Copeia, 1982(2), pp. 331–336

Diet of the Australian Freshwater Turtle *Emydura krefftii* (Chelonia: Chelidae), in an Unproductive Lentic Environment

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The abundance of *Emydura krefftii* in the nutrient-deficient dune lakes of Fraser Island, Australia, is explained in terms of the species' broad food habits and its ability to directly utilise foods of terrestrial origin. Small specimens of *E. krefftii* are carnivorous, relying principally on aquatic and terrestrial insects, and small crustaceans. As they grow, the turtles become omnivorous and eat larger varieties of insect and crustacean. The changes in diet with increasing turtle size are explained in terms of energetic efficiency, and by the fact that as the turtles grow, more robust food items become available to them. The diets of mature males and females of similar sizes do not differ appreciably.

THE diets of Australian freshwater turtles have only recently been the subject of detailed studies. Parmenter (1976) described the diet and feeding behavior of the carnivorous *Chelodina longicollis,* and Chessman (1978) compared its diet with those of *Emydura macquarii* and *Chelodina expansa.* Legler (1976) reported the feeding habits of *Elseya dentata, Emydura australis* and an unnamed species of *Emydura* from Kookabookra (New South Wales). There are no detailed reports on the diet of *Emydura krefftii.*

E. krefftii is widespread in Queensland where it inhabits large rivers and the larger waterholes and billabongs of their floodplains (Cogger 1975:133). In this paper I describe the diet of *E. krefftii* in an unusual environment—a dune lake on Fraser Island, off the Queensland coast. The study site, Lake Coomboo, is typical of the tea-colored lakes of Fraser Is. They are oligotrophic, with very dilute, acidic waters containing high proportions of dissolved allochthonous organic material (Bayly, 1964; Bayly et al., 1975). Their brown coloration severely limits penetration of sunlight, restricting photosynthetic growth to surface waters (Bayly, 1975). Limited photosynthesis, coupled with low concentrations of nutrients, results in low productivity. The invertebrate fauna of dune lakes is low in both diversity and numbers, when compared with other freshwater lakes (Timms, 1973). Molluscs, eaten by *E. krefftii* in mainland water bodies, are absent from the dune lakes of Fraser Is., and fish are typically represented by one or two species (Arthington, 1977).

Despite the low productivity, *E. krefftii* is abundant in most of the permanent lakes of Fraser Is. For example, in Lake Coomboo (8.8 ha accessible to the turtles), 683 *E. krefftii,* eleven *Chelodina expansa* and two *Chelodina longicollis* were captured. The population density of *Emydura krefftii* exceeds 81 turtles per hectare.

The aim of the present study was to determine the diet of *E. krefftii* in the dune lakes of Fraser Is., and so gain some insight into their surprising abundance in a seemingly unproductive environment.

Materials and Methods

The stomach contents of 97 turtles from Lake Coomboo (25°13′S, 153°10′E, Fraser Is.) provided data on the diet of *E. krefftii* during the warmer months of 1978 and 1979; 13 were caught in September, 28 in November, 11 in January, 6 in February, 25 in March and 14 in May. All specimens were captured in the late afternoon (after 1500 hr) in hoop traps (Legler, 1960) baited with bread. The bait was enclosed in perforated containers to prevent it from being eaten.

Stomach contents were removed by stomach flushing (Legler, 1977). Sixteen turtles yielded little or no material; either their stomachs were empty, or their stomach contents had been only partly dislodged. Data from these individuals were not included in the analysis. All turtles were flushed as soon as possible—and never more than 3 hours—after capture.

Carapace length and sex were recorded for each turtle before its release. Stomach contents were preserved in FAA solution (Luna, 1968:4) and later examined under a low-power binocular microscope. Sand and fragments of litter were assumed to have been accidentally ingested and were not included in the analysis of food items.

Percentage composition by number and percentage composition by volume (Windell and Bowen, 1978) were used to evaluate the relative proportions of different foods eaten by *E. krefftii*. The numerical method involves 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 hind wings or other identifiable parts. Solid plant material and the large decapod crustacean *Cherax robustus* were seldom eaten whole so the numbers of fragments (= bites) were included in the analysis. Items which did not occur as discrete units (such as filamentous algae and *Utricularia* sp.) could not be counted and were omitted from the numerical analysis.

The volumetric method relies on estimating the volume of taxonomically similar items from each stomach. In this study, the volume of a food item was taken to be proportional to the product of its length, width and depth. These linear measurements were obtained using a calibrated eyepiece or vernier calipers. When large numbers of prey items of similar size were found, only representative items were measured. The linear dimensions of fragmented items were either estimated from those of an intact item of similar size, or the fragments were measured separately. The volume of filamentous plant material was estimated by removing excess moisture and measuring the material's displacement in a graduated cylinder of water.

To investigate variation in diet with turtle size, stomach samples were grouped according to the size of the turtles from which they were taken (each size-class contained samples from at least ten turtles). The proportions of different foods in each size-class were then compared. The mean length of food items for which the entire length could be determined was also compared among different size-classes.

To examine differences in diet due to sex, mature specimens were first divided into males and females, then new size-classes within each sex-class were computed. The data were then adjusted so that data for each size-class contributed equally to the overall result for the sex-class. These measures were necessary to remove effects due to the particular size distribution of the turtles examined.

Results

The food *E. krefftii* in Lake Coomboo is listed in Table 1 together with an indication of the relative importance of each major food type. *E. krefftii* is clearly an omnivorous species with both plant and animal material contributing substantially to the diet. The plant food consists principally of the freshly sprouted shoots of sedges (*Lepironia articulata* and *Baumea* spp.) exposed when the turtles dig in the sand at the bases of these plants. Algae and the bladderwort, *Utricularia* sp., although contributing little to the overall diet of the Coomboo population, were found in substantial quantities in a few individuals. Caddisfly larvae (Leptoceridae), midge larvae and pupae (Chaoborinae, Chironomidae, Ceratopogonidae), dragonfly nymphs (Anisoptera), decapod crustaceans (*Cherax robustus* and *Caridina indistincta*) and terrestrial arthropods are the major animal components of the diet. Mayfly nymphs (Leptophebiidae), damselfly nymphs (Zygoptera), alderfly larvae (Sialidae) and beetle larvae (Gyrinidae) were also present in substantial quantities in the stomachs of a few individuals. The colonial ciliate, *Ophridium* sp. (in association with *Zoochlorella parasitica*) and tubificid oligochaetes deteriorate rapidly once in the stomach, so it was impossible to gauge their importance to the diet.

Variation in diet with body size.—Larger turtles tend to eat larger food items than do smaller turtles. The significance of this relationship is indicated by the non-overlap of the 95% confidence intervals in Fig. 1, and by the fact that a positive correlation between the mean length of food items (by individual) and turtle length proved significant ($r = 0.35$, $P < 0.001$, $N = 81$). In addition, food items taken from large turtles varied more in size than those from small turtles. These changes in food item size with turtle size are sufficient to explain changes in the qualitative composition of the diet.

Differences in composition between the diets of turtles in different size groups are presented in Fig. 2. There is an obvious trend away from eating aquatic insects as turtle size increases. Turtles less than 100 mm in length eat large numbers of small caddisfly larvae (principally the sand-grain encased *Oecetis* spp.) and the

TABLE 1. ITEMS FROM THE STOMACHS OF 81 SPECIMENS OF *Emydura krefftii*, WITH AN INDICATION OF THE RELATIVE IMPORTANCE OF EACH FOOD TYPE TO THE OVERALL DIET OF THE COOMBOO LAKE POPULATION. An asterisk indicates a contribution to the diet of less than 1%. Percentage by occurrence gives the number of stomachs that contained one or more items of a particular food type, expressed as a percentage of the total number of stomachs examined. Abbreviations: L, larvae; P, pupae; N, nymphs; A, adults.

Food type			Percentage by number	Percentage by volume	Percentage by occurrence
PLANT MATERIAL			**20**	**30**	**56**
Div. RHODOPHYTA	Batrachospermaceae	*Batrachospermum* sp.	—	7	6
Div. CHLOROPHYTA	Oocystaceae	*Zoochlorella parasitica*			
	Zygnemaceae	*Zygogonium ericetorum*			
		Zygogonium kumaoense			
Div. MAGNOLIOPHYTA	Cyperaceae	*Baumea* spp.	20	23	55
		Lepironia articulata			
	Lentibulariaceae	*Utricularia* sp.			
ANIMAL MATERIAL			**80**	**70**	**98**
Ph. PROTOZOA	Ophrydiidae	*Ophrydium* sp.	—	—	—
Ph. ANNELIDA	Tubificidae		*	*	2
Ph. ARTHROPODA					
Cl. Crustacea	Parastacidae	*Cherax robustus*	5	25	64
	Atyidae	*Caridina indistincta*			
Cl. Insecta					
O. Coleoptera	Dytiscidae (A)	Gyrinidae (L,A)	*	*	10
O. Diptera	Ceratopogonidae (L), Culicidae (L,P)	Chironomidae (L)	12	1	19
O. Ephemeroptera	Leptophlebiidae (N)		5	2	14
O. Hemiptera	Corixidae (N,A)	Naucoridae (N,A)	*	*	5
O. Megaloptera	Sialidae (L)		2	2	14
O. Odonata	Corduliidae (N), Gomphidae (N)	Libellulidae (N), Miscellaneous Zygoptera	5	18	48
O. Trichoptera	Leptoceridae (L)		42	9	51
Miscellaneous Terrestrial Arthropods			8	11	38
		Raw totals	1,960 (items)	54.69 (cm^3)	81 (turtles)

equally small midge larvae and pupae (principally chaoborids and chironomids). These small insects contribute negligibly to the diets of turtles exceeding 140 mm in length. Instead, the larger dragonfly nymphs make up most of the insect matter eaten by this group, and of the caddisfly larvae eaten, most are the larger *Triplectides* sp. (stick-encased type).

A trend toward omnivory is also obvious from the data presented in Fig. 2. Turtles less than 100 mm in length are almost totally carnivorous with items of plant material comprising less than 2.5% of the total number of items eaten by this group. This represents 7.2% of the volume of food eaten. Only 2.6% of the volume of food eaten by the 11 individuals smaller than 85 mm was plant material. The quantity of plant material increases, both in volume and in terms of the number of plant items (=bites) eaten, as turtle size increases. It exceeds 50% of the food eaten by turtles between 140 and 180 mm in length. In the largest size-class, however, the trend toward herbivory is overshadowed by a sharp increase in the con-

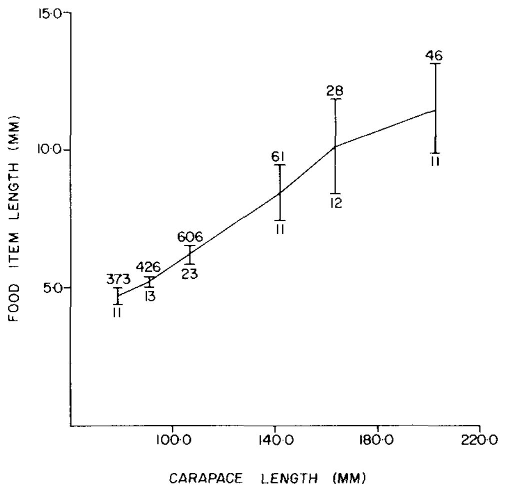

Fig. 1. The relationship between food item size and turtle body size for *Emydura krefftii*. Only data from whole items are included. The vertical bars represent two standard errors either side of the means. The numbers of food items are given above each mean, and the numbers of turtles from which the items were taken are given below each mean.

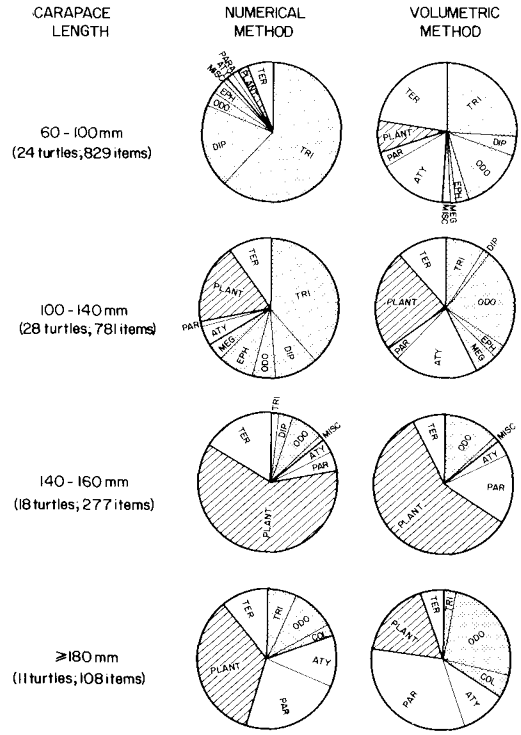

Fig. 2. Variation in the composition of the diet of *Emydura krefftii* with increasing body size. Food types are abbreviated as follows: ATY = atyid crustaceans; COL = coleoptera larvae; DIP = diptera larvae and pupae; EPH = ephemeroptera nymphs; MEG = megaloptera larvae; MISC = miscellaneous aquatic insects; ODO = odonata nymphs; PAR = parastacid crustaceans; TER = terrestrial arthropoda; TRI = trichoptera larvae.

sumption of the relatively large crustacean *Cherax robustus* (Parastacidae)—a food resource that appears to be available only to turtles longer than 140 mm.

Terrestrial insects contribute substantially to the diets of turtles of all sizes (Fig. 2). They consisted primarily of winged insects (probably blown onto the water), though some were terrestrial larvae that likely dropped from the branches of overhanging trees.

Variation in diet with sex.—Males and females of similar sizes (carapace lengths 130–190 mm) ate similar foods, both in terms of percentage composition by number and volume, and in terms of the size of items eaten (14 males, mean food item length = 9.34 ± 0.58, N = 54; 12 females, mean = 9.19 ± 0.80, N = 48).

However, males from Lake Coomboo mature at a length of about 110 mm and are not known to exceed a length of 200 mm. Females mature at the larger size of 155 mm and can reach 250 mm in length. In view of the relationship between diet and body size, mature males and females would be expected, solely on consideration of their differing body sizes, to eat different foods. Differences in the diets of mature males and females are shown in Fig. 3.

Discussion

E. krefftii, though primarily carnivorous when young, is an omnivorous species that draws on a wide variety of food resources. It obtains most of its food in the lake's littoral zone, although planktonic dipteran larvae and terrestrial arthropods are important components of its diet. The fishes *Rhadinocentrus ornatus* and *Hypseleotris* sp., both common in Lake Coomboo, are conspicuously absent from the diet, and few adult aquatic coleopterans and hemipterans are eaten. Presumably *E. krefftii,* a short-necked species, finds it difficult to catch these relatively fast prey species.

The results show a shift away from small food items as the turtle grows, and this was used to explain the qualitative changes in diet with size and the differences between the diets of mature males and females. Dietary changes from youth to maturity are common among turtles. In general, omnivorous species tend toward carnivory when young and toward herbivory as they grow older (Carr, 1952; Clark and Gibbons, 1969; Moll and Legler, 1971; Moll, 1976). Reports of variation in the size of food items with turtle size are also common. The kinosternid turtles studied by Mahmoud (1968) fed predominantly on small aquatic insects, algae and carrion when small, while large individuals fed on prey of all sizes. Similarly, *Graptemys pseudogeographica ouachitensis, Chelodina longicollis* and *Chelodina expansa* tend to eat larger food items as they grow (Moll, 1976; Chessman, 1978).

Most of the variation in diet with size/age exhibited by these species can be explained in terms of energetic efficiency and the fact that as the turtles grow in size and strength, more robust food items become available to them. In Lake Coomboo, small turtles probably lack the strength to uncover and bite off the fibrous shoots of sedges, and a very small turtle might find the tables turned if it attempted to secure a meal by confronting a large *Cherax robustus.* As the turtle grows, the energetic return from small prey items is less able to offset the energy expended in obtaining them. Hence it may be energetically inefficient for larger turtles to forage for small prey items. However, the smallest food items are available to large turtles since they were found in small quantities in the stomachs of turtles in the larger size-classes. Clearly, small turtles eat small food items by necessity; large turtles eat larger items by preference and eat small items when encountered by chance. However, more complex factors may also be involved. For example, Clark and Gibbons (1969) proposed that shift in the diet of *Pseudemys scripta* with increasing body size may be related to the changing calcium requirements of the turtles as they grow.

The dense population of *E. krefftii* in the unproductive, nutrient-deficient environment of Lake Coomboo is testimony to the species' efficiency in using the available food resources. The dune lakes of Fraser Island are unable to maintain large concentrations of waterfowl (Kikkawa et al., 1979), and the obligate carnivores, *Chelodina expansa* and *Chelodina longicollis,* are present there in much lower numbers than *E. krefftii,* although further study is required to determine whether the relative abundance of the three turtle species differ from those in more productive mainland lakes.

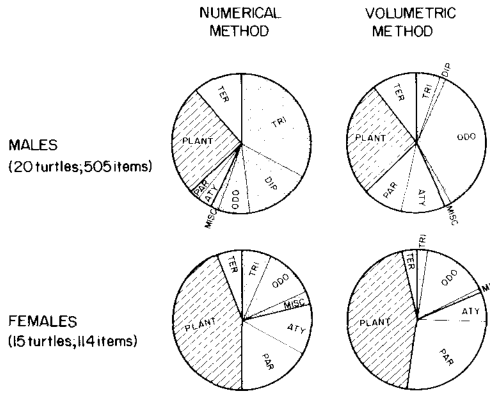

Fig. 3. Differences in the composition of the diets of mature male and female specimens of *Emydura krefftii.* Abbreviations are the same as for Fig. 2.

Terrestrial arthropods are a major food source for *E. krefftii,* contributing up to 20% to the diets of turtles in the smallest size group (Fig. 3). Wind-blown insects contribute to the success of other species inhabiting water bodies of low productivity. Terrestrial insects and pollen are a major food source for the melanotaenid *Rhadinocentrus ornatus* (Bayly et al., 1975) common in the lakes of Fraser Is., and were also for the fishes *Galaxius pedderensis* and *Galaxius parvus* in Lake Pedder, Tasmania, before its destruction (Bayly et al., 1972). The Ouachita map turtle, *Graptemys pseudogeographica ouachitensis,* inhabits a portion of the Mississippi River with a moderate current and turbid water, almost no aquatic vegetation, a constantly shifting inorganic sand bottom, and widely fluctuating water levels (Moll, 1976). It is able to survive in its harsh environment by relying on terrestrial plants and insects flooded when the water level is high, and on occasional carrion, insects and vegetable matter which fall upon the water when the water level is low. Similarly, the broad food habits of *E. krefftii* and its ability to directly utilise food resources of terrestrial origin have no doubt contributed to its success in invading the unproductive dune lakes of Fraser Is.

Acknowledgments

I am deeply indebted to Tony Thulborn for his supervision and advice during the course of this study. Trevor Clifford (magnoliophytes), Alan Cribb (algae), Kevin Lambkin (insects), and Steven Platt (insects) assisted with indentifying items among the stomach contents. I am also grateful to Bruce Chessman, Peter Dwyer, John Legler, Tony Thulborn and Grahame Webb for critically reading the manuscript, and to Glenda Georges for typing the many drafts. The study was funded by a Commonwealth Postgraduate Research Award. The University of Queensland and the Queensland Department of Forestry provided material support.

Literature Cited

Arthington, A. H. 1977. Ecology of Fraser Island Lakes. Occ. Pap. Anthropol. (Queensland University, Brisbane) 8:135–137.

Bayly, I. A. E. 1964. Chemical and biological studies on some acidic lakes of east Australian sandy coastal lowlands. Aust. J. Mar. Freshwat. Res. 15:56–72.

———. 1975. Interactions between terrestrial and aquatic environments: Queensland's coastal lakes. Proc. Ecol. Soc. Aust. 9:325–328.

———, E. P. Ebsworth and H. F. Wan. 1975. Studies on the lakes of Fraser Island, Queensland. Aust. J. Mar. Freshwat. Res. 26:1–13.

———, P. S. Lake, R. Swain and P. A. Tyler. 1972. Lake Pedder: its importance to biological science. *In:* Pedder papers: Anatomy of a decision. Australian Conservation Foundation, Melbourne.

Carr, A. F. 1952. Handbook of turtles. Comstock Press, Ithaca, N.Y.

Chessman, B. 1978. Ecological studies of freshwater turtles in southeastern Australia. Unpubl. PhD Thesis, Monash University, Melbourne.

Clark, D. B., and J. W. Gibbons. 1969. Dietary shift in the turtle *Pseudemys scripta* (Schoepff) from youth to maturity. Copeia 1969:704–706.

Cogger, H. G. 1975. Reptiles and amphibians of Australia. Reed, Sydney.

Kikkawa, J., G. J. Ingram and P. D. Dwyer. 1979. The vertebrate fauna of Australian heathlands—an evolutionary perspective, p. 231–279. *In:* Heathlands and related scrublands of the world, A. Descriptive studies. R. L. Specht (ed.). Elsevier Scientific Publishing Co., Amsterdam.

Legler, J. M. 1960. A simple and inexpensive device for trapping aquatic turtles. Proc. Utah Acad. Sci. 37:63–66.

———. 1976. Feeding habits of some Australian short-necked tortoises. Victorian Nat. 93:40–43.

———. 1977. Stomach flushing: A technique for chelonian dietary studies. Herpetologica 33:281–284.

Luna, L. G. 1968. Manual of histologic staining methods of the Armed Forces Institute of Pathology (3rd Edition). McGraw-Hill Book Co., London.

Mahmoud, I. Y. 1968. Feeding behavior in kinosternid turtles. Herpetologica 24:300–305.

Moll, D. 1976. Food and feeding strategies of the Ouachita map turtle (*Graptemys pseudogeographica ouachitensis*). Amer. Midl. Nat. 96:478–482.

Moll, E. O., and J. M. Legler. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff) in Panama. Bull. Los Angeles Co. Mus. Nat. Hist. (Sci.) 11:1–102.

Parmenter, C. J. 1976. The natural history of *Chelodina longicollis*. Unpubl. PhD Thesis, University of New England, Australia.

Timms, B. V. 1973. A limnological survey of the freshwater coastal lakes of East Gippsland, Victoria. Aust. J. Mar. Freshwat. Res. 24:1–20.

Windell, J. T., and S. H. Bowen. 1978. Methods for the study of fish diets based on the analysis of stomach contents. *In:* IBP Handbook No. 3: Methods for the assessment of fish production in fresh waters (3rd edition). T. Bagenal (ed.). Blackwell Scientific Publications, Oxford.

Zoology Department, University of Queensland, Brisbane, 4067, Australia. Accepted 22 April 1981.