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Feeding Ecology of the Turtle, *Clemmys marmorata*

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ABSTRACT.—Although *Clemmys marmorata* eats a variety of food and appears to be a dietary generalist, it does not select food items based on general availability. This species is a scavenger and an opportunistic predator with a preference for live prey captured by varied foraging tactics. Diets of males, females, and juveniles differ in prey size and proportions of food items, which may reduce intraspecific competition between the age and sex classes. Partial herbivory occurs in adults, and plants may provide an important source of readily available nutrients and some protein when animal food is unobtainable. Seston and other small animals abound in the filamentous algae eaten by *C. marmorata*, and may contribute considerable nutrient value to the diet.

Freshwater turtles display several patterns and tactics in their feeding habits: differences in diet among sympatric species (Lagler, 1943; Breckenridge, 1944; Berry, 1975; Vogt, 1981), different food habits among species with different body sizes or morphological adaptations (Mahmoud, 1968; Mahmoud and Klicka, 1979; Moll, 1976; Vogt, 1981), diets keyed to seasonal availability of prey (Graham, 1979; Mahmoud and Klicka, 1979), and selection of high-protein prey (Gibbons, 1967, 1970; Wilbur, 1975; Parmenter, 1980).

The western pond turtle (*Clemmys marmorata*) shows little sexual dimorphism in body size and apparently has no special adaptations in feeding morphology (Seeliger, 1945; Bury, 1970, 1972*a*). Individuals have been observed feeding on the pods of the yellow pond lily (*Nuphar polysepalum*), eating a dead mallard duck floating in the water (Evenden, 1948), browsing on aquatic plants that grow in the shallow, slow-moving water of a stream (Bogert *in* Carr, 1952), and feeding on water beetles and other aquatic insects (Carl, 1951). Ernst and Barbour (1972) stated that *C. marmorata* is omnivorous, with a preference for animal food (adult and larval insects, fish, worms, and crustaceans). These morphological and feeding observations suggest that this species is a food generalist with a broad feeding niche.

The diet of *C. marmorata*, however, has not been critically examined and its feeding habits may not be as general as assumed. The primary objective of the present study was to quantify the diet and foraging behavior of *C. marmorata*, and to compare its diet with known patterns of feeding ecology in other freshwater turtles.

A few investigators have examined age-sex differences in diets of turtles. *Chrysemys picta* and *Pseudemys scripta* show a dietary shift from carnivory in young to herbivory in mature individuals (Tinkle, 1958; Clark and Gibbons, 1969; Mahmoud and Klicka, 1979), while other species have dietary sex differences in adult turtles usually related to size differences between sexes (Plummer and Farrar, 1981; Vogt, 1981). Another objective of my research was to determine whether individuals of different sizes or sexes use different foods.

METHODS

Turtles were collected in Hayfork Creek and its tributaries, slow-moving streams with rocky substrates that are at about 750-m elevation in the North Coast Range, Trinity County, California. Most animals (N = 110) were taken between 5 August and 16 September 1968 and 1969, and one sample (N = 9)

TABLE 1. Diet of 77 *Clemmys marmorata* with food present in the stomach. N = number of items; F = frequency of occurrence; Vol = volume in cc.

Prey item	Juveniles (N = 30) N	Juveniles F	Juveniles Vol	Females (N = 27) N	Females F	Females Vol	Males (N = 20) N	Males F	Males Vol
Algae	1	1	2.00	9	9	18.00	1	1	4.00
Other vegetation	—	—	—	5	3	0.30	2	2	0.50
Nematomorpha (Gordididea)	8	2	0.25	1	1	0.05	—	—	—
Crustacea	14	14	2.55	10	10	10.10	6	5	5.55
Araneae	2	2	0.15	2	2	0.15	—	—	—
Odonata nymphs	61	19	10.15	21	12	4.05	19	6	5.00
Ephemeroptera nymphs	718	15	4.60	20	2	0.15	22	3	2.91
Trichoptera larvae	355	24	17.25	127	18	19.80	53	8	7.40
Hemiptera nymphs	10	8	0.58	3	3	0.40	2	2	0.10
Hemiptera adults	5	5	0.41	5	3	0.30	1	1	0.10
Orthoptera adults	3	3	1.60	3	3	0.55	2	2	0.20
Coleoptera larvae	211	21	7.95	63	15	5.15	8	4	0.75
Coleoptera adults	9	6	0.48	2	2	0.30	1	1	0.10
Diptera larvae	400	13	4.45	9	7	0.66	1285	3	9.15
Diptera adults	3	2	0.30	1	1	0.10	—	—	—
Osteichthyes	1	1	0.90	1	1	0.20	4	4	10.90
Amphibia (Anura)	4	4	1.20	8	6	4.05	8	5	7.80
Other food	7[1]	7	0.80	4[2]	4	1.35	1[3]	1	0.50
Total	1802		55.5	289		65.4	1413		54.5

[1] 1 snail, 1 adult dragonfly, 1 adult mayfly, 1 stonefly nymph, 2 ants, 1 rodent toe.
[2] 2 snails, 1 sowbug, 1 adult true bug.
[3] 1 adult true bug.

was obtained 20 May 1970. All data were pooled.

Individuals were captured by hand, usually between 1100 and 1600 h, and preserved about 1 h after capture. Stomachs were removed and dissected in the laboratory; contents were counted and identified under a binocular microscope. Algae in the stomach were scored as present, but algal clumps in the stomachs were not counted due to mastication and the large numbers of filamentous strands. Volume of food items was determined by water displacement.

Turtles smaller than 12 cm in carapace length (CL) were considered juveniles (Bury, 1972*a*). Notes on feeding in the wild were recorded in 1969–1971 during observations of social behavior (Bury and Wolfheim, 1973) and basking behavior (Bury, 1972*a*). I also observed feeding in several captive individuals kept over a 10-yr period both in aquaria and outdoor pools.

RESULTS

Sex Differences.—Females had eaten low numbers of prey items except insects, but had consumed a variety of prey, mostly aquatic invertebrates (Table 1). Vertebrate prey included one small unidentified fish (partly digested) and eight tadpoles (*Rana boylei*). Males ingested less variety of prey (15 categories) than did females (20) and juveniles (22). An exceptionally high number of fly larvae occurred in a few stomachs. Males had eaten five tadpoles and three adult *R. boylei*, a piece of an adult lamprey (*Lampetra tridentata*) and portions of three suckers (*Catostomus rimiculus*).

The foods of the adults differ by sex (Table 2). The stomachs of adult males contained many more insects than did those of females, but the male total was inflated by the large numbers of dipteran larvae (N = 1285) in the stomachs of three males. Dipterans made up 91% of all items and 93% of insect prey in adult males.

The diets of the sexes differed greatly in their plant and vertebrate components. Females had a significantly higher frequency of algae (Table 1) in their diets than did males (χ^2, $P < 0.05$).

TABLE 2. Proportional comparison of major foods[1] in 77 *Clemmys marmorata* (20 ♂♂; 27 ♀♀; 30 Juv).

Food item	% no. items			Percent frequency			% total volume		
	♂♂	♀♀	Juv	♂♂	♀♀	Juv	♂♂	♀♀	Juv
Algae	0.1	3.1	0.1	5.0	33.3	3.3	7.3	27.5	3.6
Crustacea (Decapoda)	0.4	3.5	0.7	25.0	37.0	46.6	10.2	15.5	4.6
Odonata nymphs	1.3	7.3	3.4	30.0	44.4	63.3	9.1	6.2	18.2
Ephemeroptera nymphs	1.6	6.9	39.8	15.0	7.4	50.0	5.3	0.2	8.3
Trichoptera larvae	3.7	43.9	19.7	40.0	66.6	80.0	13.6	30.3	31.1
Coleoptera larvae	0.6	21.8	11.7	20.0	55.5	70.0	1.4	7.9	14.3
Diptera larvae	90.9	3.1	22.2	15.0	25.9	43.3	16.8	1.0	8.0
Osteichthyes	0.3	0.3	0.1	20.0	3.7	3.3	20.0	0.3	1.6
Amphibia (Anura)	0.6	2.8	0.2	25.0	22.2	13.3	14.3	6.2	2.2

[1] Major foods are >5% of the diet.

Percent volume of algae (Table 2) was 3.8 times higher in females than in males, and 44% of the females had consumed some plant material whereas only 10% of the males had ingested vegetation (Fig. 1). Males consumed only a few more fish than did females, but these prey constituted the greatest volume of any food in male stomachs (Table 2). Anurans were about equal in total number and frequency in both sexes, but amphibians made up a greater proportion of the food in males than in females.

Prey volume was slightly larger for males than for females. Prey >0.4 cm^3 in volume constituted 15% of the food of males, but only 5% of the female diet. Both the head length (Fig. 2A) and head width (Fig. 2B) of adult male pond turtles are significantly larger than females of the same shell length (Analysis of Covariance, $P < 0.01$).

Size Differences.—Juvenile *C. marmorata* principally ate invertebrate prey; aquatic insects constituted the bulk of their diet. Vertebrate food consisted of one small sucker (*Catostomus rimiculus*), two tadpoles and two juvenile frogs (*R. boylei*), and the toe of an unidentified mouse. Except for the dipteran larvae in male stomachs (Table 1), juvenile diets had higher numbers of prey items than did adults. Almost all juvenile food items (93%) were small, <0.2 cm^3. All turtles smaller than 11 cm CL contained only animal matter in their stomachs, whereas adults included more plant material in their diets (Fig. 1). Although low in numbers, crayfish and amphibians were important prey both in frequency and volume in the diets of male and female adults.

Feeding Behavior.—Several foraging tactics were employed by turtles in their natural habitats. On three occasions, turtles paddled slowly below the surface of a pool with only their heads extended out of the water, bit objects floating on the water surface, then submerged with the food in their mouths. One food item was a dead fish about 10 cm long; the others were insects. I observed adult turtles in rocky riffles moving their heads back and forth in the flowing water for short bouts (1 to 3 min), sometimes biting and lunging forward as they moved, apparently striking at prey before raising the head.

Most foraging by *C. marmorata* was observed in shallow water (up to 0.5 m deep); activity at lower depths could not be reliably determined. Turtles moved with the neck outstretched and the head moving back and forth. They slowly swam around rocks and along the edges of algal mats, biting at objects which I usually could not identify. Turtles of both sexes frequently patrolled the edges of pools, covering a distance of 10 to 50 m before returning to deep water or cover where they were not visible. Routes varied from a short, direct swim, to a meandering search of the pool's perimeter that lasted 10 to 15 min.

Some individuals pushed into the

edges of algal mats and appeared to bite at objects. Both juvenile and adult turtles were seen moving or resting under algal aprons along the edges of pools, raising their heads from under the algae for varying periods. I could not observe foraging when turtles were under the algal mats.

One adult actively pursued a fish for about 5 m around several submerged large rocks until the fish escaped. The fish appeared to be diseased as it had a conspicuous white area on its back and was slow-moving. All other fish easily avoided the relatively slow swimming *C. marmorata* in open water.

One adult in an outdoor enclosure chased and caught grasshoppers on land, returning to the water to consume the prey. Turtles also grabbed live food perched on rocks above the water. One juvenile in an aquarium employed a gape-and-suck technique to catch live shrimp (tropical fish food). The turtle closely approached shrimp and swiftly opened its mouth, sucking in the small shrimp, and then expelled the water.

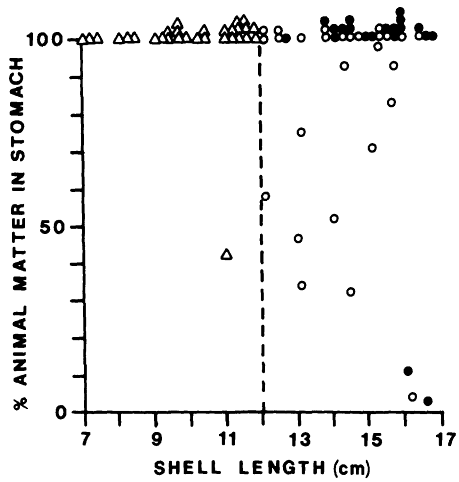

FIG. 1. Comparison of carapace length and percent volume of animal food in 77 *Clemmys marmorata.* Juveniles (triangles) are <12 cm long (dashed line); adults are >12 cm long: males, solid circles; and females, open circles.

DISCUSSION

Clemmys marmorata mostly eat aquatic food, but a few prey are terrestrial (e.g., grasshoppers) and aerial (e.g., adult flies), and are probably taken when the prey is on the water's surface. Large numbers of small-sized dipterans found in the stomachs of some juveniles and males may be due to the colonial habits or clumped distributions of this type of insect. A turtle that had access to such prey could ingest many individuals in one bite or in one feeding bout.

Western pond turtles apparently prefer live or dead animal tissue to plant material. Turtles can capture food on land (but were observed swallowing food in the water), on the water's surface, under water (most prey), or gape-and-suck in water.

From the diversity of their food and foraging maneuvers, western pond turtles appear to be food generalists and opportunistic predators, when live prey can be captured. However, some food may not be consumed in proportion to its general availability. Algae are available ad libitum to turtles, but do not predominate in the diets of young or many adult *C. marmorata.* Fishes and amphibians are common (>2/m) in Hayfork Creek (Bury, 1972*b*) yet relatively few are eaten, presumably because these vertebrate prey can elude capture. Similarly, MacCulloch and Secoy (1983) found that food items in *Chrysemys picta* are not always chosen on the basis of abundance alone, e.g., fishes and tadpoles, although abundant at their study sites, were little utilized.

Hayfork Creek *C. marmorata* apparently display sex-age differences in food habits. Females consume significantly greater volume and frequency of filamentous algae than do males. Males are not only more carnivorous than females, they also ingest prey of larger sizes than do females. This difference may be related to the relatively greater head size in males compared with females having the same shell size. Also, juvenile *C. marmorata* are principally carnivorous and feed on relatively smaller-sized prey than do adult turtles. These differences in food proportions and types eaten by turtles may serve to reduce intraspecific competition between the sex and age classes. It is not known if these differences occur in other populations or other years.

Dietary shift from carnivory in juveniles to herbivory in adults is marked, but incomplete. Adult *C. marmorata*, especially females, feed partly on plant matter, but adults of both sexes consume much more animal food than do other species of turtles with generalized body forms. For example, herbivory occurs in adult *Pseudemys, Chrysemys*, and many other aquatic genera (Lagler, 1943; Carr, 1952; Moll and Legler, 1971; Ernst and Barbour, 1972). The change from carnivory in young to herbivory in adults (Clark and Gibbons, 1969; Mahmoud and Klicka, 1979) may be due to higher metabolic demands of juveniles whose growth requires the most energy and nutrient intake possible in the least amount of time.

For maximum reproductive output by female *C. marmorata* (and other freshwater turtles), a diet including a large amount of vegetation would be less than optimal because plants usually contain less protein and less available energy than do animal foods. However, plant food may provide sufficient resources for the needs of many adult freshwater turtles. Clark and Gibbons (1969) and Parmenter (1980) reported that *P. scripta* is generally herbivorous as an adult but is an opportunistic carnivore when animal food can be obtained. Presumably, a larger turtle would use more energy to capture small, live prey (e.g., an insect) than the turtle would receive in return, and would reap a decreasing benefit to cost ratio for the energy expenditure involved in hunting animal prey. Also, larger turtles may be forced to generalize their diet to include other organisms, including plants, in order to satisfy their metabolic requirements (Schoener, 1977).

One advantage of including vegetation in the diet is that this large-sized food can be readily and predictably acquired by a turtle with a relatively small investment of time and energy. In the present study, filamentous green algae were always available to turtles during their period of summer activity; late in the season, algae choked the shorelines of the stream. The omnivorous pond turtle probably selects animal food with high caloric profitability and nutrients when these are available, but also forages on vegetation as an alternate source of bulk and nutrients. Females may exploit this available source of food when other choices are absent and if greater nutrient sources are needed for reproduction.

Parmenter (1980) presented data on nine plant foods (including algae) with

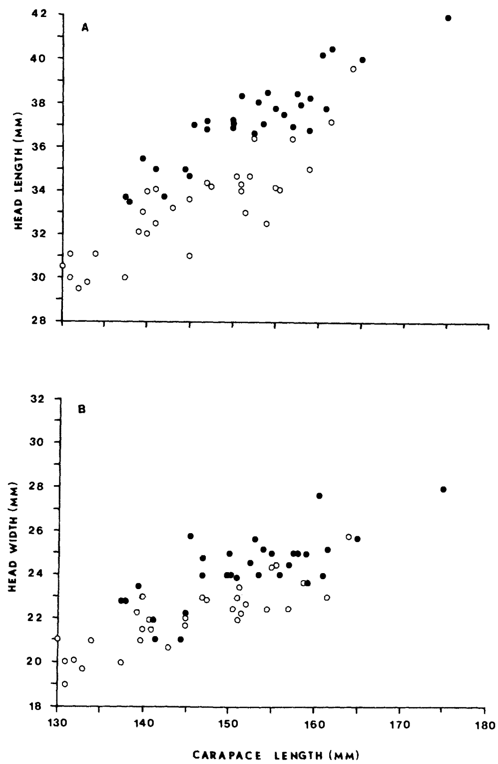

FIG. 2. Relation of head length (A) and head width (B) to carapace length in adult *Clemmys marmorata* >13 cm long. Males are solid circles; females, open circles.

energetic values (kcal/g dry wt) averaging 4.3 (3.4 to 5.3) compared with nine animal foods (eight insects, one fish) averaging 5.2 (4.9 to 5.8). Mean protein value (mg/g dry wt) for the same plant material was 138 (80 to 173) and for animal material, 520 (294 to 706). Per unit weight (g dry weight), plants provide about 80% of the energetic value and 25% of the protein value of animal food. Freshwater turtles need only to ingest a little more plant material to equal the energy value of animal food, but a fourfold increase is necessary to equal the protein uptake (i.e., 4 g plant material roughly equals 1 g of animal). If this general relationship holds in other aquatic systems, then freshwater turtles could obtain a substantial proportion of their energy and nutrient needs from vegetation alone. Digestibility and assimilation of plant matter often are less than for animal food, but again plants may be more available and in greater volume to offset these limitations.

Further, additional undetected protein may be ingested along with filamentous algae or other vegetation. Microscopic seston, small insects, immature crustaceans, and other animal matter often abound in algal clumps; many of these items are not counted in food analyses because they are rapidly digested or overlooked due to their small size. Such material may add considerable nutrient value to the diet. To adult *C. marmorata* (especially females), a few larger animal items (mature insects, crayfish, tadpoles, etc.) may provide entrees of animal protein, while large volumes of algae with seston and small prey together may also provide an adequate diet.

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