substrate, and (iv) repeatedly in clear shallow pool with minimal cover and no obvious food source. Adult male aggregations were also recorded in the context of feeding on the substrate while mixed-sex aggregations were recorded near in-flows where turtles selectively fed on plant debris washed into pools. Two apparent instances of courtship and one of mating were recorded.

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Introduction

Direct observation of the natural behaviour of freshwater turtles in the wild is often difficult and published observations of the natural behaviour of Australian freshwater turtles largely consists of descriptions of basking, nesting, and overland migration, that is, the behaviour of turtles out of the water (see Cann 1998; Cann & Sadlier 2017). Besides escape behaviour, seldom do field observations describe the natural behaviour of freshwater turtles in the water where most of their time is spent. Two exceptions to this, though not based on turtles in the wild, have been the work of Giles (2005) and Giles *et al.* (2009) who examined the underwater acoustic repertoire of one species in artificial ponds and Schaffer *et al.* (2016) who examined the effects of sedimentation on diving behaviour of turtles in the laboratory.

The Johnstone River Snapping Turtle *Elseya* sp. is a moderately large (to 340 mm carapace length), primarily herbivorous, freshwater turtle inhabiting the Johnstone River catchment of Wet Tropics region of north Queensland (Cann 1998; Turner 2006; O'Malley 2007; Freeman 2018). While the species' occurrence within the catchment has long been known, its distinctiveness has not been supported by genetic data and so it has been regarded by some authors as a disjunct population of Irwin's Turtle *Elseya irwini* (Georges & Thompson 2010; Cogger 2018), a species found in the Burdekin River drainage almost 300 km further south (Cann 1998). There has also been nomenclatural instability, with its description as a distinct species (*Elseya stirlingi*) and subsequent recognition (e.g., Cann & Sadlier 2017, Wilson & Swan 2021, Wilson 2022) or rejection (e.g., Iverson *et al*. 2001, Cogger 2014) of this name (see discussion in Cann & Sadlier (2017), pp. 172-173). I refer to it herein as *Elseya* sp.

Elseya sp. spend much of their time on the substrate of pools and flows, mostly engaged in feeding, and are occasionally seen at the surface and basking on rocks and logs; adults are both diurnal and nocturnal while immatures are strictly diurnal and remain concealed at night (Turner 2006; O'Malley 2007). Adult females attain significantly larger sizes than males (Turner 2006; O'Malley 2007). Nesting, diet, movements, general behaviour, and some aspects of the species' ecology have been reported (Cann 1998; Turner 2004, 2006; O'Malley 2007; Freeman & Curran 2009, 2010; Freeman 2012, 2018; Freeman *et al.* 2018; Turner 2020) but beyond this the behavioural repertoire of individuals and their interactions with each other remain unknown.

Field observations of *Elseya* sp. (and freshwater turtles generally) engaged in natural behaviour are difficult for several reasons: (i) their timid nature, which either results in turtles retreating or else the cessation of movement or normal activity when approached by observers, (ii) turbid water that limits the observer visibility, (iii) clear water, combined with acute vision, that enables turtles to see observers both in, and to some extent, out of the water, and (iv) potential hazards to observers from other organisms in the water (in the case of *Elseya* sp., Estuarine Crocodiles *Crocodylus porosus* and to a lesser extent, Bull Sharks *Carcharhinus leucas*; pers. obs.).

In this work observations of feeding behaviour, occurrence of aggregations, and interactions between wild adult *Elseya* sp. are described.

Methods

The observations described below occurred intermittently between 2001–2015 (inclusive), most prior to 2010. They were obtained by direct observation from elevated banks, trees overhanging pools and flows, and in some cases by snorkelling in pools and flows. When viewing turtles from banks, polaroid sunglasses were frequently used even on overcast days to reduce the surface reflection enabling turtles to be viewed more clearly. Binoculars (7 × 35 wide-angle) were also employed when circumstances permitted. Turtles were sensitive to movements occurring in the water and on the banks, usually retreating at the slightest disturbance. Those at (or near) the water's surface would immediately descend to the substrate while those on the substrate in clear water would typically retreat into deeper water. Observation therefore required minimal movement and some degree of concealment for turtles to engage in anything besides escape behaviour. Turtles were observed at night in shallow water with the aid of a spotlight or a headlamp and tended to be less inclined to flee, sometimes continuing their natural behaviour despite artificial light. Most observations relate to adult turtles because juveniles, due to their small size, were very difficult to observe underwater from a distance (i.e., from banks). They were easily observed at the surface and some were also able to be observed going about their natural behaviour on the substrate when snorkelling.

During observations the following details were recorded: number of turtles, their size (adult, subadult or juvenile), sex, type of behaviour(s), location in the water (surface, column or substrate), and in the case of feeding, the food item identified to species level where possible. Plant identifications were made using DNRM (2001), Cooper & Cooper (2004), and the Australian Tropical Rainforest Plants (2010) website. Water depths to 1.5 m were measured using a 2 m long wooden rod with 0.1 m gradations and greater depths usually estimated to the nearest 0.3 m. Lengths of objects < 1 m were measured with flexible steel tape measure to the nearest centimetre; larger distances up to 10 m were estimated to the nearest 0.5 m. Separate observation periods were treated as independent samples even though some instances repeated observations of individual turtles occurred. The justification for this is that sampling was spread out over time and occurred at widely separated sites along river and several tributaries. The term 'feeding' as used below includes the associated foraging or searching behaviour. An 'aggregation' is defined as a temporarily stable gathering of more than two turtles, sufficiently close as to be aware of (at least) one other's presence. This definition precludes brief chance encounters of multiple individuals and courtship activity involving just a male and a female. Adult females and males were readily distinguished by their size (females being significantly larger than males) and by males having longer thicker tails than females (Turner 2006; O'Malley 2007). The sex of subadult and juvenile turtles could not generally be determined due to the lack of these secondary sexual characters.

Counts of female and males feeding were compared to the 'known' sex ratio using the Chi-squared (χ^2) statistic. This statistic was also computed in the analysis of 2×2 contingency tables along with the odds ratio. The sex ratio (M:F) of Australian chelids is typically close to 1:1 (Georges *et al.* 1993) and upland populations of *Elseya* sp. exhibit this ratio (Freeman 2018), however, O'Malley (2007) found it to be skewed in favour of females (1:1.93) overall in lowland populations. Hamann *et al.* (2004) also found geographic variation in the sex ratio of congener *E. albagula* (Southern White-throated Snapping Turtle, as *Elseya* sp. [Burnett]). Given this inconsistency, counts were compared to both the 1:1 and 1:2 sex ratios. The binomial distribution was used to compute the probability of observing successive encounters with females (with p = ½ or ⅔ depending on the assumed sex ratio).

Sites

Observations were confined to lowland (< 80 m asl) sections of the main flow, anabranches, and some large tributaries of the North Johnstone River near Innisfail (146°01'E, 17°32'S). This tropical river has a strong perennial flow with large pools interspersed by riffle zones, rapids, and islands of various sizes. Water quality in the Johnstone River and its tributaries varies greatly over the course of the year, the main determinant of this being rainfall. During the wet season, which generally spans January to March (inclusive but wet conditions often extend through to July, though with reduced rainfall totals), the lower reaches of the river are often very turbid with strong flows carrying sediment laden run-off; this condition is seen at other times of the year when intense down-pours occur. Turbidity is typically lowest in the latter part of year, from about August through to December when rainfall is least. In sections of the river where observations occurred, it traverses World Heritage rainforest and in the lower reaches is fringed with riparian vegetation which forms a narrow corridor, with land above the river valley used for agriculture (mainly bananas, sugar cane, and cattle).

Observations

A total of 242 separate visits, both by day and by night, to 12 different sites along the North Johnstone River and nine tributaries resulted in more than 550 separate observations of turtles being made. While most turtles were observed to occur singly, 63 turtle aggregations were recorded, all involving adults (a few with subadults) and most of these were single-sex (85%); of these single-sex aggregations 70% were all-female.

Feeding behaviour

Almost all turtles seized food items when in the water, with small items consumed immediately where they were encountered and larger items seized at the surface, or in the water column, and then consumed on the substrate (Table 1).

(i) Surface feeding – Previous observations of *Elseya* sp. indicated that they rarely engaged in surface activity, nor did they regularly occupy the water column but instead were most likely to be encountered on the substrate (Turner 2006). While observations from the current study have confirmed this, it is clear the species does engage in surface feeding on occasions. Surface feeding was most often observed when water levels were low, and surface (plant) debris was common due to riparian tree species shedding leaves and producing flowers and/or fruit (Fig. 1). Surfacing feeding was only ever observed during the day.

There was a significant bias in the sex and size of individuals observed surface feeding, most being adult females (90%). Males were only occasionally seen surface feeding (9%) while immature turtles were rarely seen (1%; χ^2 = 50.36, 1df, P < 0.001; Table 2). Surface feeding was observed when surface debris was common and rarely when it was not (2×2 contingency table: χ^2 = 25.83, 1df, P < 0.0001); overall surface feeding was 23 times more likely to occur when surface debris was present than when it was not.

Table 1. Food items consumed by Johnstone River Snapping Turtles *Elseya* sp. A description of the feeding behaviour and circumstances is given. The number of separate observations (separate days) is denoted by *n*.

Food item	*n*	Description
River Cherry *Syzygium tierneyanum* fruits and inflorescences	4	Between 5-8 females were observed consuming floating fruits and inflorescences beneath over-hanging trees by day at the surface (n = 2); fruits were consumed on the substrate one after the other by a female and a male.
Leichhardt Tree *Nauclea orientalis* flowers	2	Both observations involved all-female aggregations (of 3 and 10 individuals resp.) beneath trees overhanging pools. Trees had nearly completed flowering and disintegrating flowers had fallen onto the water's surface. Females slowly swam just below the surface, breaching it to consume parts of the inflorescences. Occasional gusts of wind dislodged flowers and the 'rain' of debris hitting the water attracted the attention of nearby females who quickly swam towards disturbances and occasionally consumed items (see Fig. 3).
Plentiful Fig *Ficus copiosa* fruits	1	Two females were observed by day walking and swimming in clear shallow water (depth 0.1 - 0.3 m) immediately below a fruiting tree; there were no fruits in the water, but wind gusts dislodged fruits which were immediately seized and consumed by females in deeper water.
Red Satinash *Syzygium apodophyllum* fruits	1	A female was consuming submerged and floating fruits in small shallow pool (depth 0.2 m) by day containing large numbers of these fruits (10–15 mm diameter).
October Glory Vine *Faradaya splendida* fruits and inflorescences	3	Individual females were observed feeding on floating fruits which were 2–3 times the size of their head; fruits proved difficult to grasp and two methods were employed: (i) fruits were charged at side-on with open mouth, and (ii) fruits were gently approached from below with an open mouth. A subadult female was observed consuming flowers floating on the surface also.
Water Gum *Tristaniopsis exiliflora* leaf petioles	> 50	Individual females were surface feeding by day on floating leaves, nipping-off and consuming only the petioles.
Variegated Fig *Ficus variegata* and *Ficus* spp. leaves & fruits	>30	Individual females at the surface consumed portions of green leaves while others were seen consuming fruits that had sunk to the substrate.
Blue Quandong *Elaeocarpus grandis* fruits	5	Females consumed both floating and submerged fruits by day; males consumed submerged fruits also.
Guava *Psidium guajava* leaves	1	A female consumed green leaves in their entirety while surface feeding.
Black Bean *Castanospermum australe* nuts	6	Both adult males and females were observed feeding on submerged nuts in shallow water by day (n = 4) and night (n = 2).
Mueller's Damson *Terminalia muelleri* fruits	2	Fruits were observed being consumed by three adult females on the substrate.
Brown Walnut *Endiandra montana* fruits	5	Females were seen consuming portions of these fruits on the substrate

Table 2. Numbers of female and male Johnstone River Snapping Turtles *Elseya* sp. engaged in surface and substrate feeding. Numbers represent the totals from separate days of observations and include repeated sightings of individuals (from different days).

Feeding Location	Number of Males	Number of Females
Surface	18	178
Substrate (by day)	27	71
Substrate (by night)	110	184

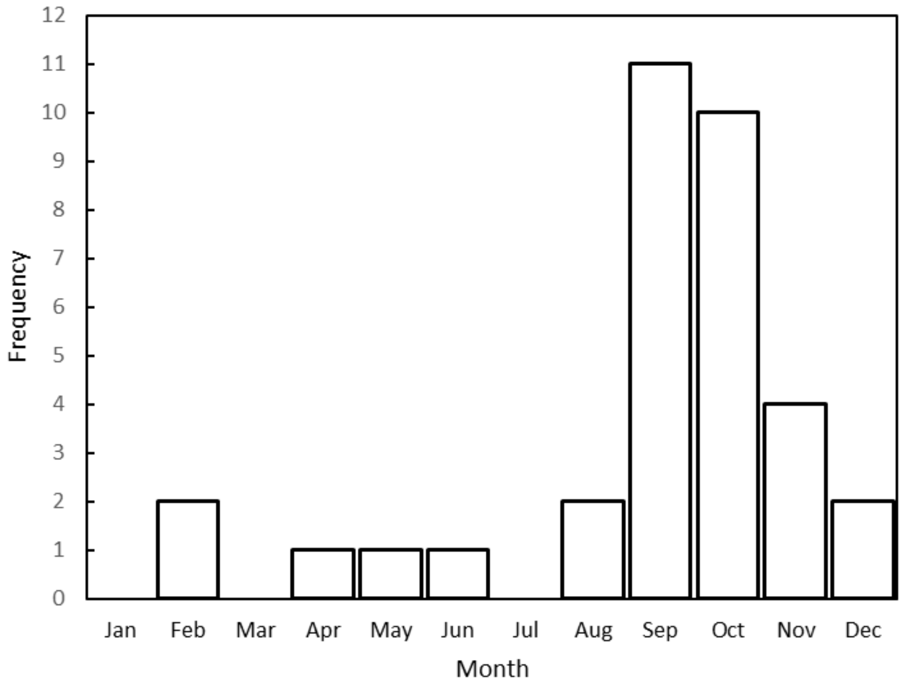

Figure 1. Frequency distribution of surface feeding in the Johnstone River Snapping Turtle *Elseya* sp. throughout the year. Frequencies represent the number of days that at least one turtle was observed surface feeding (n = 34).

A variety of fruits, inflorescences and small leaves or leaf portions were consumed at the surface (Table 1). As surfacing feeding was most often observed in females (Table 1), what follows is a description of the general pattern of surface feeding in females. They were observed to swim slowly at, or just below the surface, in broad arcs, sometimes repeatedly intersecting their own paths with no apparent pattern to their movements. Turtles were not always attracted to items closest to them and given that surface debris was often common and scattered, they would encounter it irrespective of what direction they moved in. Feeding occurred across the entire surface of pools, right-up to the water's edge. Their attention was drawn to small accumulations of floating leaves or other items which turtles would 'inspect'. When a large item was seized, they would sink to the substrate and then consume portions of it (see below). Both forelimbs were frequently used to assist with the consumption of large items. Leaves, for example, were grasped in the mouth, and then one or both forelimbs were used to stabilise the leaf against which an opposing force was applied by the head to detach a portion for consumption. Some females were observed skimming the surface with mouth slightly agape, consuming small (unidentifiable) items (n = 5). When surface feeding, turtles would swim gently just below the surface, occasionally pausing to breach the surface with the snout, moving from item to item. More rapid and clearly directed movements occurred when a breeze or wind gust displaced large quantities of debris from trees, causing a flurry of activity as turtles swam quickly, from one piece of debris to the next, 'inspecting' each item, and then either consuming or rejecting it (see below). Turtles were frequently attracted to the sound of fruits as they hit the water from overhanging trees (n > 30) and to similar sounds made by fish (Jungle Perch *Kuhlia rupestris* and Sooty Grunters *Hephaestus fuliginosus*) as they breached the surface to feed. The turtles' reaction to these sounds was to move in the direction of the source and this was observed to occur in both turbid and clear water even when turtles were not facing the direction of the sound.

Turtles were selective in the items they chose to consume. Floating surface debris was carefully 'inspected' by approaching typically within a centimetre of the item with their snout before either consuming, or more commonly, rejecting it. For example, one female consumed five items but 'inspected' and then rejected at least 36 other items in a 20-minute period of surface foraging (i.e., it consumed approximately 1 in 8 items). Whether 'inspecting' potential food items involved smelling the item and/or making visual assessment of it was unclear though the fact that surface feeding was only observed during the day would indicate that a visual appraisal was at least part of the assessment. Females showed a definite preference for leaves that were green and these were typically consumed in their entirety (n > 30; Fig. 2). By contrast, only portions of yellow leaves were consumed (n = 11); leaves of other colours were rarely consumed (n = 3). The preference for the petiole of senescent leaves from a variety of tree species, among these Water Gums *Tristaniopsis exiliflora* and fig trees *Ficus* spp., was commonly observed (n > 50). Turtles were also observed to consume various components of inflorescences and leaf fragments (see Table 1; Fig. 3).

(ii) Feeding in the water column – Turtles seizing food items from the water column was not commonly observed (n = 9), however, they were commonly observed sitting-in-wait on the substrate for food items to be flushed through inlets and into the water column (n = 17). Both adult (males and females) and sub-adult turtles were seen standing on the substrate near in-flows to pools where they adopted a characteristic stance with front limbs and the neck fully extended, and head facing towards the in-flow (i.e., into the current), often close to each another (< 0.3 m; n = 11). Up to six individuals were seen standing perfectly still except for head movements that would often follow the path of pieces of debris as they were carried in by the current. Occasionally they were observed to chase in-flowing debris through the water column. As with feeding behaviour described above, each item was 'inspected' closely and then either consumed or let pass. If the latter occurred, then they would resume their stance on the substrate with their head directed into the flow.

(iii) Feeding on the substrate – The analysis of frequencies of females and males feeding on the substrate was equivocal (Table 2). With an assumed sex ratio of 1:1, substrate feeding in females was significantly more common than in males both by night and by day (night χ^2 = 18.20, 1df, P < 0.0001; day χ^2 = 18.86, 1df, P < 0.001); with an assumed sex ratio of 1:2 they were not significantly different from expected frequencies (night χ^2 = 2.20, 1df, P = 0.155; day: χ^2 = 1.23, 1df, P = 0.267). When substrate feeding by day, both males and females were observed to either walk along or swim slowly low above the substrate, 'inspecting' items as they moved. As for surface feeding, they were very selective in what they chose to consume. They appeared to be attracted to items that were strongly contrasting in colour with the (dark) stony substrate, such as pale or brightly colour fruits or (fresh) green leaves. These were inspected closely in same manner as items floating on the water's surface. The most common form of substrate feeding observed was grazing on filamentous algae growing on submerged stones and logs (n > 60) typically in shallow water. Both males and females grazed algae from stones both during the day and night (Figs. 4 & 5). Algae covered much of the visible surface of stones that were in clear water and algal filaments were generally short (< 20 mm) and frequently covered in a fine layer of silt. Much longer algal strands occurred only in near stagnant, clear, shallow water. During the driest months of the year, algae grew prolifically on submerged stones that were subject to sluggish flows such as cul-de-sacs formed in anabranches. Turtles were also observed standing in leaf litter accumulations, selectively feeding on leaves. The regurgitated stomach contents of eight turtles comprised leaf fragments with a cleanly cut crescent-shaped edge (where leaves had been severed). Small leaves (typically < 5 cm in length) were often consumed in their entirety by adults; however, most leaves were too large to be consumed whole and only a portion of them was consumed.

(iv) Emerging from water to seize food items – On six separate occasions *Elseya* sp. were observed to partially, or completely, emerge from the water during daylight hours to seize food items (Table 3). The only live food that was observed being consumed was a species of moth commonly seen aggregating on the underside of logs and on vegetation (esp. *Lomandra* sp. and Weeping Bottlebrush *Callistemon viminalis*) that lined the water's edge. Para Grass *Brachiaria mutica* was also observed being consumed. This invasive perennial grass (DNRM 2001) is patchily distributed along the river and some of its tributaries where it grows along the edge of disturbed banks and is readily accessible to turtles.

(v) Nocturnal movement to and from feeding areas – Adult *Elseya* sp. are known to move into shallow water at night to feed (Turner 2006). This movement typically occurred early in the evening

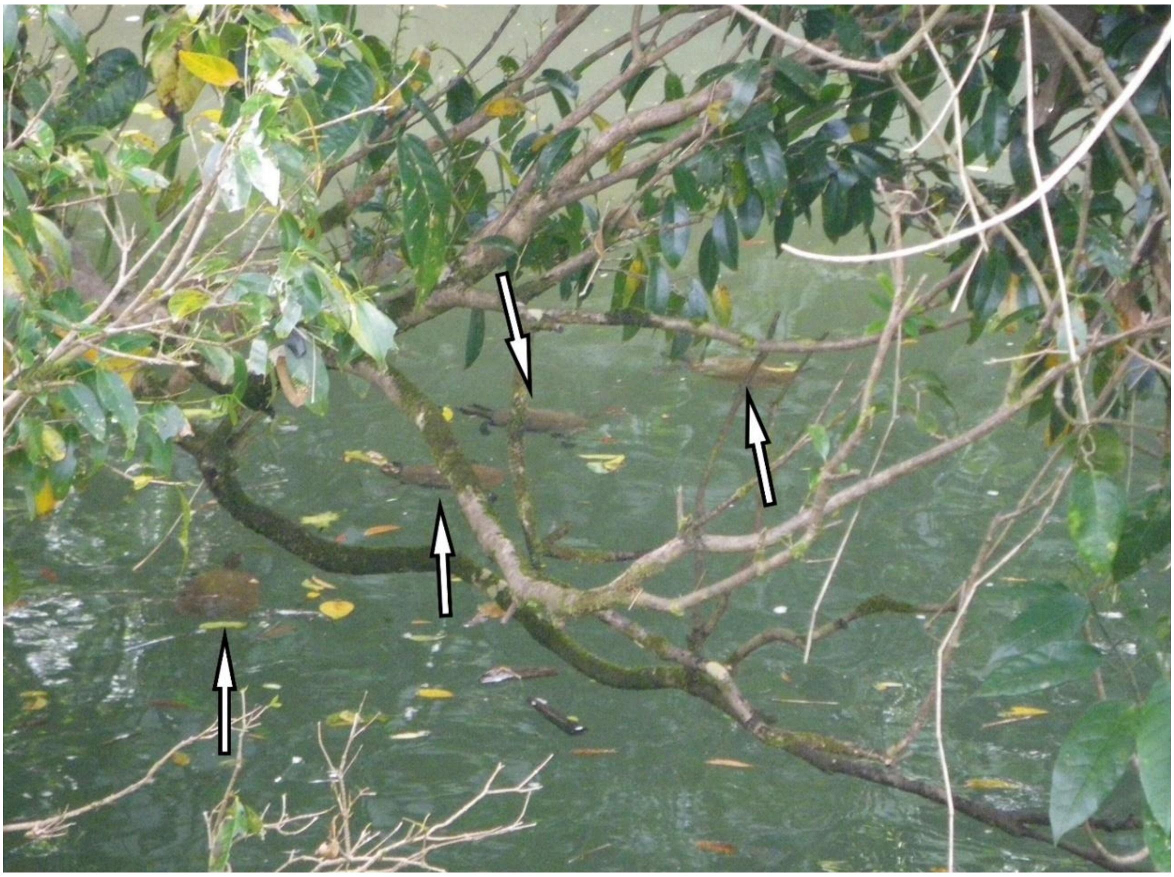

Figure 2. An aggregation of seven adult female Johnstone River Snapping Turtles *Elseya* sp. surface feeding (mainly on leaves and leaf fragments). Four females are visible at the surface in this photograph.

Figure 3. An aggregation of 10 adult female Johnstone River Snapping Turtles *Elseya* sp. surface feeding on inflorescences of the Leichhardt Tree *Nauclea orientalis*. Eight turtles are visible at the surface in this photograph.

Figure 4. A young adult female Johnstone River Snapping Turtle *Elseya* sp. feeding on algae growing on the surface of a stone in shallow water at night. This female had moved from the main flow of the river into an anabranch to feed on algae and was not deterred by the beam of the spotlight.

Figure 5. An adult female Johnstone River Snapping Turtle *Elseya* sp. foraging amongst stones in a shallow pool by day. This female was foraging mid-morning in shallow (< 0.3 m) water where it consumed leaf fragments and algae from the surface of stones. Note the top of the carapace protruding from the water.

(usually between 7 to 9 pm EST) and was from the main flow of the river into shallow pools and the cul-de-sacs of anabranches (Fig. 6). In the shallow pools filamentous algae grew abundantly on submerged stones and turtles were observed feeding on it. In some instances, because water levels were low, the movement into anabranches resulted in turtles climbing partly or wholly out of the water (usually just the carapace) but where possible the head was always held beneath the water. The pools of the anabranches by day (at that time of year) contained no adult turtles, being shallow and having little cover, but at night up to 20 adult turtles were recorded in these pools either feeding or heading up-stream (n > 30).

Table 3. Food items seized by Johnstone River Snapping Turtles *Elseya* sp. that were partially or completely out of water. A description of the circumstances and behaviour is given. The number of observations is denoted by n.

Food Item	Turtle	Description
Moth aggregation	Sub-adult n = 1	The turtle used its front limbs to propel itself upwards breaching the surface and lunging several times at an aggregation of small moths (≈ 50; approx. 15 mm in length) that were on the underside of log overhanging a pool (0.1-0.2 m above the surface). Moths were consumed in the water.
Kebeas vine *Decalobanthus peltatus*	Adult female n = 1	A female repeatedly approached the water's edge where it sat with its head and neck out of the water apparently looking up the bank. It then emerged from the water and moved approx. 0.5 m up the bank on five separate occasions and bit: (i) the terminal shoot which ran along the ground (n = 2), (ii) a leaf (approx. 5 cm long; n = 2), and (iii) a second leaf (approx. 15 cm long) on the vine. It immediately returned to the water to consume each item.
Para Grass *Brachiaria mutica*	Adult females n = 3	Females were seen to partially emerge from the water, nip-off single blades, and then return to the water to consume them; they were also observed consuming blades that protruded into the water.

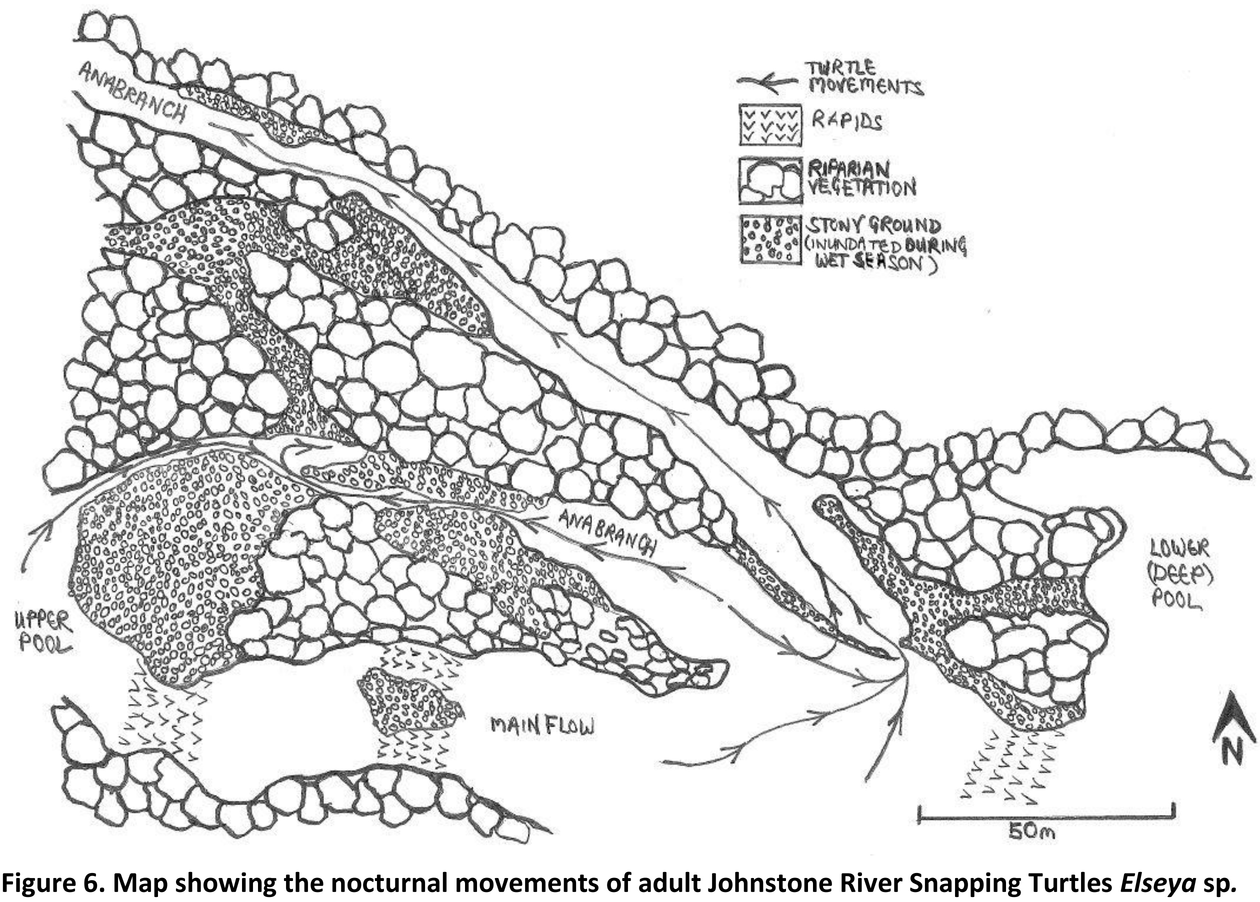

Figure 6. Map showing the nocturnal movements of adult Johnstone River Snapping Turtles *Elseya* sp. to feeding areas in anabranches. A section of the North Johnstone River with a primary and secondary anabranch joining the main flow. The nocturnal movements of turtles are indicated by arrows.

Some turtles were recorded more than 150 m up the anabranch. By the next morning adults were not located in any of the pools and were presumed to have returned to the river since the same movements from the river into the anabranch were observed the next evening (n > 20).

Aggregations of adult females

Apart from adult females aggregating near food sources (as described above), they also formed aggregations in several other contexts, and these are described separately below.

(i) Pre-nesting – The largest aggregation of adult females was observed on 19 May in pool formed by a non-flowing anabranch adjacent to nesting grounds on the North Johnstone River. Approximately 30 to 40 females were observed aggregated at the surface of a large pool in the late afternoon (4–5 pm) about two weeks before rain stimulated nesting (on 4 June). Apart from seeing so many females close together in one pool (spread out over about 10 m^2) what was unusual about the sighting was the fact that many were breaching the surface at the same time, a behaviour usually only seen briefly in the context of surface feeding. This aggregation was not seen following nesting, though smaller numbers of adult females and males were routinely seen on the substrate in the shallows of the pool at night. Smaller aggregations of between five and 12 adult females were observed in smaller, shallower, pools adjacent to known nesting sites within days of nesting occurring but they were on the substrate and were not seen to breach the surface (n = 14). In several regularly visited pools, non-resident females (i.e., females not recorded in pools previously nor recorded after nesting occurred) were seen several weeks prior to nesting (n = 9).

(ii) Day-time 'processions' – The occurrence of aggregations of females all moving in the same direction along the substrate were observed on five occasions and involved aggregations of between 4 and 11 females (Table 4). Four of these 'processions' occurred in anabranches while one occurred in the main flow. The direction of the movements were both up (n = 3) and downstream (n = 2).

(iii) Occupation of a small pool – I previously reported an observation of an aggregation of eight adult females occupying a small, relatively clear, shallow pool (Turner 2006). The pool was situated in a small (tertiary) anabranch whose junctions with a larger secondary anabranch was via a narrow (1 m wide) inlet. The pool had a maximum depth of 1.5 m and was approx. 10 m by 4 m with a white sandy substrate. Besides a few submerged branches and small accumulations of leaf litter, there were no refugia large enough to conceal a single adult female. Subsequent observations based on 16 visits to the pool over 14 years confirmed the occurrence of adult female aggregations (up to 8 individuals) in this pool (Table 5). The probability that the occurrence of only females in this pool is due to chance is extremely small (binomial n = 71, $p = ½$ or ⅔, $P << 0.0001$). Whether, over the 14 years, these observations were of the same or different individuals (or a mix of the two) is not known. What is peculiar about this aggregation is that the pool they inhabited was lacking refugia or stones and was small relative to the number of adult turtles in it. This meant turtles were very exposed compared to the situation in which they are typically encountered (i.e., on stony substrates where they are much less conspicuous). Females sought what little cover was available on the substrate (resulting in only partial concealment) and there they remained stationary. It is not known if the females occupied the pool in all months of the year. It seemed likely that they moved to and from the secondary anabranch as on two occasions several females were observed moving into the pool via the inlet. Despite repeated observation, no interactions between females were observed even though they were often near each other.

Other aggregations

Aggregations of males ranging in number from three to five individuals were observed at night moving from the main flow up into anabranches (n = 3) and one aggregation was seen near several females that were surface feeding by day. Other small aggregations of males were observed at night in shallow pools where at least one was feeding (n = 14). Another two observations that occurred on the same night (27 October) involved single-sex aggregations; one of males, the other of females. Each aggregation had nine individuals: the males were within centimetres of each other at the head of a set of rapids while females were located some 60 m away in a pool at the bottom of the rapids. The purpose, if any, of these aggregations was not apparent.

Table 4. Occurrence of adult female 'processions' of Johnstone River Snapping Turtles *Elseya* sp. Female were all observed on or near the substrate in close proximity to each other and heading in the same direction.

Observation	No. of females	Description
1	>9	Most females were walking downstream along the substrate, but several were swimming low above it in water 0.6 m deep. The pale brown silt-covered carapace of the females was easily distinguished from the darker (stony) substrate when initially seen from 15 m away.
2	5	All were within 3 m of each other and were walking along the substrate in 0.4 m of water heading downstream.
3	6	All were within 2.5 m of each other and were walking along the substrate in 0.5 m of water heading downstream.
4	11	Turtles were spread out over 8 m in 0.5 m of water in the main flow above a set of rapids. Most were walking along the substrate while several were stationary and had their heads down in between stones. They were moving upstream.
5	4	All were within 1.5 m of each other walking along the substrate and heading upstream in 0.5 m of water.

Table 5. Occurrence of adult female Johnstone River Snapping Turtles *Elseya* sp. in a small pool over 14 years. The small pool was situated in a secondary anabranch of the North Johnstone River (see text for details).

Date	No. of females	Description
29/10/05	8	Initially all females were active either walking or swimming just above the substrate.
17/9/06	5	Females were either stationary on the substrate or swimming low above it. One female entered the pool from a narrow in-flow.
1/11/08	>6	Females were all stationary on the substrate having likely been disturbed by me on approach.
28/9/09	2	Two females were attempting to conceal themselves on the substrate.
31/10/09	8	Two females were swimming low above the substrate < 1 m apart; the other six were on the substrate and were active.
12/12/09	6	Six adult females all on the substrate; at least four were active.
19/9/11	7	Seven females all on the substrate; three were either side of the deepest part of the pool and moved to it within minutes of my approach, attempting to conceal themselves; a few other females continued to move around slowly on the substrate.
25/9/11	7	Six females were active on the substrate in the deepest part of the pool; a seventh was active at the surface.
1/10/11	≥3	At least three females on substrate; visibility was poor.
24/9/12	7	Six females were active on the substrate in the deepest part of the pool; a seventh was initially active at the surface and then sought cover on the substrate.
13/10/12	≥4	At least four females on the substrate.
27/10/12	≥3	At least three females active and they immediately retreated to the substrate of the deepest part of the pool; visibility was poor.
30/9/13	≥3	At least three females were active on the substrate.
25/10/14	2	Two females were seen retreating; visibility was poor.
10/12/15	3	Three females only were visible on the substrate.
2/10/18	≥5	Two females were surfacing feeding (chasing leaves that were carried in by the inflow channel) while at least three others were on the substrate.

Interactions between turtles

Few interactions were observed among females when surface feeding even though they were often near each other (< 0.1 m) despite many observations (n > 120). The only interactions observed between females occurred when one had seized a green leaf resulting in a nearby female attempting to seize the item in a short, unsuccessful pursuit (n = 2). As with females, interactions among males were few and apart from skirmishes over food items (n = 3). One observation involved a male feeding on the substrate that chased away approaching males with mouth agape (n = 5); on two occasions females approached this male but elicited no aggressive response or chasing, although he kept a watchful eye on them. Males were typically very circumspect around females and would almost invariably approach them from the rear, rather than the front. When one male approached the head of the female, the response was immediate: the female chased the male over a short distance (< 1 m) and male thereafter kept its distance.

Males pursuing females and courtship behaviour

Observations of males pursuing females were observed on three occasions during the months of October, February and March. On each of these occasions, males were situated at the rear of the female, with their head typically no more than 0.2 m from its tail. Females appeared to go about their normal movements: all were surface feeding with males in pursuit. In one instance, on 2 February, a male which had been observed pursing a female for several minutes, then mounted her and appeared to copulate, with his tail curled down and under her rear marginals. Two separate instances of apparent courtship behaviour were observed on 23 February and 17 April. Each of these observations involved turtles initially at the surface with the female and male head-to-head, snouts almost touching; in one instance both heads and part of neck protruded from the water. It was not determined whether barbels were aligned when turtles were head-to-head. The male was briefly seen to repeatedly move its head from side to side. Otherwise, it was nuzzling the female while remaining perfectly still. This behaviour was observed for several minutes before the pairs slowly sank to the substrate while maintaining the head-to-head arrangement. Frontal contact and male head-bobs are two behaviours recorded in courtship sequences of several Australian chelids (see Murphy & Lamoreaux 1978).

Discussion

The feeding behaviours described in this work indicate that during the drier months of the year, at least, leaves or portions of them, along with fruit, flowers and filamentous algae are likely to comprise a substantial portion of the diet of *Elseya* sp. This is consistent with the results of the analysis of stomach contents of *Elseya* sp. examined by O'Malley (2007) who found plant material, primarily of terrestrial origin, to comprise > 90% of the species' diet. Wet season observations of surface feeding are likely to significantly add to the number of plant species consumed by *Elseya* sp. since different riparian species flower and fruit during this period. Fruit and flower feeding is common in several other *Elseya* species, and the trend in the genus is for larger species to be primarily herbivorous while the smaller species tend to be more omnivorous (Legler 1976; Cann 1998; Allanson & Georges 1999; Freeman 2010; Freeman *et al.* 2014).

The occurrence of female *Elseya* sp. aggregations surface feeding is the first detailed documented occurrence of this behaviour in the species. O'Malley (2007) noted the occurrence of 'large aggregations of *Elseya* sp. under fig trees and other fruit trees exploiting windfall fruit' but no further details (e.g., composition, behaviour, etc.) are given. Legler (1976) described several small Gulf Snapping Turtles *E. lavarackorum* (as *E. dentata*) feeding at the surface on floating figs (*Ficus* spp.) in the Gregory River and suggested the species congregates beneath laden trees for figs to drop. Legler (1976) and Freeman (2010) observed this species congregating under fruiting fig trees and consuming fruit that fell into the water. Freeman (2010) described the occurrence of antagonistic behaviour at the start of the fruiting period (when fruits were few) between individual *E. lavarackorum* (and Worrell's Turtle *Emydura subglobosa worrelli*) when small feeding aggregations occurred beneath Cluster Fig Trees *Ficus racemosa*. The observations described above provide direct evidence that *Elseya* sp. exploit fruit-fall from a variety of tree species and will wait in the vicinity of trees in anticipation of fruit fall.

Fish of various sizes, including those that *Elseya sp.* would be capable of consuming, are common in the river at certain times of the year and were often seen to be in close proximity (< 0.1 m) to turtles but turtles were never observed to make any attempt to seize them. On the contrary, it was observed that some species of small fish (and the juveniles of some larger species) fed on the algae, and possibly the flaking skin, that grew on the limbs, neck, inguinal pocket, and carapace of turtles (n = 8). Whether this apparent grooming by fish extends to the consumption of ectosymbiont flatworms *Bdellasimillis barwicki* that commonly occur in the inguinal pockets of *Elseya* sp. (Turner 2006) is not known but fish were seen in and around axilla/inguinal pockets of turtles on the substrate.

Feeding was the primary reason for the nocturnal movement of turtles from the river into anabranches and tributaries. The minimum displacement for most of these individuals was 50 m and some exceeded 150 m in a single night. Freeman *et al.* (2018) tracked the movements of eight individual *Elseya* sp. (4 females, 4 males) inhabiting smaller upland waterways and found the daily displacement of turtles was between 9 and 31 m while the linear home ranges varied from 387 to 1128 m. Individuals inhabiting the main flow of the lowland Johnstone River therefore had considerably larger daily displacements than those in upland waterways. The anabranch pools in which turtles fed at night were never occupied by day at that time of year (and rarely at other times) being shallow (< 0.5 m) and lacking in cover (i.e., no submerged logs or undercut banks). O'Malley (2007) suggested that the reason for algae feeding in shallows at night, rather than by day, was to reduce the risk of predation. This explanation may be true, however, other explanations such as higher temperatures and lower levels dissolved oxygen in shallow water might also account for this behaviour. Furthermore, daytime algae feeding in shallow water does occur in smaller waterways (see Fig. 5).

The observed lack of surface feeding by male *Elseya* sp. compared to females may result in dietary differences, though this may not necessarily be reflected in either the variety or proportions of food types consumed. Females presumably eat more owing to their significantly larger size and the demands of egg production (as well as nesting, the movement to and from nesting grounds, etc.; see Moll & Moll 2000) and so this may be reflected in a greater volume of food consumed and/or a greater frequency of food items at certain times of the year. O'Malley (2007) found the dietary composition of male and female *Elseya* sp. from turtles inhabiting smaller tributaries of the river to be quite similar. Some differences were, however, apparent though were not always consistent between sites: (i) females ate more stems (by volume) and less fruit (by both volume and frequency) than males, and (ii) males ate more algae (by volume) and grass/grass shoots (by volume) compared to females. Females were frequently observed consuming petioles when surface feeding, but the low consumption of fruit is at odds with the observations of females aggregating around fruiting trees. The greater consumption of algae by males is consistent with the observations of their feeding behaviour since they tended to feed on the substrate where algae grew on stones but is at odds with their greater consumption of grass which is usually only accessible to turtles at or near the surface along the edges of pools. Differences in diet between the sexes were found in the Northern Snapping Turtle *E. dentata* with females consuming a higher percentage mass of fig fruits than males, and males consuming more leaves and fruits of the Leichhardt Tree *Nauclea orientalis* than females (Kennett & Tory 1996). No differences in diet were found between male and female Southern White-throated Snapping Turtle (Armstrong & Booth 2005).

Few observations of *Elseya* sp. partially or completely emerging from water to seize food items occurred (see Table 3) but the behaviour is known to occur in other species of *Elseya*. White (1999) observed *E. lavarackorum* cropping fruit from an overhanging fruit tree and the species has been observed emerging completely from water at night to consume figs (Little & Chew in Freeman *et al.* 2010). This behaviour might occur in response to highly valued food items or perhaps occurs only during periods when food shortage is acute, as its apparent rarity would suggest that it is not without risk.

Aggregations of turtles have been recorded in many different contexts: emergence from the nest, aerial basking, moving (including migrations and emigrations), feeding/foraging, estivation, brumation, aquatic basking, nesting, and mating (Goode

1967; Harless 1979; Heaphy in Georges *et al.* 1993, Green 1994, 1995; Cann 1998; Doody *et al*. 2001; Giles 2005; Johnston *et al.* 2018). In many of these contexts, aggregations are the result of the spatial concentration of resources (e.g., suitable basking sites, nesting sites, food, etc.) and therefore do not necessarily involve any social interactions between individuals. Frequently both sexes and a range of ages are represented in such aggregations (Harless 1979). Surface feeding aggregations of adult female *Elseya* sp. are the obvious result of the (spatial) concentration of resources i.e., flowering/ fruiting trees. Similarly, the observed pre-nesting aggregations of females in pools adjacent to nesting areas are another example of a concentrated resource, in this case, preferred nesting areas. In *E. albagula* aggregations of females have been recorded at widely scattered nesting banks In April-May (Limpus 2008). In *Elseya* sp. aggregations of nesting gravid females have been frequently observed but given this activity occurs at night it cannot be certain that females are aware of each other's presence and so do not constitute aggregations in the sense referred to in this work (see Methods); observations indicate that it is more a case of multiple females using the same nesting area at different times (pers. obs.).

The occurrence of adult female aggregations has not been previously reported in Australian chelids except in the context of nesting (Cann 1978, 1998; Georges *et al.* 1993). Why adult female 'processions' occur and why females should aggregate in a small pool with minimal cover and no food source is unclear. The time of year that observations were made precluded the possibility of either being related to nesting. It is possible that aggregations afford individuals greater protection from predators through increased vigilance. It was also not unusual to find small numbers of adult males (typically two or three) in close proximity to each other (< 1 m apart; pers. obs.) but why they are excluded, or otherwise, from adult female aggregations is unclear. Direct exclusion of males by females is likely given that adult females attain significantly larger sizes than males (Turner 2006; O'Malley 2007) and have been observed behaving aggressively towards males (above). I have observed pale crescent-shaped scars particularly on the tail and rear limbs of males, and to a lesser extent on females, that are likely the result of bites from conspecifics (given the size and shape of these scars; Turner 2006). These observations suggest the possibility that more complex social interactions exist within *Elseya* sp. Additional observations of individual interactions in *Elseya* sp., both in the wild and in captivity, are needed to understand the occurrence of single-sex aggregations. Furthermore, underwater vocalisations are known to be produced by one species of Australian turtle and a particular vocalisation produced during the breeding season was hypothesised to function as an advertisement 'call' (Giles 2005; Giles *et al.* 2009). Whether *Elseya* possess such vocalisations is presently unknown, but they might potentially play a role in the occurrence of aggregations as well as other social interactions.

The use of the limbs by turtles when feeding has been recorded in both freshwater and marine turtle species (Fujii *et al*. 2018). In *Elseya* sp. the limbs were used to stabilise large food items such as leaves so that pieces could be torn-off and then consumed. Fujii *et al*. (2018) listed ten types of limb-use observed by marine tetrapods when feeding and of these 'leveraging' would best describe this behaviour in *Elseya* sp. Also observed in *Elseya* sp. was the use of claws to scratch algae from the surface of submerged logs followed by a feeding response (pers. obs.), a behaviour Fujii *et al*. (2018) describe as 'digging'.

Both portable camera and remotely operated vehicle (ROV) technology have been used to record the behaviour of sea turtles (Seminoff *et al.* 2006; Hochscheid 2013; Thomson & Heithaus 2014; Patel *et al.* 2016; Dodge *et al.* 2018) but both technologies are at present unsuited for use in turtles such as *Elseya* sp*.* due to the species' relatively small size. Nonetheless these technologies offer the best prospect of learning about the natural aquatic behaviour of freshwater turtles in the future provided the miniaturisation of portable cameras and/or transponders can be achieved, battery life is improved, and, in the case of ROVs, the cost becomes less prohibitive.

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