

Resource partitioning among five sympatric species of freshwater turtles from the wet–dry tropics of northern Australia

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Abstract

Context. Resource partitioning of diet and microhabitat was examined for five sympatric species of freshwater turtles in the Daly River in the northern end of Northern Territory (Top End) in Australia. The Daly River supports a high diversity of freshwater turtles, making it the ideal place to study a freshwater turtle community.

Aims. To determine the dry-season diet and microhabitat use of *Carettochelys insculpta*, *Elseya dentata*, *Chelodina oblonga*, *Emydura victoriae* and *Emydura subglobosa worrelli* and examine intraspecific and interspecific niche overlap and ontogenetic dietary shift.

Methods. Gut contents were collected by stomach flushing, and microhabitat use was determined by recording where each turtle was first seen before capture. Diet and microhabitat use were compared using an index of relative importance. Niche overlap was measured with Horn's overlap index.

Key results. *Carettochelys insculpta* is an opportunistic omnivore that feeds mostly on ribbonweed (*Vallisneria spiralis*) and aquatic snails. *Elseya dentata* is herbivorous, feeding primarily on aquatic algae. The diets of *C. insculpta* and *E. dentata* overlapped moderately, but the overall niche overlap was low because they occupied different microhabitats within the river. *Chelodina oblonga* fed very little, and may use the Daly River as a dry-season refuge. *Emydura victoriae* is molluscivorous, consuming more molluscs as it grows. This ontogenetic dietary shift was associated with megacephaly (extreme broadly expanded head that is too large to fit into the carapace) and expanded triturating surfaces. This specialisation allows adult *E. victoriae* to feed exclusively on molluscs and so their diet overlapped little with other species. *Emydura subglobosa worrelli* was omnivorous, consuming mostly freshwater sponge and apparently preferring more lentic water.

Conclusions. The freshwater turtles of the wet–dry tropics are usually reported as being heavily reliant on the seeds, fruits and leaves of riparian vegetation; however, the present study showed that the dry-season diet in perennial rivers is primarily of aquatic origin.

Implications. The study suggested that populations of *C. insculpta*, *E. dentata* and *E. victoriae* could be threatened by broad-scale development in northern Australia if there were substantive impacts on aquatic macrophytes and molluscs in the Daly River system.

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Introduction

There have been many dietary studies of Australian freshwater turtles in the past 35 years (Georges 1982; Georges *et al.* 1986; Georges and Kennett 1989; Heaphy 1990; Kennett and Tory 1996; Spencer *et al.* 1998; Allanson and Georges 1999; Armstrong and Booth 2005; Wilson and Lawler 2008); however, few have quantitatively studied interspecific resource partitioning (Chessman 1978; Tucker *et al.* 1999; Lees 2008). There is a lack of knowledge of species interactions among Australian turtles, compared with turtles of other continents (Berry 1975; Vogt 1981; Vogt and Guzman 1988; Moll 1990; Fachin-Teran *et al.* 1995; Lindeman 2000a). Resource-partitioning studies are important because they provide a better understanding of species

interactions, identify major resource dimensions along which species segregate, and provide a background for generating testable hypotheses concerning factors that shape community structure (Ross 1986). Quantitative dietary studies are also lacking for many freshwater turtle species from tropical northern Australia (Georges and Kennett 1989; Kennett and Tory 1996). Such studies are required to identify habitats in need of preservation or management and the contribution of elements of those habitats to maintaining species richness, and to provide insight into the cause of species declines (Kenneth Dodd 1990; Georges and Rose 1993; Kennett and Tory 1996; Allanson and Georges 1999; Tucker *et al.* 1999; Chessman 2011; Spencer *et al.* 2014), as well as describing and understanding

conceptual food webs and carbon budgets in ecosystems (Pettit *et al.* 2011). The Daly River, in the northern part of Northern Territory (Top End) in Australia, supports a high diversity of freshwater turtles (Georges *et al.* 2000), making it an ideal place to study a freshwater turtle community.

The primary aim of the present study was to describe the diet and microhabitat use of the pig-nosed turtle, *Carettochelys insculpta*, northern snapping turtle, *Elseya dentata*, northern snake-necked turtle, *Chelodina oblonga* (previously *rugosa*; ICZN 2013), northern red-faced turtle, *Emydura victoriae*, and diamond-head turtle, *Emydura subglobosa worrelli*, in the Daly River. Specifically, dry-season diet and microhabitat use of turtles were described, and both intraspecific and interspecific measures of niche overlap were calculated. Trophic morphology of turtles was examined and related to diet, particularly in *E. victoriae*, a species with ‘megacephaly’ and enlarged crushing mouth plates. These adaptations are associated with molluscivory in other freshwater turtles such as map turtles of the genus *Graptemys* (Lindeman 2000b).

Materials and methods

Study area

Turtles were captured over the dry season from July to November of 1998 at the Daly River. The Daly is a major perennial monsoonal river system; in the dry season, the river is 1–4 m deep and is dominated by groundwater discharge, 20–80 m wide, whereas in the wet season, floodwaters raise the water level substantially (sometimes over 20 m) above dry-season levels. The climate is typical of the wet–dry tropics of northern Australia, with a mean annual rainfall of 1245.8 mm (Australian Government Bureau of Meteorology, http://www.bom.gov.au/climate/averages/tables/cw_014901.shtml, accessed 4 May 2017). Freshwater turtles in the Top End are known to vary their diet between seasons (Georges and Kennett 1989; Kennett and Tory 1996). The present study was conducted in a typical dry season so the data here samples only dry-season turtle niche utilisation.

The majority of turtles were captured at Ooloo Crossing (14°04'40"S, 131°15'00"E), where, in the dry season, the river is typically 1–3 m deep, with abundant ribbonweed (*Vallisneria spiralis*) and aquatic algae beds on sand and rock flats. Turtles were also captured at Policeman's Crossing (13°45'09"S, 130°41'15"E), near the township of Daly River, where, in the dry season, the river is mostly deeper than 3 m, slower flowing and with very little ribbonweed.

Methods

Turtles were captured with dip-nets from a boat, or by hand while diving with the aid of mask and flippers. Direct capture methods were used in preference to trapping so as to reduce the time lapse between the initial capture and stomach flushing, which may lead to a bias that overestimates the importance of foods that digest slowly (Hyslop 1980; Vogt 1981; Kennett and Tory 1996). Identification of *Emydura subglobosa worrelli* (hereafter referred to as *E. subglobosa*) was complicated by the presence of the externally similar species *Emydura tanybaraga*, a species discovered in the Daly River in an electrophoresis study (Georges and Adams

1996) and described by Cann (1997). Identification followed the key from Thomson (1996). Only four *E. tanybaraga* individuals were captured; so, dietary analysis of the species was excluded from the present study.

Standard measurements on each turtle captured were recorded. Carapace length (CL) was measured to the nearest 0.01 mm; however, *C. insculpta* individuals were too large to be measured with vernier callipers, and consequently, curved carapace length (CCL) was measured with a measuring tape to the nearest 1 mm. Mass was measured to the nearest 1 g (turtles <3 kg) or 100 g (turtles >3 kg) or by using an electronic scale or spring balance. Males were identified as having an elongated precloacal length relative to their body length. The minimum size of visually identifiable males was used as the upper size limit for all juveniles.

Gut contents were usually retrieved within 1 h of capture by stomach flushing (Legler 1977), and preserved in 70% ethanol. Turtles with an empty gut were excluded from the analysis. Food items with a slow rate of digestion may be overestimated in gut-content sampling because they build up in the pylorus (Hyslop 1980; Georges *et al.* 1986), so food items that were found in the form of a pyloric plug (a small, elongated, mucous covered mass of partially digested food) were ignored. Food items were identified with a stereo-microscope, and weighed (wet) on electronic scales (± 0.01 g). Before weighing, food items were placed on blotting paper to reduce surface moisture (Hyslop 1980). Food items were categorised into the following eight groups:

- (1) ribbonweed (*Vallisneria spiralis*);
- (2) aquatic algae;
- (3) miscellaneous aquatic plants;
- (4) terrestrial vegetation (mostly wind-fallen leaves and fruit);
- (5) small molluscs (snails under 5 mm greatest diameter);
- (6) large molluscs (snails over 5 mm greatest diameter and all bivalves);
- (7) active aquatic invertebrates; and
- (8) miscellaneous animal matter (e.g. carrion, freshwater sponge and other sessile invertebrates).

For each turtle species, the frequency of occurrence of a food category was expressed as a percentage of the total number of turtles (%f). The mass of each food category consumed by a species was expressed as a percentage of the total mass of all food items consumed by the species (%m). Index of relative importance (IRI) (Cortés 1997, 1998; Hart *et al.* 2002) based on %f and %m was calculated for each food category for each species. The IRI used in the present study is based on that in Bjørndal *et al.* (1997), but adapted to be suitable for describing turtle diets, and was calculated as follows:

$$IRI = \frac{50(\%f \times \%m)}{\Sigma(\%f \times \%m)} + \frac{50(\%f + \%m)}{\Sigma(\%f + \%m)}$$

Microhabitat use was examined on the basis of where each turtle was first seen before capture. Microhabitat use was described by calculating the number of turtles that were captured in each microhabitat category, expressed as a percentage of the total number of turtles (%f). Microhabitat was divided into the following six categories:

- (1) fallen trees (both living and dead submerged branches);
- (2) ribbonweed patch (a common freshwater macrophyte that forms large patches);
- (3) overhanging bank (occur where erosion has cut into the bank below the dry season water level);
- (4) rock flats;
- (5) sand flats; and
- (6) *Pandanus* roots (a common riparian tree, *Pandanus aquaticus* where root systems grow well into the water).

Niche overlap (Krebs 1989) was measured to estimate the inter-specific or intra-specific niche overlap of resource use among animals (Berry 1975). Horn's index of niche overlap was used for the present study, because it has minimal bias, even when sample sizes are small, and can be used for data that are not expressed as number of individual prey items (Smith and Zaret 1982; Krebs 1989). Horn's overlap was measured for diet and microhabitat use among all species (where sample size was at least 20 turtles of both species). The product of dietary overlap and microhabitat overlap was also calculated, representing a measure of multidimensional niche overlap (Holt 1987). Horn's overlap was measured using IRI's for dietary niche overlap, and using %f for microhabitat niche overlap. The minimum overlap score ($R=0$) represents no overlap, and the maximum score ($R=1$) represents complete overlap. Horn's overlap was calculated as follows:

$$R = \frac{\sum (x_i + y_i) \log(x_i + y_i) - \sum x_i \log x_i - \sum y_i \log y_i}{2 \log 2}$$

where R = Horn's index of niche overlap between turtle species x and y , x_i = proportional use of resource category i by species x (IRI for diet and %f for microhabitat), y_i = proportional use of Resource category i by Species y (IRI for diet and %f for microhabitat).

It is important to have a complete representation of life-history stages in resource-partitioning studies because turtles, like fish, may undergo ontogenetic shifts in diet and microhabitat preference (Ross 1986). Turtles were arbitrarily divided into size-classes to examine dietary shift in relation to turtle size. Size-class boundaries were chosen to divide turtles found from Ooloo Crossing into roughly even groups, or, in the case of *C. insculpta*, six animals were found that were clearly smaller than the others, and were, hence, categorised as juveniles. *Carettochelys insculpta* was divided into juveniles (CCL < 14 cm), small adults (CCL 27–38.1 cm) and large adults (CCL > 38.1 cm). *Elseya dentata* was divided into juveniles (CL < 112 mm), small adults (CL 114–200 mm) and large adults (CL > 200 mm). No *C. oblonga* individuals smaller than 150 mm were found, so this species was divided into small adults (CL < 231 mm) and large adults (CL > 235 mm). *Emydura victoriae* was divided into juveniles (CL < 100 mm), small adults (CL 100–150 mm) and large adults (CL > 150 mm). Contingency analysis (Fisher's two-tailed exact test) was used to determine significant intraspecific variation in frequency of use of food categories among size classes or between sexes.

Some species of *Emydura* are known to have ontogenetic megacephaly (extreme growth of the head) that may be related to a molluscan diet (Legler 1976; Lindeman 2000b). Head size and trophic morphology of *E. victoriae* and *E. subglobosa* were

examined in relation to the presence of molluscs in the diet, and compared with those of *Elseya dentata* so as to compare them to a species of short-necked chelid from another genus. Regressions between carapace length (CL) and maximum head width (HW) and alveolar length (from the anterior extent of the mandibular tomium to the posterior extent of mandibular symphysis, measured externally) were used to investigate the relationship between head size and body size. Sexual dimorphism in the ontogenesis of the head of *E. victoriae* was examined using analysis of covariance (Snedecor and Cochran 1984). Head measurements were taken with vernier callipers (± 0.01 mm).

All statistical analyses followed the procedures of Krebs (1989) and Snedecor and Cochran (1984). Fisher's exact test was calculated using eXactoid (2008), whereas niche-overlap calculations were made on a spreadsheet. All other statistical tests were performed with Statistical Analysis Systems (version 6.12, SAS Inc., SAS Institute, Cary, NC). All means are given with their standard error.

Results

Carettochelys insculpta

In total, 74 *C. insculpta* individuals were sampled from Ooloo Crossing, of which 72 (97%) had food in their gut. Mean turtle body mass was 6.1 ± 0.3 kg (0.61–11.0 kg) and mean curved carapace length was 36.8 ± 0.9 cm (8.6–44.7 cm). Gut contents averaged 19.8 ± 1.90 g (0.1–71.6 g).

Carettochelys insculpta was omnivorous, feeding mostly on ribbonweed, large molluscs (*Notopala* and *Thiara*) and algae (*Oedogonium* and *Batrachospermum* sp.). There was evidence of dietary shift with size, consisting of an increase in the consumption of ribbonweed, and a decrease in the consumption of algae (Table 1). Molluscs were only a minor part of the diet for juveniles and small adults, but appeared to be quite important for large adults. Large molluscs were eaten significantly ($P=0.0108$) more frequently by large adults than small adults, but otherwise, the diets of small and large adults were similar ($R=0.96$). Females were, on average, larger (curved carapace length 40.8 ± 0.7 cm) than males (37.3 ± 0.4 cm; $t=4.2$, d.f.=38, $P<0.001$) and the diets of female and male *C. insculpta* were similar ($R=0.98$).

Elseya dentata

In total, 149 *Elseya dentata* individuals were sampled, of which 127 (85%) had food in their gut. Mean gut content was 5.38 ± 0.61 g (0.01–33.39 g) and mean turtle body mass was 1.30 ± 0.12 kg (0.04–4.80 kg). Mean gut content mass of *E. dentata* from Ooloo Crossing (5.9 ± 0.7 g) was considerably higher than at Policeman's Crossing (1.0 ± 0.4 g). *Elseya dentata* individuals from Ooloo Crossing were also larger (mean CL = 210.3 ± 7.9 mm, range = 68.9–322.0 mm) than those at Policeman's Crossing (137.6 ± 7.8 mm, range = 77.7–200.0 mm).

Elseya dentata was herbivorous, consuming mostly algae (*Oedogonium* and *Spirogyra* sp.) and ribbonweed, and very little animal matter. At Ooloo Crossing, there was evidence of dietary shift with size, consisting of an increase in the consumption of algae, with a decrease in the consumption of

Table 1. The diet of *Carettochelys insculpta* from Ooloo Crossing

%f, percentage of turtles that contained a food item; %m, percentage of the total mass of all food consumed; IRI, index of relative importance

Food item	Juveniles			Small adults			Large adults		
	%f	%m	IRI	%f	%m	IRI	%f	%m	IRI
Ribbonweed	33.3	12.4	11.2	76.5	89.5	77.0	93.8	74.4	73.0
Aquatic algae	66.7	44.5	46.2	50.0	5.4	11.7	28.1	10.6	8.5
Miscellaneous aquatic plants	16.7	1.0	3.0	2.9	0.0	0.5	0.0	0.0	0.0
Terrestrial vegetation	50.0	31.1	27.8	11.8	1.9	2.6	6.3	0.1	1.1
Small molluscs	33.3	2.8	6.6	20.6	1.6	4.1	25.0	1.0	4.6
Large molluscs	0.0	0.0	0.0	11.8	1.4	2.4	40.6	13.9	12.9
Active aquatic invertebrates	0.0	0.0	0.0	2.9	0.0	0.5	0.0	0.0	0.0
Miscellaneous animal matter	16.7	8.2	5.2	5.9	0.2	1.1	0.0	0.0	0.0
Sample size (turtles)	n = 6			n = 34			n = 32		
Total mass of stomach contents (g)	9.9			741.5			669.8		

Table 2. The diet of *Elseya dentata* from Ooloo Crossing and Policeman’s Crossing

%f, percentage of turtles that contained a food item; %m, percentage of the total mass of all food consumed; IRI, index of relative importance

Food item	Juveniles			Ooloo Crossing Small adults			Large adults			Policeman’s Crossing		
	%f	%m	IRI	%f	%m	IRI	%f	%m	IRI	%f	%m	IRI
Ribbonweed	70.6	74.4	69.9	82.1	35.4	37.3	48.0	19.7	18.9	38.1	54.9	42.2
Aquatic algae	35.3	18.3	15.0	85.7	63.0	57.5	90.0	72.0	73.4	4.8	0.4	1.0
Miscellaneous aquatic plants	5.9	0.5	1.2	0.0	0.0	0.0	8.0	1.8	1.9	4.8	0.1	1.0
Terrestrial vegetation	23.5	6.6	6.7	10.7	0.8	2.0	8.0	2.9	2.2	33.3	12.7	13.8
Small molluscs	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Large molluscs	0.0	0.0	0.0	3.6	0.0	0.6	2.0	0.2	0.4	0.0	0.0	0.0
Active aquatic invertebrates	35.3	0.0	6.4	0.0	0.0	0.0	0.0	0.0	0.0	19.0	0.0	3.7
Miscellaneous animal matter	5.9	0.2	1.1	14.3	0.8	2.6	12.0	3.4	3.1	57.1	31.8	38.3
Sample size (turtles)	n = 17			n = 28			n = 50			n = 21		
Total mass of stomach contents (g)	14.5			107.9			524.6			25.0		

ribbonweed (Table 2), a pattern opposite to that of *C. insculpta* (Table 1). Juveniles ate mostly ribbonweed and algae, but some also ate active aquatic insects. The diet of small and large adults varied little ($R=0.96$). *Elseya dentata* was the only turtle species to not feed on molluscs, and only at Policeman’s Crossing was animal matter (sponge) an important part of its diet (Table 2).

The diet of *E. dentata* at Policeman’s Crossing was broader, and quite different from that at Ooloo Crossing ($R=0.53$, Table 2), comprising of ribbonweed and sponge.

Females were larger on average (straight-line carapace length 23.7 ± 0.90 cm) than were males (19.2 ± 1.40 cm; $t=2.875$, d.f.=90, $P=0.003$), and variation in diet between males and females was minimal ($R=0.94$).

Chelodina oblonga

In total, 97 *C. oblonga* individuals were sampled, of which 46 (47%) had food in their gut. Mean gut content was only 0.22 ± 0.05 g (0.01–1.74 g) and mean turtle body mass was 1.86 ± 0.107 kg (0.45–4.3 kg). Apart from one smaller individual (CL = 15.13 cm), all *C. oblonga* individuals were clearly adults (CL 18.35–30.81 cm; Kennett 1994). Relative to body mass, the mass of food consumed by *C. oblonga* was very low compared with the other species. *Chelodina oblonga* was carnivorous (Table 3), with adults feeding primarily on molluscs

and active aquatic invertebrates (mostly freshwater prawns *Macrobrachium* sp.).

Emydura victoriae

In total, 228 *E. victoriae* individuals were sampled, of which 150 (66%) had food in their gut. Mean gut content was 0.78 ± 0.07 g (0.01–4.14 g) and mean turtle body mass was 399 ± 28 g (19–1356 g).

Emydura victoriae at Ooloo Crossing exhibited a dramatic diet shift, with size from aquatic algae and miscellaneous animal matter as juveniles, to molluscs as adults (Table 4). Juveniles consumed mostly algae, freshwater sponge and insects (*Odonata* and *Trichoptera* nymphs), but virtually no molluscs. Small and large snails were eaten significantly more frequently by large adults than small adults ($P=0.0075$, $P=0.0001$ respectively).

Emydura victoriae individuals from Policeman’s Crossing were smaller (11.94 ± 0.90 cm, 5.19–21.54 cm) than those from Ooloo Crossing (14.0 ± 0.33 cm, 6.79–21.19 cm). The turtles there fed almost entirely on snails (both *Thiara* and *Notopala*) and sponge.

Female *E. victoriae* individuals were, on average, larger (straight-line carapace length 15.49 ± 0.5 cm) than males (14.04 ± 0.31 cm; $t=2.325$, d.f.=130, $P<0.01$). Large molluscs were eaten significantly more frequently by females than

Table 3. The diet of *Chelodina oblonga* from Ooloo Crossing and Policeman's Crossing
 %f, percentage of turtles that contained a food item; %m, percentage of the total mass of all food consumed; IRI, index of relative importance

Food item	Ooloo Crossing						Policeman's Crossing		
	Small adults			Large adults			%f	%m	IRI
	%f	%m	IRI	%f	%m	IRI			
Ribbonweed	16.7	0.0	3.3	10.5	0.0	2.1	11.1	2.3	2.6
Aquatic algae	16.7	0.0	3.3	5.3	0.0	1.1	0.0	0.0	0.0
Miscellaneous aquatic plants	0.0	0.0	0.0	5.3	0.0	1.1	22.2	0.0	3.8
Terrestrial vegetation	38.9	15.7	21.5	26.3	6.5	9.9	11.1	0.0	1.9
Small molluscs	27.8	49.4	39.2	31.6	29.0	29.8	55.6	81.4	67.2
Large molluscs	27.8	23.7	21.7	31.6	22.1	24.2	33.3	6.5	9.0
Active aquatic invertebrates	22.2	11.2	11.0	21.1	29.0	21.8	11.1	0.0	1.9
Miscellaneous animal matter	0.0	0.0	0.0	15.8	13.4	10.0	44.4	9.9	13.6
Sample size (turtles)	n = 18			n = 19			n = 9		
Total mass of stomach contents (g)	2.5			5.1			2.6		

Table 4. The diet of *Emydura victoriae* from Ooloo Crossing and Policeman's Crossing
 %f, percentage of turtles that contained a food item; %m, percentage of the total mass of all food consumed; IRI, index of relative importance

Food item	Ooloo Crossing									Policeman's Crossing		
	Juveniles			Small adults			Large adults			%f	%m	IRI
	%f	%m	IRI	%f	%m	IRI	%f	%m	IRI			
Ribbonweed	3.6	0.0	0.7	0.0	0.0	0.0	3.6	0.0	0.6	0.0	0.0	0.0
Aquatic algae	42.9	51.8	40.6	44.1	37.0	32.6	14.5	8.3	4.9	8.7	1.0	2.1
Miscellaneous aquatic plants	3.6	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terrestrial vegetation	14.3	0.0	2.7	2.9	0.2	0.6	7.3	1.4	1.6	4.3	0.6	1.0
Small molluscs	10.7	1.1	2.3	70.6	38.8	49.5	92.7	61.3	66.0	39.1	38.7	33.1
Large molluscs	0.0	0.0	0.0	14.7	7.4	5.5	56.4	26.3	24.7	21.7	21.8	14.3
Active aquatic invertebrates	32.1	9.0	10.7	0.0	0.0	0.0	1.8	0.0	0.3	4.3	0.7	1.1
Miscellaneous animal matter	60.7	38.1	42.4	23.5	16.6	11.8	7.3	2.8	1.9	65.2	37.2	48.4
Sample size (turtles)	n = 28			n = 34			n = 54			n = 23		
Total mass of stomach contents (g)	3.6			30.5			53.6			23.3		

males, but otherwise dietary overlap between male and female *E. victoriae* was high ($R = 0.96$).

Emydura subglobosa

In total, 53 *E. subglobosa* individuals were sampled, of which 29 (55%) had food in their gut. Mean gut content mass was quite low compared with other species (0.45 ± 0.10 g, range 0.01–2.12 g) and mean turtle body mass was 0.514 ± 0.050 kg (0.310–1.314 kg).

Most *E. subglobosa* individuals sampled were from Policeman's Crossing (Table 5), so comparison of the diet with that of other species (most of which were captured at Ooloo Crossing) was difficult. *Emydura subglobosa* was omnivorous, and consumed mostly sponge, snails, algae and ribbonweed (Table 5).

Microhabitat use

Microhabitat use by adult *C. insculpta* differed from the chelid turtles; *C. insculpta* mostly occupied ribbonweed patches and other open areas such as rock flats, whereas the chelids were usually found around the shelter of submerged, fallen trees or *Pandanus* roots near the bank (Tables 6, 7).

Niche overlap

There was a reasonably high level of dietary overlap between *C. insculpta* and *E. dentata* (Table 8) because both species had a primarily herbivorous diet; however, with growth, the diet of *C. insculpta* apparently shifts to ribbonweed, whereas *E. dentata* shifts to algae with size (Tables 1, 2). The two species have only a moderate level of microhabitat overlap (Table 9), resulting in low multi-dimensional overlap (Table 10). Although the sample size was small, juvenile *C. insculpta* individuals appear to have a diet similar to and occupy a microhabitat similar to those of the chelid turtles, so may have a high level of overlap with them.

Elseya dentata was almost entirely herbivorous, so its diet overlapped little with those of other species, except for *C. insculpta* (Tables 8, 11), as discussed above. The diet of *C. oblonga* overlapped most with *E. victoriae* (Tables 8, 11). Adult *E. victoriae* individuals were mollusc specialists, and so had little dietary overlap with the other common turtle species, i.e. *E. dentata* and *C. insculpta* (Tables 8, 11). Overall, the combination of dietary and microhabitat differences resulted in low interspecific multidimensional niche overlap between most species at Ooloo Crossing (Table 10).

Table 5. The diet of *Emydura subglobosa* from Ooloo Crossing and Policeman’s Crossing
 %f, percentage of turtles that contained a food item; %m, percentage of the total mass of all food consumed;
 IRI, index of relative importance

Food item	Ooloo Crossing			Policeman’s Crossing		
	%f	%m	IRI	%f	%m	IRI
Ribbonweed	50.0	30.6	25.7	4.0	0.0	0.7
Aquatic algae	75.0	29.4	35.3	28.0	24.4	15.7
Miscellaneous aquatic plants	25.0	0.0	3.8	8.0	0.3	1.5
Terrestrial vegetation	25.0	0.0	3.8	36.0	8.1	10.7
Small molluscs	50.0	40.0	31.3	12.0	0.0	2.2
Large molluscs	0.0	0.0	0.0	8.0	1.6	1.9
Active aquatic invertebrates	0.0	0.0	0.0	4.0	0.4	0.8
Miscellaneous animal matter	0.0	0.0	0.0	72.0	65.2	66.5
Sample size (turtles)	n = 4			n = 25		
Total mass of stomach contents (g)	2.4			10.7		

Table 6. The percentage frequency of microhabitat utilisation of turtles from Ooloo Crossing

Microhabitat	<i>Carettochelys insculpta</i>	<i>Elseya dentata</i>	<i>Chelodina oblonga</i>	<i>Emydura victoriae</i>
Fallen trees	11.1	72.6	62.7	59.4
Ribbonweed patch	63.9	3.2	2.4	0.0
Over-hanging bank	0.0	8.4	21.7	11.2
Rock flats	22.2	8.4	0.0	9.8
Sand flats	2.8	2.1	3.6	7.0
<i>Pandanus</i> roots	0.0	5.3	9.6	12.6
Sample size (n)	72	95	83	143

Table 7. The percentage frequency of microhabitat utilisation of turtles from Policeman’s Crossing

Microhabitat	<i>Elseya dentata</i>	<i>Emydura victoriae</i>	<i>Emydura subglobosa</i>
Fallen trees	52.2	29.4	67.5
Ribbonweed patch	4.3	2.9	7.5
Over-hanging bank	0.0	2.9	0.0
Rock flats	0.0	17.6	0.0
Sand flats	4.3	0.0	2.5
<i>Pandanus</i> roots	39.1	47.1	22.5
Sample size (n)	23	34	40

Table 8. Dietary (interspecific) niche overlap (Horn’s overlap of dietary index of relative importance, IRI) among turtle species from Ooloo Crossing

Species	<i>Carettochelys insculpta</i>	<i>Elseya dentata</i>	<i>Chelodina oblonga</i>	<i>Emydura victoriae</i>
<i>C. insculpta</i>	X	0.71	0.44	0.41
<i>E. dentata</i>		X	0.29	0.41
<i>C. oblonga</i>			X	0.84
<i>E. victoriae</i>				X
Sample size (n)	74	94	36	117

Table 9. Microhabitat utilisation (interspecific) niche overlap (Horn’s overlap of percentage of turtles that contained a food item, %f) among turtle species from Ooloo Crossing

Species	<i>Carettochelys insculpta</i>	<i>Elseya dentata</i>	<i>Chelodina oblonga</i>	<i>Emydura victoriae</i>
<i>C. insculpta</i>	X	0.48	0.33	0.59
<i>E. dentata</i>		X	0.93	0.96
<i>C. oblonga</i>			X	0.92
<i>E. victoriae</i>				X
Sample size (n)	74	94	36	117

Table 10. Product of dietary and microhabitat utilisation (interspecific) niche overlap among turtle species from Ooloo Crossing

Species	<i>Carettochelys insculpta</i>	<i>Elseya dentata</i>	<i>Chelodina oblonga</i>	<i>Emydura victoriae</i>
<i>C. insculpta</i>	X	0.34	0.15	0.24
<i>E. dentata</i>		X	0.27	0.39
<i>C. oblonga</i>			X	0.77
<i>E. victoriae</i>				X

Table 11. Dietary (interspecific) niche overlap (Horn’s overlap of dietary index of relative importance, IRI) among turtle species from Policeman’s Crossing

Species	<i>Elseya dentata</i>	<i>Emydura victoriae</i>	<i>Emydura subglobosa</i>
<i>E. dentata</i>	X	0.49	0.70
<i>E. victoriae</i>		X	0.75
<i>E. subglobosa</i>			X
Sample size (n)	21	23	25

At Policeman’s Crossing, *E. dentata*, *E. subglobosa* and *E. victoriae* had a moderate level of niche overlap (Table 11) because of the common consumption of miscellaneous animal matter (mostly freshwater sponge) (Tables 2, 4, 5). The microhabitat overlap among these three species was also

moderate (Table 12), resulting in levels of multidimensional overlap (Table 13) generally higher than what was found at Ooloo Crossing.

Table 12. Microhabitat utilisation (interspecific) niche overlap (Horn's overlap of percentage of turtles that contained a food item, %f) among turtle species from Policeman's Crossing

Species	<i>Eelseyia dentata</i>	<i>Emydura victoriana</i>	<i>Emydura subglobosa</i>
<i>E. dentata</i>	X	0.85	0.97
<i>E. victoriana</i>		X	0.79
<i>E. subglobosa</i>			X
Sample size (n)	21	23	25

Table 13. Product of dietary and microhabitat utilisation (interspecific) niche overlap among turtle species from Policeman's Crossing

Species	<i>Eelseyia dentata</i>	<i>Emydura victoriana</i>	<i>Emydura subglobosa</i>
<i>E. dentata</i>	X	0.42	0.68
<i>E. victoriana</i>		X	0.59
<i>E. subglobosa</i>			X

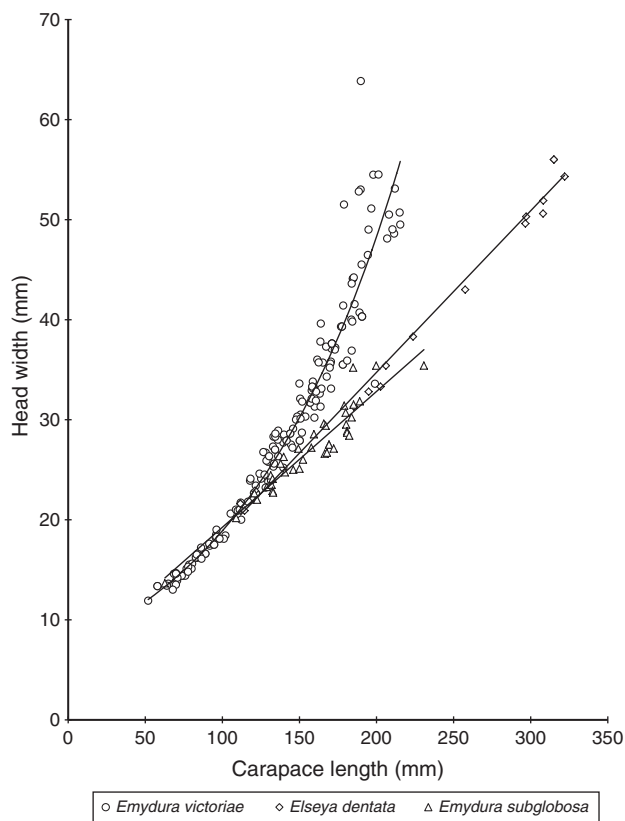


Fig. 1. Regressions of head width (HW) and carapace length (CL) for *Emydura victoriana* (HW (log10)=0.869+0.004CL), *Eelseyia dentata* (HW = 2.436+0.162CL) and *Emydura subglobosa* (HW = 5.664+0.136CL).

Trophic morphology of Emydura turtles

Head width to carapace length for *E. victoriana* followed a significant log-linear regression ($F_{1,147}=0.48, P=0.49$), whereas the regressions of other species were linear (Fig. 1). Head width to carapace length linear regressions were significant for *E. dentata* ($F_{1,15}=1434.61, P=0.00$) and *E. subglobosa* ($F_{1,36}=327.42, P=0.00$; Fig. 1). The length of dentary symphysis of the lower jaw to carapace length for *E. victoriana* also followed a significant log-linear regression ($F_{1,111}=2215.40, P=0.00$), and, for *E. subglobosa*, it followed a significant linear regression ($F_{1,29}=79.24, P=0.00$; Fig. 2). Analysis of covariance showed that male and female *E. victoriana* individuals exhibit the same pattern of development of megacephaly ($F_{1,147}=0.48, P=0.49$) and dentary symphysis ($F_{1,93}=1.43, P=0.23$), but because females grow larger, they exhibit a greater degree of megacephaly and mouth plate size.

Discussion

The results of the present study supported previous research that showed that *C. insculpta* is omnivorous, with a tendency towards herbivory (Georges and Kennett 1989; Heaphy 1990; Georges and Rose 1993). In billabongs in the wet season, *C. insculpta* relies on windfall leaves and fruit (Georges and Kennett 1989), whereas the present study showed that, in the dry season in large rivers, it feeds principally on aquatic

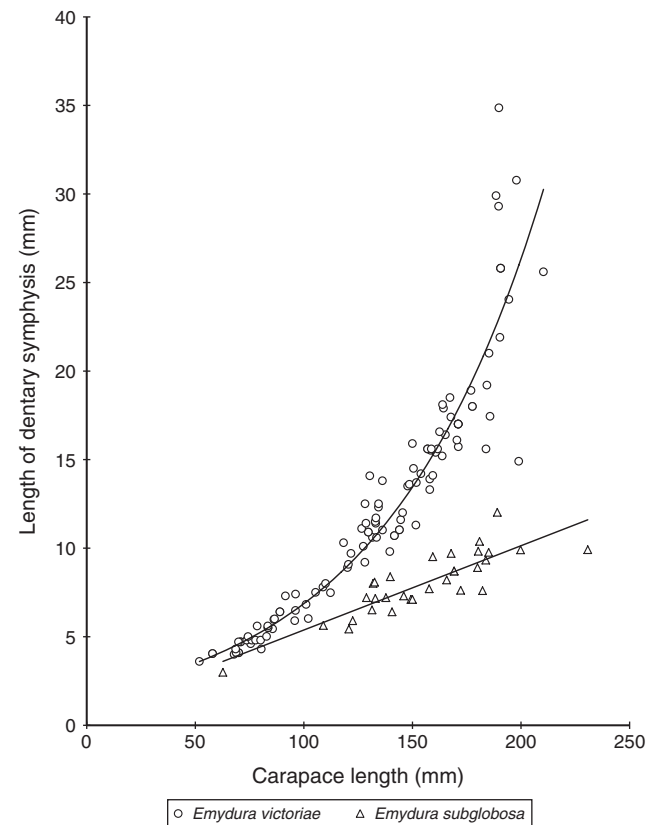


Fig. 2. Regressions of dentary symphysis (LDS) and carapace length (CL) for *Emydura victoriana* (LDS (log10)=0.253+0.006CL) and *Emydura subglobosa* (LDS = 0.622+0.048CL).

vegetation. Mean food mass of *C. insculpta* from the present study was almost two and half times that found in Kakadu billabongs in the wet season by Georges and Kennett (1989; 8.3 g, $n=24$) using the same weighing methods, despite their mean turtle mass being greater (7400 ± 600 g) than in the present study. Even though this indicated that a greater mass of food is consumed in the dry season, 'big' wet seasons are also likely to be important feeding times for *C. insculpta*. Radio-tracking data have shown that *C. insculpta* moves out of the main river channel and into billabongs and low-lying areas when the river is flooded (Doody *et al.* 2002), where it probably forages on riparian and aquatic vegetation. Doody *et al.* (2003) found that *C. insculpta* had larger clutches in both egg number and mass, after big wet seasons.

The present study and radio-telemetry work (Doody *et al.* 2002) suggest that *C. insculpta* spends a great deal of time within patches of ribbonweed. According to optimal foraging theory, an animal's ideal food is one that is abundant enough so that there is no resource depletion during the time the animal spends in a food patch (Pyke 1984). Considering that *C. insculpta* is a large freshwater turtle that requires a large volume of food, ribbonweed may be a favourable food item because it is very abundant and occurs in large discrete patches. Ribbonweed patches also provide good shelter for turtles. We observed that when grazing in ribbonweed, *C. insculpta* is extremely well concealed from above and below the surface.

Tucker *et al.* (1999) showed that ribbonweed (*Vallisneria spiralis*) is a lower-energy food than freshwater algae (which is also very abundant in the Daly during the dry season). A diet of ribbonweed alone is insufficient for the metabolic requirements of *Emydura macquarii*, which requires a supplementary intake of animal matter for growth (Spencer *et al.* 1998). In the Daly River, molluscs are abundant within patches of ribbonweed, occurring in the order of 500–800 molluscs per m^2 (Heaphy 1990). By consuming molluscs while grazing on ribbonweed, *C. insculpta* is supplementing its diet with animal matter, and we conclude that molluscs are probably actively consumed. This differs from the conclusions of Heaphy (1990) who suggested that the consumption of molluscs by *C. insculpta* was incidental.

The present study supports the results of Kennett and Tory (1996), namely that *E. dentata* is primarily herbivorous, and has provided a fuller understanding of the diet of the species. The diet of *E. dentata* in the Daly River (in the dry season at least) was primarily aquatic vegetation, whereas previous reports have suggested that *E. dentata* relies mostly on food of terrestrial origin (Legler 1976; Kennett and Tory 1996). The present study also suggests that *E. dentata* does not shift from carnivory as a juvenile to herbivory as an adult, as was suggested by Kennett and Tory (1996), who had no data from animals smaller than 140 mm. Even though juveniles did eat more invertebrates than did adults, they were still primarily herbivorous.

The herbivorous diet with an almost complete absence of molluscs is a reflection of the trophic morphology of *E. dentata*. *Elseya dentata* has median alveolar and lingual ridging on the bottom jaw that fits into secondary ridging of the upper jaw, an adaptation which is associated with herbivory in other turtles (Legler and Georges 1993). The absence of molluscs in the diet of *E. dentata* suggests that such a trophic morphology is ineffective for ingesting molluscs. As discussed above,

ribbonweed is a lower-energy food than are aquatic algae (Spencer *et al.* 1998). The lack of animal food in the diet of *E. dentata* suggests that it should be feeding on the most nutritious plant matter available, and in the dry season in the Daly, this may be algae.

Dietary overlap between *C. insculpta* and *E. dentata* reflects the generally herbivorous nature of their diets. Previous dietary studies have shown that the diets of the two species in the Top End of the Northern Territory seems to be similar, with a heavy reliance on terrestrial fruit and leaves (Kennett 1994; Georges and Kennett 1989). In the present study, *C. insculpta* and *E. dentata* had a fairly high dietary overlap owing to the common consumption of aquatic vegetation. Unpublished quantitative behavioural observations made by Ashe Pepper suggested that these two species may compete for foraging resources within ribbonweed patches in the Daly River. In the present study, large *C. insculpta* individuals were observed exhibiting territorial behaviour within ribbonweed patches, chasing the smaller *E. dentata* individuals from preferred foraging places. Microhabitat partitioning between *C. insculpta* and *E. dentata* was evident in our study. *Carettochelys insculpta* occupied discrete patches of ribbonweed, whereas *E. dentata* was usually found near the riverbank, under the shelter of submerged tree branches. This partitioning of microhabitat resulted in a low multidimensional niche overlap between the two species.

Trophic morphology and previous examination of diet suggested that *C. oblonga* prefers fast-moving prey (Kennett 1994). Like other long-necked chelid turtles, *C. oblonga* is capable of accurate strikes at fast-moving prey and engulfing prey by suck and gape ingestion (Legler and Georges 1993). However, in the present study, *C. oblonga* mostly ate food items that were not fast moving (molluscs). Mean food mass from the present study was far less than what Kennett (1994) found from *C. oblonga* in ephemeral billabongs in the dry season (3.8 ± 0.8 g, $n=29$). In the coastal floodplains of the Top End of the Northern Territory, *C. oblonga* is known to either aestivate beneath the mud or migrate over land to permanent water bodies during the dry season (Kennett 1994; Kennett *et al.* 2014). It is likely that *C. oblonga* uses the Daly as a dry-season refuge, and suspends foraging until more favourable conditions return. *Chelodina oblonga* is rarely seen in open water, preferring to hide among the branches or roots of fallen trees or beneath undercut banks, and only came out when disturbed, suggesting that it was not feeding in open water. We observed that *C. oblonga* was occasionally partially buried in mud at the water's edge, with only the tip of the snout visible (also noted by Cann 1998). This behaviour has also been observed for *Chelodina expansa*, and may be associated with an ambush-predation strategy (Legler and Georges 1993).

The present study showed that *E. victoriae* is an opportunistic omnivore that becomes more molluscivorous as it grows, and, as a large adult, is a mollusc specialist. Large adult *E. victoriae* is best described as a 'carnivorous grazer' (Legler 1972), because most of its food consists of sessile or slow-moving animals. *Emydura victoriae* has enlarged triturating surfaces that fuse medially in the upper jaw, and dentary symphysis in the lower jaw, that act as crushing surfaces and increase leverage between the jaws, and large adults of the species are megacephalic, having

a large and broadly expanded head that is too large to fit into the carapace (Legler and Georges 1993). In the present study, dietary shift towards molluscivory with age coincided with increasing megacephaly and protrusion of triturating surfaces. This supports the theory that such a trophic morphology (that has evolved convergently in several turtle genera) is an adaptation to molluscivory (Berry 1975; Vogt 1981; Marion *et al.* 1991; Fachin-Teran *et al.* 1995; Lindeman 2000b).

Juvenile *E. victoriae* individuals were omnivorous but consumed few molluscs. Juveniles may consume more insects than do adults because smaller turtles make better active predators (Georges 1982; Hart 1983). Ontogenetic dietary shift to carnivory has also been observed for the freshwater turtle *Pseudemys rubiventris* (Fachin-Teran *et al.* 1995), a species that consumes large crayfish as adults. Juvenile *Pseudemys rubiventris* is unable to consume animal prey because it is unable to capture crayfish, which aggressively defend themselves (Fachin-Teran *et al.* 1995). In the case of *E. victoriae*, juveniles could lack the mouth gape to ingest molluscs and the jaw strength to crush them, because even very small *Thiara* snails are quite hard. Large adult *E. victoriae* ate large molluscs, including *Notopala* snails and the largest molluscs found in the Daly River, *Lortiella* mussels. Presumably, these larger molluscs are too large to be crushed by small adult *E. victoriae* individuals that lack the large mouth gape and megacephaly of large adults. In very large individuals of *E. victoriae*, there is often wear to the tomial edges of the jaw sheaths, which do not meet (Legler and Georges 1993), and which would prevent the animals from biting off pieces of vegetation. This could explain why large *E. victoriae* consumed virtually nothing but molluscs, and why no turtles larger than 189 mm consumed any plant material. Female *E. victoriae* individuals more frequently developed extreme megacephaly than did males, because females grow to a larger size. This pattern of variation in trophic anatomy caused by sexual size dimorphism has been reported for *Trionyx ferox* (Dalrymple 1977). Even though females consumed more large molluscs than did males, the present study showed that the sexual dimorphism of trophic morphology has not led to a substantial divergence in dietary preference between males and females, when comparing overall dietary overlap.

All molluscs in *E. victoriae* guts were crushed, whereas, in *C. oblonga* (who lack crushing plates), they were always uncrushed. If turtles can eat molluscs whole, it raises the question of why *E. victoriae* and other turtles that eat molluscs need crushing plates? There are three likely explanations. (1) Larger molluscs can be eaten because, when crushed, they are more easily taken into the mouth. The ability to crush the edge of mussel shells allows turtles to open them and remove the flesh and avoid eating parts of the shell (Dalrymple 1977). We found evidence for such a feeding strategy, in that complete mussels were never found in *E. victoriae*, only the soft body parts and a few fragments of shell. *Emydura victoriae* has been observed opening very large bivalves in this manner in captivity (Scott Thomson, pers. comm.). (2) Crushed molluscs may pass quicker and more efficiently through the digestive system than do whole ones, so crushing molluscs may be the only way turtles can eat large quantities of them. (3) Digestible matter may be released in the crushing process, providing calorific or nutritional components that would otherwise pass through the turtle. Crushed molluscs

may provide an extra source of calcium for gravid female turtles during eggshell production (Legler 1972) during the dry season, when *E. victoriae* appears to nest (Doody and Welsh 2005).

Megacephaly combined with crushing plates allows adult *E. victoriae* to exploit a molluscan food resource to a level not possible by other species. This advantage is at the expense of the ability of large, extremely megacephalic individuals to withdraw their heads into their shells for protection. Adult *E. victoriae* consumed mostly snails of the genus *Thiara*, which are small and very hard-shelled. These snails are much harder than *Notopala* snails, so *E. victoriae* may be the only species of turtles in the Daly that can crush and, hence, consume large quantities of them. In evolutionary terms, the advantage of being able to exploit molluscs to such a degree must outweigh the disadvantage of being unable to withdraw the head into the shell. Only fairly large individuals cannot withdraw their heads and, hence, only a small proportion of populations are affected, whereas the ability to exploit molluscs would benefit all but juveniles of the species.

Emydura subglobosa was found to be an opportunistic omnivore. It has a trophic morphology indicative of a general diet: it lacks crushing plates and megacephaly (Thomson 1996) typical of molluscivorous turtles like *E. victoriae*, the dentary ridging of herbivores like *E. dentata*, or the long and agile neck of active predatory turtles like *C. oblonga*. In a habitat with many sympatric species such as the Daly River, the lack of a specialised feeding apparatus may disadvantage *E. subglobosa*, and this may be limiting its ability to exploit resources as effectively as do other species in the dry season. Poor foraging success is evident in the low gut-content mass and in the low proportion of *E. subglobosa* individuals that had food in their gut. The greater foraging success and relative abundance of *E. subglobosa* at Policeman's Crossing may be due to the presence of a food resource (sponge) that does not appear to be the favoured food of the other turtle species, and it may reflect a preference for more lentic waters. It is possible that *E. subglobosa* feeds primarily in the wet season. We observed that *E. subglobosa* does seem relatively more common in billabongs in the vicinity of the Daly River, so this could be more preferable habitat for the species.

In floodplain rivers, a large proportion of the primary productivity that supports consumers occurs outside the main channel (Pettit *et al.* 2011). The freshwater turtles of the wet-tropics are usually reported as being heavily reliant on the seeds, fruits and leaves of riparian vegetation (Kennett and Georges 1989; Georges and Wombey 1993; Georges *et al.* 1993; Kennett and Tory 1996). The present study has shown that the dry-season diet of turtles in perennial rivers is primarily of aquatic origin, and *E. victoriae*, *C. insculpta* and *E. dentata* are likely to rely substantially on ecological resources within the main channel.

Much of the land adjacent to the Daly River is privately owned, and land use has had little impact on the aquatic biota of the river (Schult and Townsend 2012). However, the Daly River catchment is subject to an increasing development pressure from land clearing, agriculture and groundwater extraction, and this is likely to continue under Australian Government plans to develop the north of Australia (Australian Government 2015). Tucker (1999) found that river modifications in Queensland had an impact on freshwater turtles that are ecological specialists. The present study found that *C. insculpta*, *E. dentata* and *E. victoriae*

are ecological specialists that rely heavily on dry-season aquatic food resources, in particular on aquatic macrophytes (*Vallisneria* sp. and aquatic algae) and molluscs. This emphasises the need for any broad-scale development in the Daly River region to carefully consider potential impacts to aquatic macrophytes and molluscs of the Daly River, and how any impacts to those resources might affect freshwater turtle populations.

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