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Diet of *Elseya purvisi* and *Elseya georgesi* (Testudines: Chelidae), a Sibling Species Pair of Freshwater Turtles from Eastern Australia

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Turtle abundance is determined in part by availability of potential foods and the ability of the turtles to access them. If resources are limiting and are subsequently reduced through habitat modification, then reproductive output may decrease, growth rate of juveniles or condition of the adults in the population may suffer, mortality may rise, and the population may decline. Australian rivers, streams, and wetlands, particularly in southeastern Australia, have been greatly modified by human activity (Williams, 1980). Removal of macrophytes, increased turbidity and sedimentation, salinization, clearing of riparian vegetation, dramatically altered flow regimes, introduction of invasive competitors such as European carp, and lowered temperatures below dams and impoundments can all be expected to alter the composition and abundance of available turtle foods. Knowledge of the diet of a species may provide important insights into the potential consequences of habitat modification and the causes of population decline.

Animals with catholic tastes or that are opportunistic in their use of available foods are likely to be less vulnerable to habitat modification than are those with specialized dietary requirements. There is considerable variation in the degree of dietary specialization among Australian freshwater turtles. *Elseya dentata* is primarily herbivorous, feeding upon the fruit and leaves of riparian vegetation, filamentous algae, and carrion when available (Kennett and Tory, 1996). *Chelodina expansa*, *C. rugosa*, *C. longicollis*, *Pseudemydura umbrina*, and *Rheodytes leukops* are strict carnivores (Legler, 1978; Legler and Cann, 1980; Burbidge, 1981; Georges et al., 1986; Kennett and Tory, 1996). Within the confines of carnivory, *Chelodina expansa* and *C. rugosa* selectively feed on highly motile prey such as decapod crustaceans, aquatic bugs, and small fish, although they will take carrion when available (Legler, 1978; Chessman, 1983; Kennett and Tory, 1996). *Chelodina longicollis* on the other hand, has a diverse and opportunistic diet (Chessman, 1984; Georges et al., 1986). Although carnivorous, *P. umbrina* and *R. leukops* are short-necked species that lack the specialized morphological adaptations of *Chelodina* and the other long-necked chelids necessary for securing fast-moving prey (Pritchard, 1984). *Carettochelys insculpta* and species in the genus *Emydura* are opportunistic omnivores (Legler, 1976; Georges, 1982; Chessman, 1986; Georges and Kennett, 1989), although they may be carnivorous when young with increasing tendencies toward herbivory as they age (Georges, 1982). Their opportunism provides great scope for their diet to vary from locality to locality, in response to differences in available foods, and presumably provides the ability to respond to changes in available foods resulting from human-induced impacts.

Despite these studies, and with the exception of *P. umbrina* (Burbidge, 1981), detailed dietary data are lacking for threatened species with restricted distributions or low or declining populations, yet it is in the management of such threatened species that this information will be of greatest utility. Part of the reason for our lack of knowledge is that many species that occupy single drainages have only recently been described (e.g., *R. leukops* and *Elusor macrurus*) or have yet to be described (Legler and Cann, 1980; Cann and Legler, 1994; Georges and Adams, 1996). In this study, we determine the diets of two recently described species with close affinities to *Elseya latisternum* (Georges and Adams, 1992).

Elseya georgesi (Cann, 1997) is found only in the Bellinger drainage of coastal New South Wales. *Elseya georgesi* and a second form (*E. purvisi*) from the Manning-Barnard drainage 160 km to the south are a sibling species-pair that for many years were regarded as the same taxon (Cann, 1978; Legler, 1981). They are morphologically difficult to distinguish on external characters (Cann, 1978) but are very distinctive electrophoretically (Georges and Adams, 1996) and in their neural bone exposure (Thomson and Georges, 1996). The Manning-Barnard species was given the name *Elseya purvisi* by reference to published photographs and with scant diagnosis (Wells and Wellington, 1985). Despite these shortcomings, this name is available, and our use of it follows that of Cann (1997). This should in no way be taken as support for the many other names provided by Wells and Wellington (1985) without adequate description or diagnosis.

Materials and Methods. — Specimens of *Elseya purvisi* were obtained in January 1993 by diving with the aid of mask and fins from one location in each of the Manning and Barnard Rivers; *Elseya georgesi* were obtained by similar means in the same month from one location in the upper reaches of the Bellinger River. Turtles were captured from several kilometers of river at each location, spanning a number of pools and the full range of habitat variation present. Stomach contents of a total of 72 specimens were obtained by stomach flushing (Legler, 1977). A 12 V submersible pump (L.V. Motors model 105) was used to supply a steady flow of water, which was passed into the stomach through a flexible plastic tube. Water flow was adjusted for turtles of different sizes by interchanging tubes of different diameters. The 72 animals comprised 12 juveniles (73–130 mm carapace length [CL]), 38 males (137–172 mm CL) and 22 females (155–217 mm CL). Three individuals, in addition to these, yielded little or no material. Either their stomachs were empty, or their stomach contents were not dislodged. Data from these individuals were not included in the analysis. All turtles were flushed as soon as possible, and never more than 2 hrs after capture, then released. Stomach contents were fixed and preserved in FAA Solution (Luna, 1968) and later examined under a stereo microscope for identification by the authors. Sand and other indigestible items were considered to have been accidentally ingested, and were excluded from analysis.

Percentage composition by number and percentage occurrence (Windell and Bowen, 1978) were used to evaluate the relative importance of different foods. The numerical method involved counting the number of items belonging to each taxonomic group. Aquatic insects and small crustaceans usually remained intact and were easy to count. The numbers of terrestrial arthropods, when fragmented, were determined from the numbers of hindwings or other identifiable parts. Items that did not occur as discrete units (filamentous algae, ribbon weed [*Vallisneria* sp.], fig fragments [*Ficus* sp.], and barley from livestock feces) could not be counted and were simply recorded as present or absent. As such, they did not contribute to the numerical estimates, but did contribute to estimates of importance based on percentage occurrence. The percentage occurrence method involved expressing the number of turtles that had eaten one or more items of a particular food as a percentage of the number of animals examined. Windell and Bowen (1978) discussed the relative merits of these two methods, among others.

Differential rates of digestion and passage through the gut for different types of food contribute an element of bias into estimates of the relative importance of food types calculated from stomach contents. The importance of foods with a relatively slow rate of passage will be overestimated. This source of bias was held to a minimum by excluding from the analysis partly digested invertebrates found in the mucous plug which occupies the pyloric stomach before it is dislodged by the flushing process. The importance of foods that deteriorate rapidly in the stomach, such as oligochaetes, cannot be determined.

Results and Discussion. — Table 1 lists foods of *Elseya georgesi* and *E. purvisi*, together with an indication of the relative importance of each major food type. Both species are omnivorous, though with strong leanings toward carnivory. Trichopteran larvae (primarily Leptoceridae and Calamoceratidae) were the most important prey items, both in terms of percent occurrence and numerically. Lepidopteran larvae (Pyralidae) were also important, particularly at the Manning River site. There were no striking differences in the composition of invertebrate foods across localities or species except that terrestrial insects that fell upon the water were found in 15.8% of stomachs from the Manning River locality, in trace amounts only from the Barnard River locality, and were absent from the Bellinger River locality. Indeed, the taxa represented in the diets were remarkably uniform across species and localities at

Table 1. Relative importance of prey items in the diets of *Elseya georgesi* and *Elseya purvisi* from coastal New South Wales, Australia. Percentage occurrence is the number of turtles with a particular food type in their stomachs expressed as a percentage of the total number of turtles examined. Percentage numerical is the number of items in a category expressed as a percentage of the total number of items counted. Abbreviations: A = adults, L = larvae; P = pupae, * = trace only, blank = zero occurrence, – = not counted.

	Elseya georgesi		***Elseya purvisi***			
	Bellinger River		**Barnard River**		**Manning River**	
Prey Type	% Occurrence	% Numerical	% Occurrence	% Numerical	% Occurrence	% Numerical
ANIMAL MATERIAL	**100.0**	–	**100.0**	–	**89.5**	–
Coleoptera	**22.6**	**0.8**	**54.5**	**1.6**	**57.9**	**2.3**
Dytiscidae spp (A, L)	3.2	*			5.3	0.1
Elmidae spp. (L)	12.9	0.6	31.8	1.1	10.5	0.3
Hydrophilidae spp. (A,L)	6.5	*	13.6	0.2	15.8	0.4
Hygrobiidae spp. (A,L)					10.5	0.3
Psephenidae spp. (L)			9.1	0.2	26.3	0.8
Staphylinidae spp. (L)					5.3	0.1
Terrestrial (A)			*	*	15.8	0.4
Diptera	**25.8**	**0.9**	**72.7**	**5.5**	**31.6**	**2.3**
Athericidae spp. (L)	3.2	*				
Ceratopoginidae spp. (L)			9.1	0.2		
Chironomidae spp. (L,P)	25.8	0.7	68.2	5.0	31.6	2.2
Tabanidae spp. (L)	3.2	0.1	13.6	0.3		
Ephemeroptera	**6.5**	**0.1**	**45.5**	**6.3**	**15.8**	**0.8**
Caenidae: *Tasmanocoenis* sp. (L)	6.5	0.1	22.7	0.6	5.3	0.3
Leptophlebiidae spp. (L)			31.8	5.7	15.8	0.5
Lepidoptera						
Pyralidae (Nympulinae)	**16.1**	**5.1**	**40.9**	**10.5**	**52.6**	**29.4**
Odonata	**12.9**	**0.6**	**77.3**	**6.6**	**47.4**	**2.8**
Aeshnidae: *Austroaeschna* sp. (L)			*	*		
Coenagrionidae: *Austrocnemis splendida* (L)	3.2	*				
Corduliidae: *Cordulephya pygmaea* (L)			18.2	0.4	5.3	0.3
Gomphidae: *Austrogomphus ocraceus* (L)			36.4	1.6	26.3	0.9
Protoneuridae: *Isosticta simplex* (L)	9.6	0.5	50.0	4.4	31.6	1.7
Synlestidae			*	*		
Trichoptera	**96.8**	**92.4**	**100.0**	**69.5**	**78.9**	**62.6**
Atriplectidae spp. (L)	19.4	1.7	54.5	7.8		
Calamoceratidae spp. (L)	58.1	9.5	90.9	26.6	57.9	17.9
Conoesucidae spp. (L)	9.6	0.2	*	*	5.3	0.1
Ecnomidae spp. (L)			22.7	1.0	5.3	0.1
Glossosomatidae spp. (L)			*	0.5	5.3	0.1
Helicophidae spp. (L)	19.4	1.7			10.5	0.3
Helicopsychidae spp. (L)	16.1	0.4			47.4	9.9
Hydropsychidae spp. (L)					10.5	0.4
Hydroptilidae spp. (L)	9.6	0.2	18.2	1.1	5.3	0.1
Leptoceridae spp. (L)	96.8	76.3	95.5	29.6	78.9	30.4
Pupae (unidentified)	48.4	2.7	45.4	2.8	42.1	3.2
PLANT MATERIAL	**35.5**	–	**36.4**	–	**63.2**	–
TOTALS	31 turtles	1415 items	22 turtles	1045 items	19 turtles	780 items

the family level. Those differences that did occur could probably be explained by differences in availability of foods at the different localities, although this was not quantified.

Plant material was present in the stomachs of approximately 35% of turtles from the Bellinger and Barnard Rivers and in 63% of turtles from the Manning River. Figs, many of which had been parasitized by wasps (*Idarnes australis*), algae, and ribbon weed (*Vallisneria* sp.) were the principal plant foods, though many turtles in the Manning River had eaten partially digested barley from cattle feces.

Although sample sizes precluded detailed statistical analysis, it was evident that larger animals had a greater propensity to consume plant matter. Algae and ribbon weed were found in substantial quantities in three of the largest females from both the Bellinger and Manning Rivers. Large females (CL > 200 mm) had eaten no ephemeropteran or lepidopteran larvae. Juveniles (CL < 135 mm) consumed very little plant material and ephemeropteran larvae, and odonate nymphs were generally absent from their stomachs. Females with CL in the range of 160–200 mm consumed a greater proportion of pyralid (Lepidoptera) larvae than males in the same size group, and mature females in general had a greater propensity (72.7% of stomachs) to consume plant material than mature males (33.3%) or juveniles (16.7%). There were no appreciable differences in the diet of males, females, or juveniles when compared separately across rivers.

Both *E. georgesi* and *E. purvisi* are essentially omnivores, gaining a high proportion of their food from benthic macro-invertebrate communities (>95% by occurrence), but with some terrestrial fruit and aquatic vegetation eaten. They feed upon prey that are relatively sedentary and live in immediate association with the substratum, such as cased caddis-fly larvae (Leptoceridae) and lepidopteran larvae (Pyralidae) (Table 1). Like *Emydura*, these turtles lack the specialized morphological adaptations and behavior of *Chelodina* (Legler, 1976; Pritchard, 1984) required to secure fast-moving prey such as fish and adult coleopterans and hemipterans. Within these constraints, the wide range of foods taken gives no indication that *E. georgesi* and *E. purvisi* are selective in what they eat, though substantive data to allow a comparison between diets and prey availability are lacking (see Georges et al., 1986).

Ontogenetic dietary shifts in turtles are common (Clark and Gibbons, 1969; Georges, 1982; Chessman, 1984, 1986; Kennett and Tory, 1996), with juveniles of omnivorous species tending toward carnivory and adults tending more toward herbivory. This variation in diet within single populations has been explained in terms of optimal foraging, energetic efficiency (Clark and Gibbons, 1969; Georges, 1982; Parmenter and Avery, 1990), microhabitat differences in prey availability (Hart, 1983), and increasing strength as the turtles grow larger, enabling them to take advantage of a wider range of foods (Georges, 1982; Chessman, 1986). Dietary shift was evident but not pronounced in the present study, with the two species of *Elseya* examined falling more toward the carnivorous end of the spectrum overall than other omnivorous Australian *Emydura* species so far examined (Georges, 1982; Chessman, 1983, 1984). Dietary shift toward herbivory was only strongly evident when the very largest females were examined. There was evidence of prey size difference among turtles of different sizes. Lack of ephemeropteran and odonate larvae in the foods of juvenile turtles, and their presence in the diets of larger turtles probably reflects the general tendency of smaller turtles to feed upon smaller prey items (Moll, 1976; Georges, 1982; Chessman, 1983, 1984). This may also explain the reverse trend whereby smaller turtles tended to have more items in their stomachs than larger turtles, true also of *Chelodina expansa* (Chessman, 1983).

Both the Bellinger and Manning-Barnard systems are clear-water, continuously flowing rivers in their middle and upper reaches, with an instream macro-invertebrate fauna that is diverse and appears to have been little impacted by human activity within their respective catchments. The present study shows that both *E. georgesi* and *E. purvisi* currently draw the bulk of their foods from the macro-invertebrate fauna closely associated with the river bed. Increased sedimentation can result from bank erosion, removal of vegetation and consequential increased run-off and erosion within the catchment, altered flow regimes, livestock access, and the introduction of European carp (Williams, 1980; Fletcher et al., 1985). Sedimentation from such disturbances can be expected to smother the stream bed by filling interstitial spaces and restricting growth of aquatic macrophytes, both of which provide refugia and habitat for aquatic macro-invertebrates. Consequential changes in the sedentary benthic macro-invertebrate fauna, as have occurred in many other Australian streams, may substantially impact these turtle populations. Their reliance on sedentary benthic macro-invertebrates may exacerbate their vulnerability, already high because both species each occupy single small drainages.

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