

# *Bioenergetics*

## 20

# The Feeding Ecology of the Slider Turtle

**ROBERT R. PARMENTER**  
Department of Biology  
Utah State University  
Logan, Utah 84322

*Current address:*  
Department of Biology  
University of New Mexico  
Albuquerque, New Mexico 87131

**HAROLD W. AVERY**  
Department of Biology  
University of California, Los Angeles  
Los Angeles, California 90024-1606

---

### Abstract

Slider turtles (*Trachemys scripta*) are widely foraging opportunistic omnivores, consuming a diversity of aquatic vegetation, invertebrates, and, to a lesser extent, vertebrate food matter. Although their food preference is generally for animal matter, changes in feeding habits toward herbivory are observed in response to changes in proximate environmental factors (e.g., seasonal changes in food availability), as well as to ontogenetic changes and associated constraints (e.g., increased body size). Ambient temperature has a profound influence on the behavioral timing and duration of foraging, as well as on the physiological rates associated with digestion. Population studies of free-living slider turtles inhabiting comparatively warmer aquatic environments show relatively higher growth rates and/or higher reproductive output compared with those of turtles that inhabit cooler aquatic environments. Data from controlled nutritional studies indicate that associated increases in trophic productivity of food items in warmer environments may also enhance the net productivity of slider turtle populations. Dietary protein content is probably a major factor in food selection, especially among juveniles.

---

### Introduction

The slider turtle (*Trachemys scripta*), long known for its opportunistic feeding habit, has been the subject of numerous ecological studies concerning its foraging behavior, prey selection, and digestive physiology. Research has focused on the influence of environmental factors

(e.g., spatial and temporal differences in temperature regimes and food availability) on diets, growth rates, and digestive processes. Results of these studies not only have expanded our knowledge of reptilian feeding ecology but also have provided insights into ecosystem changes due to anthropogenic perturbations.

The purpose of this chapter is to review in detail the literature to date on the feeding ecology of sliders and to identify areas of relevant future research. Of necessity, this report will concentrate on *Trachemys scripta*. For general surveys of turtle feeding behavior and reptilian digestion, the reader is referred to the excellent reviews by Mahmoud and Klicka (1979) and Skoczylas (1978).

### Diet Analysis Techniques

The basic data for virtually all studies on slider feeding ecology are derived from diet analyses. The examination of ingested food items can provide data on the kinds, the amounts, and ultimately the nutritional quality of food resources. Historically, assessments of slider diets have been accomplished using dissection procedures, wherein the stomachs and intestines of killed turtles are opened and examined for food items. Such dietary analyses are generally performed in concert with other studies dealing with anatomical descriptions, systematic evaluations, and reproductive capacities. Although dissection produces a complete sample of the entire digestive tract, it has the disadvantage of permitting only a single sample per turtle. Because of immense variability in diets among individuals, age classes, populations, and seasons, large numbers of turtles must be killed to characterize the diet adequately. In view of the modern ecologist's concern for wildlife conservation, techniques that result in large-scale destruction of study populations are becoming increasingly undesirable. Fortunately, alternative methods are available.

One such technique, using live captive specimens, involves laboratory feeding trials, in which the researcher offers a variety of foods to the turtles and records which items are consumed. This method yields food preference data and general diet information, although application of such data to wild populations depends largely on the researcher's ability to select a menu representative of the actual food items available in the field.

Another method of diet determination involves the analysis of feces obtained from live, recently captured specimens. Microscopic inspection of the feces can yield a reasonable species list of food items. This type of analysis has the advantages of being nondestructive to the turtle and allowing multiple samples to be taken from the same individuals over long periods of time. Unfortunately, it is exceedingly difficult to reconstruct the original meal quantitatively (including numbers, volumes, or masses of each food item) from the postdigestive remnants found in

the feces. Soft-bodied insects, fruit, and meat leave little residual material, and counts of insects or seeds (reassembled from small fragments) may contain considerable sample errors.

Stomach flushing techniques (Fig. 20.1) can be used to obtain recently ingested food items (for details, see Legler, 1977; Parmenter, 1980). This method, when properly applied, has proved effective in extracting nearly all of the food items from a turtle's stomach while inflicting no permanent injury on the turtle. Food items can be readily sorted, identified, and measured. Stomach flushing allows multiple samples to be taken from individual turtles over their lifetimes and can be integrated with other non-destructive techniques for studying turtle natural history, such as radiotelemetry for movement patterns (Schubauer, 1981b; Standora, 1982) and x-ray photography of egg production (Gibbons and Greene, 1979).

### The Slider's Diet

#### DIET COMPOSITION

The slider turtle is an opportunistic omnivore, consuming a wide variety of invertebrates, vertebrates, and vegetation (Table 20.1). Plant materials in the diet include both blue-green and green algae, as well as leaves, stems, roots, fruits, and seeds of vascular plants. Larger invertebrates are taken deliberately (flushed from or plucked off both submerged and emergent vegetation), and smaller invertebrates may be inadvertently consumed along with aquatic plants. Small fish, tadpoles, and frogs can be actively pursued and captured, although larger vertebrate food items in the diet usually result from feeding on carrion. A notable exception is given in an account by Pritchard and Trebbau (1984), in which they report that in Venezuela the Colombian slider (*T. scripta callirostris*) captures waterfowl by biting the birds' legs and pulling them underwater to drown. Although the vast majority of reported food items are aquatic organisms, some terrestrial insects and plants can be observed in the diet on occasion. These prey items presumably represent allochthonous inputs to the aquatic environment. Sliders are known to venture considerable distances on land (e.g., Bennett et al., 1970; Gibbons, 1970d), but there are few data to suggest that they regularly forage away from water, although Cagle (1944b) observed individuals moving onto land to eat terrestrial vegetation.

#### SEASONAL CHANGES IN DIET

Seasonal shifts in slider diet composition have been illustrated in a South Carolina population of *T. s. scripta* (Parmenter, 1980; Schubauer and Parmenter, 1981; see Table 20.1). The summer diet includes vegetation and a sub-

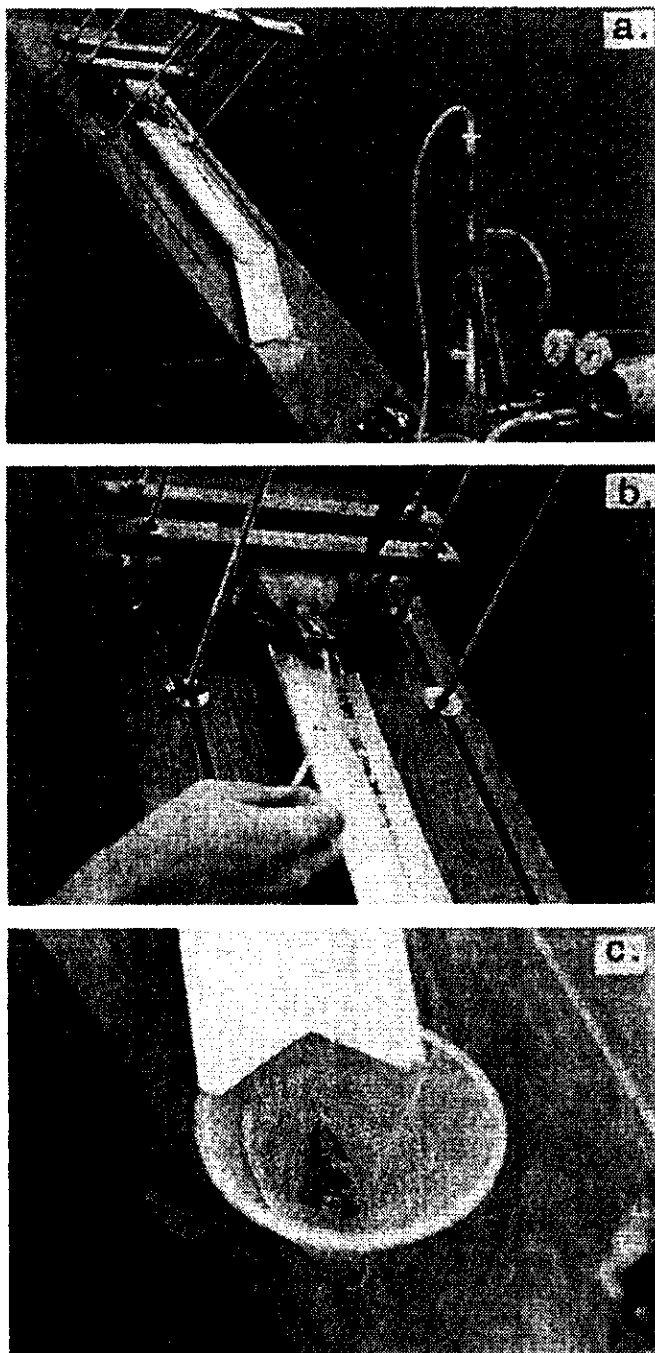


FIGURE 20.1. Turtle stomach flushing apparatus and procedure. *a*, turtle is secured in restraining braces, mouth held open by cables and fishhooks; hooks are attached to bony parts of mandible and maxilla to avoid injury to soft tissues. *b*, a flexible plastic tube connected to a running water faucet is slowly inserted down the esophagus into the stomach; food items from the stomach are flushed out of the turtle and carried down the plastic gutter into a funnel. *c*, food items are collected in a screen placed in the funnel; excess water is pulled through by a vacuum pump and collected in the sidearm flask shown in *a*.

stantial quantity and variety of animal prey. In contrast, the winter diet is composed entirely of aquatic vegetation. A similar shift from summer omnivory to winter herbivory has been observed in kinosternids (Mahmoud, 1968a). Seasonal diet changes of sliders can be partially attributed to changes in prey availability; abundance of animal prey, especially insects, decreases during winter (perhaps more so in northern regions). However, reduced prey availability does not entirely explain the observed diet shifts. Drastic declines in trapping success using fish or meat baits of otherwise omnivorous turtles (Cagle, 1950; Ernst, 1972) suggest that foraging activity or hunger levels may also be reduced. If so, consumption of easily acquired aquatic vegetation may be sufficient to meet lower energy demands.

#### BODY SIZE AND DIET SHIFTS

As sliders increase in body size from juveniles to adults, the diet composition changes from a fairly balanced mix of plant and animal matter to one dominated by vegetation (Fig. 20.2; Marchand, 1942; Clark and Gibbons, 1969; Moll and Legler, 1971; Hart, 1983).

Because the demand for amino acids is probably greater for faster-growing juvenile turtles than for slower-growing adults (Wood, 1974), such a dietary shift could be predicted. Energetic constraints may also partially explain why adult turtles stop feeding predominantly on animal prey. Small turtles, having less mass, use less total energy than large adults in pursuit of an animal prey item. Hence, for the same prey item, the juvenile may achieve a greater energy gain than an adult. In addition, the size of the meal is proportionally larger for the juvenile (with respect to the slider's body mass), which further enhances the energetic benefit-cost ratio of the prey encounter.

Alternatively, nonrandom distributions of animal prey in the environment may contribute to the observed diet shifts. For example, adult sliders may avoid shallow-water habitats, normally teeming with invertebrate prey, because of maneuverability constraints (Hart, 1983). Such a scenario of microhabitat exclusion could conceivably produce diet composition differences among age classes without invoking energetic models. In any case, the perhaps fortuitous outcome of juvenile carnivory is an increase in the diet of proteins and essential nutrients, particularly calcium (Clark and Gibbons, 1969), which results in faster growth and carapace development for the young slider. Similar omnivore-to-herbivore diet shifts can be observed in *Graptemys pseudogeographica* (Moll, 1976b), *Emydura krefflii* (Georges, 1982), and *Mauremys caspica* (Sidis and Gasith, 1985), whereas the reverse situation is found in *Chrysemys rubriventris* (Graham, 1971). In this latter case, juveniles (3 years old and younger) were predominantly herbivorous; but in their fourth year, they achieved sufficient body size to prey successfully on

Table 20.1. Food items of *Trachemys scripta*

Subspecies	Reference	Study location	Study period	N	Food items			
					Vegetation	Invertebrates	Vertebrates	Miscellaneous
<i>T. s. scripta</i>	10	South Carolina	July-Aug.	65	Algae (unspecified) <i>Bacopa caroliniana</i> <i>Brasenia schrefferi</i> Grass (unspecified) <i>Najas guadalupensis</i> <i>Nymphaea odorata</i> (seeds and leaves) <i>Potamogeton</i> sp. <i>Sagittaria</i> sp. <i>Utricularia</i> sp.	Gastropoda: Physidae Insecta: Coleoptera Diptera Hemiptera Hymenoptera ( <i>Bombus</i> ) Odonata: Anisoptera Zygoptera Orthoptera: Locustidae	Pisces Unknown claws Unknown bones	Turtle scutes Pebbles, sand Wood
	11		Dec.-Feb.	17	<i>Bacopa caroliniana</i> <i>Potamogeton</i> sp. <i>Sagittaria</i> sp. <i>Utricularia</i> sp.			
	2	Florida	Oct., Feb.	2	Algae (unspecified) <i>Ceratophyllum</i> sp. <i>Lemna</i> sp. <i>Najas</i> sp.	Gastropoda (crayfish and shrimp) Insecta: Odonata: Anisoptera Zygoptera		Turtle scute
<i>T. s. roosei</i>	3	Louisiana	Oct.-June	104	Algae: <i>Cladophora</i> sp. <i>Oscillatoria</i> sp. <i>Spirogyra</i> sp. <i>Celastis occidentalis</i> <i>Ceratophyllum demersum</i> <i>Cornus asperifolia</i> <i>Persicaria</i> sp. <i>Piaropus crassipes</i>	Amphipoda Arachnida Decapoda (crayfish) Insecta: Coleoptera Diptera Ephemeroptera Hemiptera Homoptera Hymenoptera Lepidoptera Odonata Orthoptera Isopoda Isopoda	Amphibia (frog eggs) Reptilia: <i>Nerodia</i> <i>rhombifera</i> Unknown bone	Detritus Paper Watermelon rind
	2	Tennessee	June-July	22	Algae: <i>Spirogyra</i> sp. <i>Azolla caroliniana</i> <i>Callitriche</i> sp. <i>Callitriche natans</i> <i>Ceratophyllum</i> sp. <i>Lemna</i> sp. <i>Spirodela</i> sp. <i>Wolffia</i> sp. Seeds (unspecified)	Amphipoda Decapoda (crayfish and shrimp) Insecta: Diptera Odonata: Zygoptera Trichoptera		Detritus
	1	Illinois	-	-	Aquatic vegetation (unspecified)	Decapoda (crayfish) Insecta (aquatic) Mollusca	Pisces Amphibia (tadpoles)	
<i>T. s. elegans</i>	8	Louisiana	Feb.-Dec.	88	Algae (unspecified) <i>Ceratophyllum</i> sp. <i>Egeria</i> sp. <i>Eichhornia</i> sp. <i>Lemna</i> sp. <i>Limnophilum</i> sp. <i>Najas</i> sp. <i>Nyasa</i> sp. <i>Potamogeton</i> sp. <i>Spirodela</i> sp. <i>Taxodium</i> sp. <i>Wolffia</i> sp.	Amphipoda Bryozoa Cladocera Decapoda (crayfish) Gastropoda Insecta: Coleoptera Diptera Hemiptera Homoptera Hymenoptera Odonata Orthoptera Isopoda Ostracoda Pelecypoda	Pisces	Wood

Table 20.1 -- Continued

Subspecies	Reference	Study location	Study period	N	Food items			
					Vegetation	Invertebrates	Vertebrates	Miscellaneous
	8	Illinois	Mar.-Oct.	26	<i>Myriophyllum</i> sp.	Porifera: Spongillidae Decapoda Insecta: Diptera Pelecypoda		
	5	Oklahoma	June-July	3	<i>Lippia incisa</i>			Fishhook
<i>T. s. gaigeae</i>	4	Mexico, Texas	June	--	Aquatic vegetation (unspecified)			
<i>T. s. taylori</i>	4	Mexico	Sept.	--	Vegetation (unspecified)			
<i>T. s. grayi</i>	10	Mexico	--	--	Vegetation (unspecified) <i>Ficus</i> sp. (fruit)	Insecta (aquatic)		
<i>T. s. ssp.</i>	6	Mexico, British Honduras, Nicaragua, Costa Rica, Panama	--	78	Vegetation (unspecified, mostly grasses) Fruits, seeds ( <i>Ficus</i> sp. and palm nuts)	Decapoda (crayfish) Insecta Mollusca	Vertebrates (unspecified)	
<i>T. s. ssp.</i>	6	Panama	Aug.-Aug.	58	Algae: <i>Oscillatoria</i> sp. <i>Elodea</i> sp. <i>Najas</i> sp. <i>Paspalum</i> sp.	Gastropoda Insecta: Blattodea Coleoptera Odonata Orthoptera Pelecypoda	Pisces	Mud
<i>T. s. callirostris</i>	12	Venezuela	--	--			Aves (waterfowl)	
<i>T. s. chichiriviche</i>	12	Venezuela	--	--	Grass (unspecified)	Decapoda (crayfish)	Pisces	

References: 1, Cahn, 1937; 2, Marchand, 1942; 3, Minyard, 1947; 4, Legler, 1960b; 5, Webb, 1961; 6, Moll and Legler, 1971; 7, Avalos, 1975; 8, Hart, 1979; 9, Smith and Smith, 1979; 10, Parmenter, 1980; 11, Schubauer and Parmenter, 1981; 12, Pritchard and Trebbau, 1984.

crayfish. A concomitant acceleration of growth was observed following the diet shift (Graham, 1971).

## Foraging Behavior

### GENERAL FORAGING

Slider turtles tend to forage during the day, patrolling areas of shallow water (less than 1-3 m deep), particularly in the vicinity of aquatic vegetation (if present). The shallow, littoral environment not only harbors the greatest quantities of potential food items but also possesses sufficient sunlight for sliders to identify and target their prey. Large expanses of deep, open water are generally rapidly traversed or avoided altogether. Adult and juvenile sliders further partition the foraging microhabitat, in that juveniles frequent quieter, shallower waters than adults do (Moll and Legler, 1971; Hart, 1983). Hatchling juveniles commence foraging almost immediately after

emerging from the eggs. Cagle (1946) reported that *T. s. elegans* hatchlings in Illinois had stomachs and intestines packed with food even though they still possessed unused yolk masses.

Sliders spend a considerable portion of their activity time in foraging. Moll and Legler (1971) observed three juvenile sliders that allocated a mean of 6.8 hours (range = 4 to 8.5 hours) of an 11-hour day to foraging activity. Submergence times during foraging ranged from 20 seconds to 5 minutes for juveniles, and 5 to 6 minutes for adults (Moll and Legler, 1971).

During foraging, the slider swims slowly beneath the water's surface, periodically poking its head into clumps of aquatic vegetation in an apparent effort to flush out hidden invertebrates. Sliders, especially juveniles, are attracted to prey movements and will pursue small fish, tadpoles, and frogs (much in the manner of painted turtles, *Chrysemys picta*; see Sexton, 1959b). However, such pursuits are abandoned if the prey is obviously faster than the turtle. Once captured, small prey items are swallowed

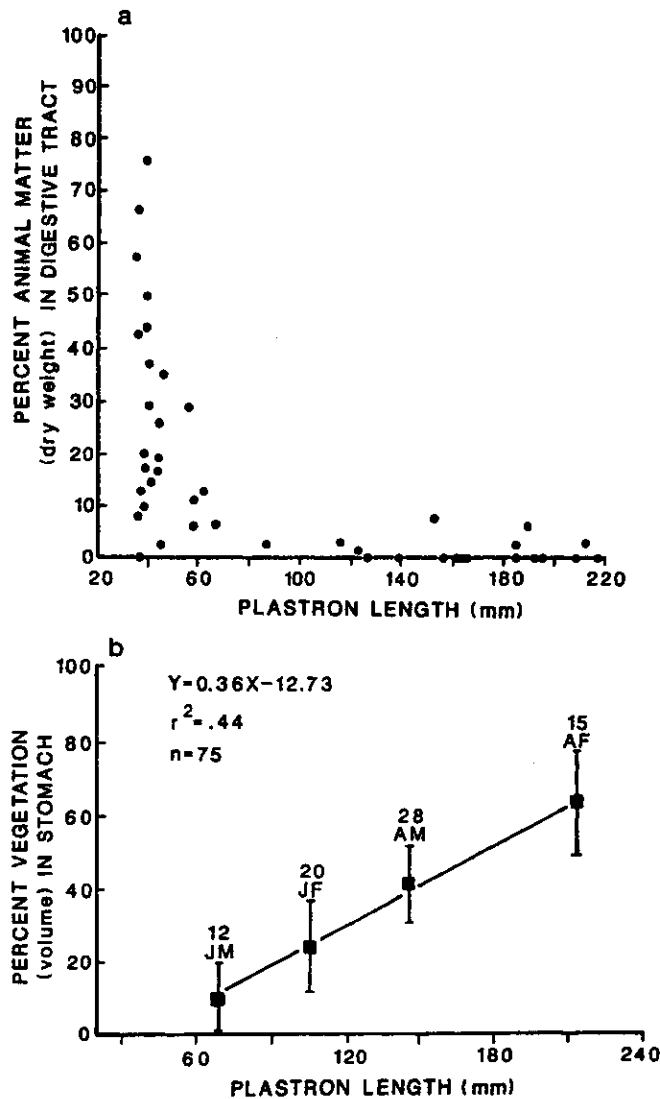


FIGURE 20.2. The relationship between diet and body size in *Trachemys scripta*, showing the diet shift from juvenile carnivory to adult herbivory. *a*, data for *T. s. scripta* from the Savannah River Plant, South Carolina; from Clark and Gibbons (1969) with permission. *b*, data for *T. s. elegans* from Lafourche Parish, Louisiana; group means ( $\pm 2$  SE) of plant volumes are presented for juvenile males (JM), juvenile females (JF), adult males (AM), and adult females (AF) at the mean plastron length of each group; from Hart (1983) with permission.

intact, but larger prey (including plants and vertebrate carrion) are ripped into smaller pieces by the slider's powerful jaws and muscular, clawed forelegs.

Another aspect of foraging behavior, although scarcely reported for sliders, is neustophagia (Belkin and Gans, 1968), a foraging maneuver similar to that of a baleen whale. The turtle ingests tiny particles of food floating on the water's surface (neuston) by skimming the surface with its lower jaw (mouth agape), collecting water and food particles in the pharynx. When the turtle closes its

mouth, the water is forced out through the nostrils and between the jaws. The remaining food particles are then swallowed. The entire system functions as a crude filtration process. Neustophagia in turtles was first reported in *Podocnemis unifilis* and *Chrysemys picta* (Belkin and Gans, 1968), which were induced to feed on finely powdered foods in outdoor pond enclosures. Subsequently, this feeding strategy was reported for natural populations of *T. s. scripta* and *Chrysemys floridana peninsularis* feeding on duckweed (Lemnaceae) in a dystrophic pond in Florida (Auth, 1975). It seems probable that sliders can use this technique extensively, especially populations feeding mainly on free-floating algae and duckweed.

A potential, but as yet unobserved, slider feeding behavior is geophagy, the deliberate consumption of stones or pebbles. Such objects in reptilian stomachs may assist in mechanical grinding of larger food items, thereby promoting faster and more efficient digestion. Geophagy has been reported in *Terrapene ornata* (Skorepa, 1966), *Testudo hermanni*, *Gopherus agassizii* (Sokol, 1971), and a variety of other reptiles. Analyses to date of slider stomach contents have produced little evidence of geophagy; Parmenter (1980) noted pebbles in the stomach contents in only 2 of 65 sliders from South Carolina. No other reports on slider diet mention stones or pebbles (see Miscellaneous in Table 20.1). Hence, geophagy in sliders, if it exists at all, appears to be extremely rare.

#### PREY DETECTION

There is little doubt that visual detection of food items, particularly moving prey, is of paramount importance to the foraging success of the slider turtle. In *Pseudemys nelsoni* even the visual perception of other feeding turtles provides sufficient stimulus to elicit feeding behavior and increase food ingestion (Bjorndal, 1986). Olfaction also plays a role in prey detection, though its importance relative to vision is as yet unknown (Burghardt, 1970; Manton, 1979). Although turtles possess a well-developed olfactory structure in the central nervous system (Goldby and Gamble, 1957; Scott, 1979), the range and sensitivity of their olfactory organs have yet to be rigorously tested. Sliders are capable of detecting odors underwater (Cagle, 1950; Boycott and Guillery, 1962), as are kinosternids (Mahmoud, 1968a) and *Podocnemis unifilis* (Belkin and Gans, 1968). However, preliminary comparative tests suggest that sliders may be less responsive to olfactory cues than other freshwater turtle species are (e.g., *Chelydra serpentina*, *Kinosternon subrubrum*, *Deirochelys reticularia*, *Pseudemys floridana*, and *Sternotherus odoratus*—Cagle, 1950). Nevertheless, free-ranging sliders do respond to odors from fish-meat baits placed in perforated containers (Parmenter, 1980), indicating that location of carrion can be facilitated by olfactory cues.

## PREY SELECTION

As with any opportunistic omnivore, the selection of food items by the slider turtle is greatly influenced by local availability of prey, with the result that the most common plants and invertebrates in the environment make up the bulk of the diet (Cahn, 1937; Minyard, 1947; Avalos, 1975; Parmenter, 1980). Although most field studies of adult turtle diets show that vegetation makes up the majority of the diet (see Table 20.1), results of laboratory feeding experiments indicate that sliders actually prefer fish meat and insects to aquatic vegetation (Parmenter, 1980). These results are supported by the successful use of fish meat as turtle bait in a variety of field studies. Presumably, the prevalence of vegetation in adult slider diets reflects both the greater abundance and ease of acquisition of edible plants relative to animal prey.

Food preferences in turtles appear to be established early in the turtle's life. Laboratory studies on hatchling sliders (*T. s. elegans*—Mahmoud and Lavenda, 1969) and snapping turtles (*Chelydra serpentina*—Burghardt and Hess, 1966, and Burghardt, 1967) suggest that food preferences are greatly influenced by early feeding experiences, preferences can change with increased exposure to a wider variety of foods, and there may be innate (genetically determined) preferences for some food types.

### Temperature Effects on Feeding and Digestion

The importance of environmental temperature regimes on the slider's feeding ecology cannot be overstated. Temperature influences not only foraging behavior but also virtually every physiological aspect of digestion. Seasonal changes in temperature directly affect overall foraging activity levels and diet composition (as discussed above), and daily temperature cycles control short-term behavior and digestive physiology.

Basking behavior facilitates the deviation of a turtle's body temperature away from the ambient air or water temperature, allowing the turtle to select a more potentially optimal body temperature (Boyer, 1965; Spotila et al., 1984; Schwarzkopf and Brooks, 1985; also see Chapter 22). Laboratory studies have indicated that sliders spend more time basking after ingesting food. Moll and Legler (1971) found that *T. scripta* juveniles basked significantly longer within a 48-hour period after ingesting food than when not fed for 48 hours. Gatten (1974) showed that *T. s. elegans* increases its selected body temperature from 24.5° to 29.1° C after ingesting a meal, an increase that could easily be accomplished by basking on a clear day in the wild (Auth, 1975; Standora, 1982). Hammond et al. (1988) found that fed *T. scripta* basked significantly longer than unfed sliders in spring and early summer months, but basking duration did not differ between fed and unfed groups in fall and winter months.

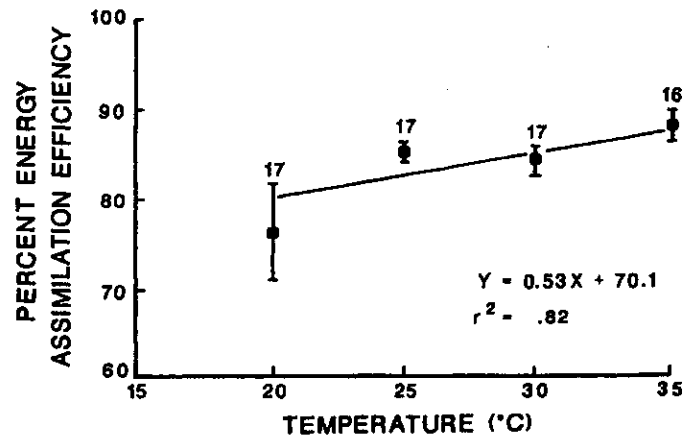


FIGURE 20.3. The effect of temperature on energy assimilation efficiency in laboratory specimens of *Chrysemys picta*, a close relative of the slider turtle. Squares are means, vertical lines are  $\pm 2$  SE, and numbers are sample sizes. From Kepenis and McManus (1974) with permission.

Various physiological aspects of turtle digestion exhibit temperature-mediated responses that could be regulated by basking behavior. For example, higher body temperatures induce greater gastric acid and enzyme secretion (Kenyon, 1925; Chesley, 1934; Anderson and Wilbur, 1948; Wright et al., 1957), faster stomach evacuation times (Fox and Musacchia, 1959), and higher intestinal motility rates (Studier et al., 1977). Protein digestion, sugar absorption, and energy assimilation proceed at faster rates with warmer body temperatures (Riddle, 1909; Fox and Musacchia, 1959; Fox, 1961; Avery, 1987). Assimilation efficiency also exhibits a modest increase at warmer temperatures (Fig. 20.3; Kepenis and McManus, 1974). As a result, the total digestive turnover time (ingestion to defecation) becomes shorter at higher temperatures (Fig. 20.4; Parmenter, 1981). These studies support the hypothesis of Cagle (1950) that basking may be an important behavior that allows sliders to optimally regulate the physiological processes of digestion through the control of body temperature.

The rate of food intake in the slider is also a function of body temperature (Fig. 20.5), with maximal ingestion occurring at 29° C (Parmenter, 1980). A similar relationship exists in the painted turtle (*Chrysemys picta*—Kepenis and McManus, 1974). Basking could enhance the ingestion rate of food, because body temperatures of postbasking sliders reentering the water remain elevated over the water temperature for several minutes (Spray and May, 1972; Schubauer and Parmenter, 1981) to a few hours (Moll and Legler, 1971).

Given the above considerations, we can hypothesize that the ultimate effect of elevated turtle body temperature would be a faster growth rate and earlier attainment of sexual maturity (assuming an adequate food supply). In support of this, Porter and Tracy (1983) demonstrated



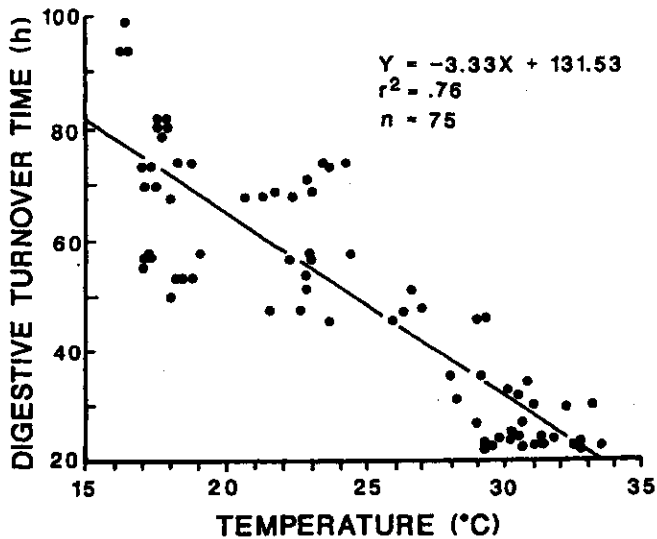


FIGURE 20.4. The effect of temperature on the digestive turnover time in laboratory specimens of *Chrysemys picta*. Turnover time is the residence time of a food item in the turtle from ingestion to defecation. From Parmenter (1981) with permission.

that growth and the attainment of sexual maturity in desert iguanas (*Dipsosaurus dorsalis*) are significantly accelerated in thermally favorable microenvironments in the laboratory; desert iguanas sexually matured in about seven months instead of the four to seven years required in nature, presumably at the same body size. However, definitive laboratory studies addressing the magnitude of temperature effects on slider growth rates and age at sexual maturity are presently lacking.

### Diet Quality and Environmental Effects on Slider Growth

#### NUTRITIONAL REQUIREMENTS

In addition to temperature, the quality and quantity of available food in the slider's environment can have a profound effect on growth rate and maturation time. Unfortunately, age-specific feeding behavior and nutritional requirements of turtles are among the least-known aspects of their feeding ecology. The quantities and nutritional qualities of ingested foods are critical components of ecological energy budgets and growth models (Porter and Tracy, 1983), yet these data are often lacking in such studies (e.g., Glidewell, 1984). Requisite parameters for such models include prey caloric values; proportions of carbohydrates, fats, and proteins; and concentrations of essential dietary components, that is, vitamins, mineral salts, and specific amino and fatty acids that cannot be biosynthesized. The determination of the feeding rates and nutritional quality of food consumed by wild slider populations, combined with an understanding of the

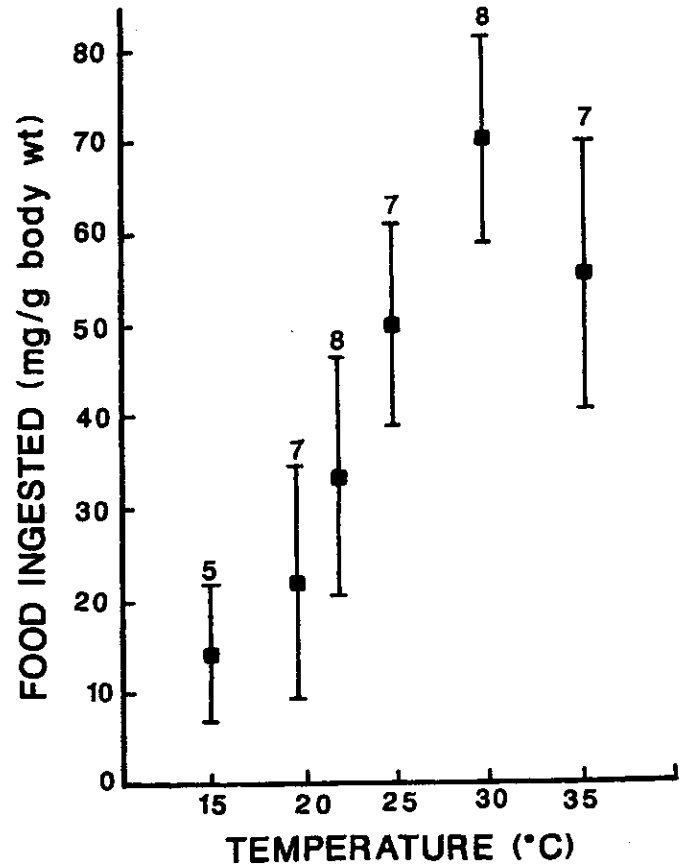


FIGURE 20.5. The effect of temperature on ingestion in laboratory specimens of the slider turtle *Trachemys scripta scripta*. Points are means, vertical lines are  $\pm 2$  SE, and numbers are sample sizes. From Parmenter (1980) with permission.

effects of environmental fluctuation and perturbation on these values, is therefore essential for the development of energy budgets and growth models.

The first dietary study on turtle growth rates was conducted by Pearse et al. (1925). Diets containing a mix of protein, carbohydrates, vitamins, and essential nutrients promoted faster turtle growth than "pure" diets consisting of a single food type. Recent work by Avery (1987) has demonstrated that the protein content of the slider's diet dramatically influences its growth rate, with high-protein foods promoting rapid increases in both turtle body size and mass (Fig. 20.6). In addition, sliders that were fed on foods containing only 10% crude protein exhibited a curling of the posterior plastron, thereby reducing their overall shell size (Fig. 20.6b; Avery, 1987).

From Figure 20.6 it is clear that slider turtles require more than 10% crude protein in their diet in order to grow properly. Boyd (1970) found that the mean crude protein content of aquatic plants from Par Pond, South Carolina, was  $13.1\% \pm 1.3\%$ , a concentration similar to that of the lowest-protein diet fed to turtles in Avery's study. Fish carrion is the other predominant food source available to

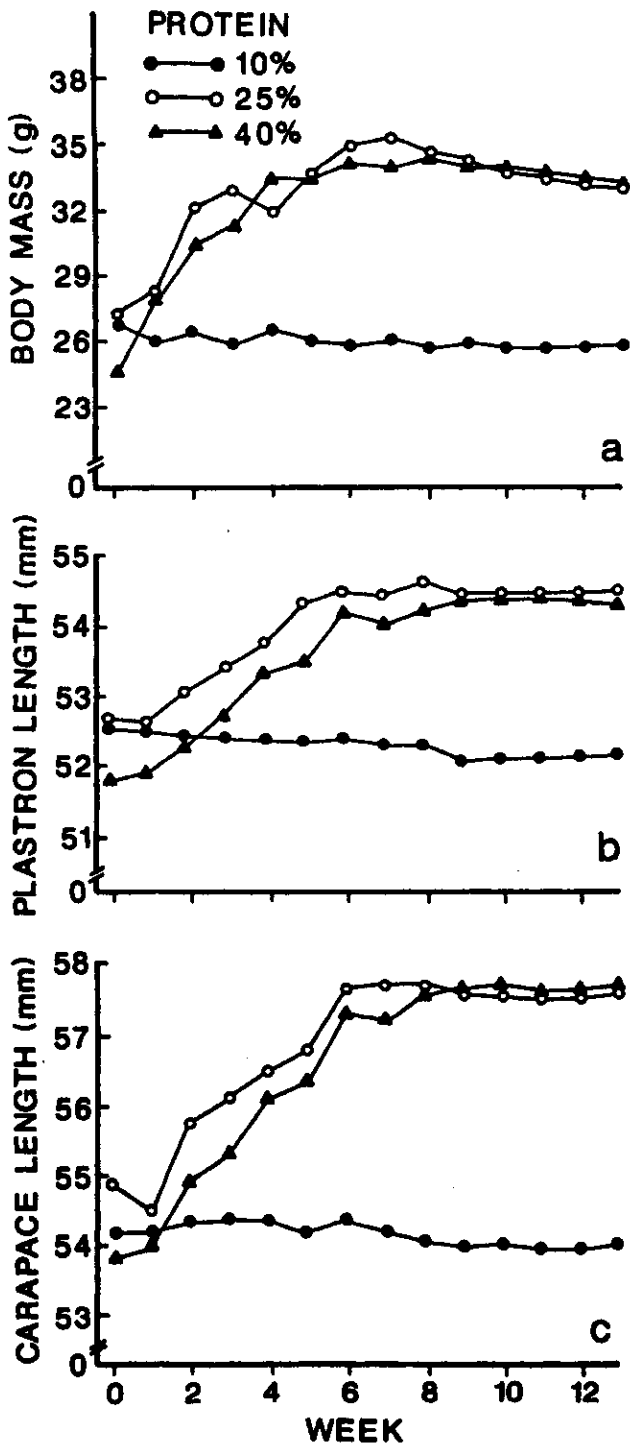


FIGURE 20.6. Growth-related changes in body mass (a), plastron length (b), and carapace length (c) of captive juvenile sliders (*T. scripta*) raised on ad libitum rations of variable protein diets. Ration energy content and other nutrient concentrations were equal for all treatment groups. Sliders given diets of 25% and 40% protein exhibited significantly faster growth than sliders fed a diet of 10% protein (one-way ANOVA and Tukey test for treatment differences,  $p < .0001$ ,  $N = 20$  sliders per group; Avery, 1987).

Par Pond juvenile sliders and has a crude protein concentration of about 20%, which is comparable to that of the 25% crude protein diet in Figure 20.6. Data from this study indicate that carnivory, or omnivory with a significant amount of fish or other dietary protein, may be essential to maintain the high juvenile growth rates exhibited by free-living juvenile sliders. These growth data therefore provide nutritional reasons for the marked carnivory observed in the first year of slider growth (Clark and Gibbons, 1969) and support the hypothesis that varying dietary protein availability accounts for differences in growth rates of sliders from different populations in the same geographic area (Gibbons, 1970b; Parmenter, 1980).

Data on other nutrient requirements of sliders are currently unavailable; however, nutritionally essential amino acids have been identified for the green turtle *Chelonia mydas* (Wood, 1974), and quantitative requirements for each amino acid have been determined for optimal weight gain in juveniles (F. Wood and Wood, 1977; J. Wood and Wood, 1977). Some of the amino acids essential for juvenile green turtle growth are found in only limited quantities in plants (J. Wood and Wood, 1977). As a result, green turtle growth rates and reproductive output decrease because of the nutrient limitation in their diets (Bjorndal, 1985). If juvenile sliders have similar qualitative and quantitative amino acid requirements, high amounts of animal protein in the diet should facilitate rapid growth. Hence, juvenile carnivory would be advantageous for attaining larger body size and earlier sexual maturity.

Although dietary nutritional requirements for sliders are as yet undetermined, some insight into the importance of diet quality on slider health and growth can be obtained from accounts of reptile nutritional disorders reported in the veterinary medicine literature (e.g., Frye, 1973; Jackson and Cooper, 1981). We now know that reptiles, like other vertebrates, are susceptible to various maladies resulting from nutritional deficiencies or excesses. For example, dietary protein deficiencies lead to body emaciation and muscle atrophy, and insufficient quantities of vitamins A and B<sub>1</sub> cause degradation of a variety of body tissues. Scurvy (caused by a vitamin C deficiency) appears to be rare in reptiles. However, rickets (caused by a vitamin D deficiency) has been reported in reptiles, as have goiters (from iodine deficiency) and steatitis (from vitamin E deficiency). Calcium deficiencies are particularly well documented in sliders. A dietary imbalance in the calcium-phosphorus ratio, which normally should remain between 1:1 and 1.5:1, causes osteodystrophy in turtles and results in shell and bone deformations (Frye, 1973). Similarly, excess concentrations of some dietary nutrients cause debilitating diseases in reptiles, such as an excess of vitamin D, which results in anorexia and lameness (Jackson and Cooper, 1981). In summary, it is clear

that diet nutritional quality can have a major influence on the growth and physical health of the slider turtle; however, we emphasize that the extent of nutritional disorders in natural populations of slider turtles is currently unknown.

#### ENVIRONMENTAL EFFECTS ON DIET AND GROWTH

Correlations between growth rates in wild turtles and diet quality (or estimates of environmental food abundance) show that highly productive habitats tend to produce larger turtles with accelerated growth rates. Exceptionally rapid growth rates have been observed in turtle populations inhabiting environments characterized by naturally high organic levels (Moll, 1976b) or artificially altered environments, such as chemically polluted rivers (Gibbons, 1967b; Knight and Gibbons, 1968) and thermally altered reservoirs (Gibbons, 1970b; Christy et al., 1974; Avalos, 1975; Thornhill, 1982).

Turtles inhabiting thermally altered habitats may experience an interaction effect between temperature and diet, in that thermal loading of the environment may (1) promote greater productivity at all trophic levels, thereby increasing the quantity and quality of available food resources, (2) extend the turtle growing season into early spring and late autumn (for high-latitude populations), and/or (3) raise turtle body temperatures, influencing behavior, metabolic rates, and digestive processes. For example, sliders exhibiting high growth rates from Par Pond, South Carolina (a highly productive nuclear reactor cooling reservoir), ingest twice as much protein (fish carrion and insects) in their diet as slower-growing sliders from a farm pond and a Carolina Bay (Parmenter, 1980). Water temperatures differ somewhat (4° to 6° C) among these habitats, and although reservoir turtles in this study were not captured in the thermally altered areas, temperature effects on this population may have influenced their feeding behavior. Winter activity and feeding occur in the Par Pond population (Schubauer and Parmenter, 1981) but are not observed in other nearby populations. In contrast, slider populations from both a reactor cooling reservoir (Lake Baldwin, Illinois) and two natural lakes have similar diets, yet individuals in the reservoir population exhibit a faster growth rate (Avalos, 1975; Thornhill, 1982). In this case, temperature differences alone among habitats (4° to 8° C) may allow increased foraging by reservoir turtles and/or cause a longer growing season.

In addition to populations in artificially heated en-

vironments, there are examples of slider populations that inhabit naturally warm, shallow-water habitats, rich in high-protein food resources, and also show high growth rates and large body size. Sliders living in shallow roadside ditches in Illinois consume massive quantities of insects (Cagle, 1946), and sliders in pools on the Atlantic coast barrier islands feast on an inexhaustible supply of euryhaline fishes (Gibbons et al., 1979).

The synergistic effect of diet quality and temperature on slider feeding ecology has been examined recently in laboratory experiments. Avery (1987) measured consumption rates, digestion rates, and digestive efficiencies in captive sliders at four temperatures (15°, 22°, 28°, and 34° C) while using three diet qualities (10%, 25%, and 40% ration protein content). Not only did Avery find that sliders displayed greater consumption rates, digestion rates, and digestive efficiencies at warmer temperatures, but he also discovered a significant interaction effect of temperature and diet quality on digestion rates and digestive efficiencies. He demonstrated that sliders feeding on high-protein rations exhibit a disproportionately greater temperature response in their digestion rate than sliders feeding on low-protein rations. Such a physiological synergism would undoubtedly contribute to the observed growth rates and large body sizes recorded in slider populations from highly productive, warm-water habitats.

Thus, environmental temperature and trophic productivity are fundamentally important environmental factors influencing the feeding ecology of *T. scripta*. Further studies are needed to determine the interactive effects of temperature, food abundance, and food quality on feeding rates, digestive physiology, growth, and development of sliders under natural thermal conditions, with natural food types from different habitats, and with different age classes. Determining the essential nutritional requirements for slider growth and development and assessing the naturally ingested food types for the availability of these nutrients (e.g., essential amino acids, calcium) would greatly enhance our understanding of differential growth exhibited among and within wild slider populations.

#### Acknowledgments

Research and manuscript preparation were made possible by contract DE-AC09-76SROO-819 between the University of Georgia and the U.S. Department of Energy and by National Science Foundation grant DEB-79-04758.