Ontogenetic Diet Shifts and Digestive Constraints in the Omnivorous Freshwater Turtle *Trachemys scripta*

Sarah S. Bouchard*
Karen A. Bjorndal
Department of Zoology, University of Florida, Gainesville, Florida 32611

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ABSTRACT

Many reptiles undergo an ontogenetic diet shift from carnivory to herbivory. In this study, we used the yellow-bellied slider turtle, *Trachemys scripta*, as a model to evaluate whether juvenile turtles are carnivorous because physiological constraints preclude herbivory. We conducted feeding trials in which we fed juvenile and adult turtles a duckweed plant, *Lemna valdiviana*, or a freshwater grass shrimp, *Palaemontes paludosus*, for 5 wk. During the trials, we measured mass-specific intake, digestibility, and digestible intake for both size classes, as well as juvenile growth. At the end of the trials, we measured the nutrient composition of the juvenile turtles. Juveniles fed shrimp grew 3.2 times faster than those fed duckweed and had equivalent lipid stores. Digestive processing in juveniles was extremely efficient on the shrimp diet, with higher mass-specific intakes than adults and very high digestibilities (97%). Juveniles digested duckweed as well as adults did; however, their intake of this diet was limited, possibly by the time required for fermentation. We concluded that although juveniles can process plant material, an animal diet allows for greater juvenile growth, which in turtles is linked to higher survivorship and increased future reproductive success.

Introduction

Ontogenetic diet shifts are common in vertebrates; as animals grow, shifts can occur between foods that are nutritionally similar or dissimilar. For example, some fish are carnivores throughout life but sequentially shift from eating zooplankton to invertebrates to fish prey (Gilliam 1982). Most frogs, on the other hand, experience more extreme shifts from herbivorous to carnivorous diets when they metamorphose from tadpoles to adults (Duellman and Trueb 1986). Similarly dramatic shifts, but in the opposite direction, also occur in lizards (Rocha 1998; Durtsche 2000; Fialho et al. 2000; Cooper and Vitt 2002) and fishes (Horn 1989; Benavides et al. 1994). Most mammals initially consume a milk diet before switching to the natural adult diet, and many doves and pigeons begin life consuming crop milk (Sales and Janssens 2003).

Ontogenetic diet shifts from carnivory to herbivory are widespread in several turtle families, including Emydidae (Moll 1976; Parmenter and Avery 1990), Chelidae (Kennett and Tory 1996; Spencer et al. 1998), and Cheloniidae (Bjorndal 1997*b*). These diet shifts in freshwater turtles are often accompanied by habitat shifts from shallow to deeper water (Hart 1983; Congdon et al. 1992). Therefore, ecological hypotheses such as differences in prey availability between these zones have often been proposed to explain chelonian diet shifts (Hart 1983; Parmenter and Avery 1990). Although ecological factors are probably important, digestive physiology may also play a critical role (Whelan et al. 2000).

Juvenile turtles may be carnivorous because they cannot process sufficient plant material to meet their nutritional needs. In most herbivorous reptiles, microbial symbionts in the hindgut play an important role in the digestion of plant material (Bjorndal 1997*a*). These symbionts ferment plant cell-wall constituents, producing short-chain fatty acids as a waste product, which the host absorbs and uses as an energy source. The capacity of the fermentation chamber must be sufficiently large to delay passage of digesta so that cell-wall components can be digested and microbes can reproduce. If passage is too rapid, microbial populations will be flushed from the digestive tract. In both mammals and reptiles, fermentation chamber capacity is directly proportional to body size (Parra 1978; Bjorndal 1997*a*); however, metabolic demands scale allometrically with body size to a power less than 1 (Bennett and Dawson 1976; Nagy et al. 1999). Consequently, the ratio of fermentation chamber capacity to metabolic rate decreases in smaller animals (Justice and Smith 1992).

Pough (1973, 1983) hypothesized that ontogenetic diet shifts occur in reptiles because small gut capacity limits the ability of juveniles to meet their high mass-specific metabolic rates on plant diets. However, since Pough (1973, 1983) published his studies, many examples of small herbivorous lizards have been documented, and some species expected to experience an ontogenetic diet shift actually have herbivorous young (Troyer

* Corresponding author. Present address: Life and Earth Science Department, Otterbein College, Westerville, Ohio 43081; e-mail: sbouchard@otterbein.edu.

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1984*b*; Mautz and Nagy 1987; Wikelski et al. 1993; Cooper and Vitt 2002). Results from these studies indicate that small reptiles can offset unfavorable ratios of gut capacity to metabolic rate by increasing mass-specific intake and shortening gut transit times relative to adults. Because time for fermentation is reduced, this strategy could decrease digestibility of the diet. However, small reptiles can compensate by maintaining higher body temperatures that facilitate digestion (Troyer 1987; Avery et al. 1993; Wikelski et al. 1993). Additionally, juveniles can maintain high intake without sacrificing digestibility because their small bite size allows them to ingest smaller food particles that are more rapidly fermented (Bjorndal et al. 1990), to feed more selectively on plant parts that are higher in nitrogen and energy (Troyer 1984*b*; Mautz and Nagy 1987; Bjorndal and Bolten 1992), and to penetrate structural barriers to digestion more effectively (Bjorndal and Bolten 1992). Bite size in reptiles is very important because reptiles cannot reduce particle size by chewing (Throckmorton 1980; Norman and Weishampel 1985).

Although studies indicate that juvenile reptiles can process and subsist on a plant diet, the question remains why juvenile turtles are carnivorous. Studies addressing this question to date have focused on the slider turtle, *Trachemys scripta*, a species in which the shift has been well studied (Clark and Gibbons 1969; Hart 1983; Parmenter and Avery 1990). As juveniles, these turtles are carnivores that feed on aquatic invertebrates, but as they mature, they become opportunistic omnivores that feed primarily on aquatic plants. Although adult *T. scripta* can process and subsist on both carnivorous and herbivorous diets (Bjorndal 1991), it is unclear if juveniles can do so; previous studies of juveniles using artificial diets have produced conflicting conclusions. McCauley and Bjorndal (1999) found that juvenile *T. scripta* fed a gelatin-based diet had higher mass-specific intake relative to adults. This study suggested that juveniles can subsist on herbivorous diets because intake increased in response to nutrient-dilute diets with energy levels similar to plants. However, the digestibility of this diet was so high that potential limits on intake imposed by fermentation and gut capacity were not relevant. In another study, Avery et al. (1993) found that juvenile *T. scripta* fed a pelleted diet of 10% crude protein did not grow and concluded that protein levels in plants were not sufficient to maintain juvenile growth. Therefore, even if juvenile *T. scripta* can process plant material, individuals feeding on plants may be in poorer condition than are those feeding on animal material.

In this study, we conducted feeding trials in which we fed juvenile and adult *T. scripta* plant and animal diets. The goal of these feeding trials was to answer two questions: (1) whether juvenile growth and composition vary with plant and animal diets, and (2) to what extent juveniles and adults are able to process plant and animal material. If juveniles are carnivorous because they are unable to subsist on plant material, then juveniles fed plants would grow more slowly or have lower energy stores than juveniles fed animal material. Additionally, Clark and Gibbons (1969) proposed that juvenile *T. scripta* are carnivorous in order to obtain sufficient calcium for shell mineralization; juveniles fed plant material may therefore also be lower in calcium relative to those fed animal material. If differences exist in growth and composition between juveniles fed plant and animal material, then comparisons of digestive processing may provide insight into the mechanism responsible. Juveniles may have reduced ability to digest plant material relative to adults either in the quantity processed or in the extent to which it is digested.

Material and Methods

Experimental Animals, Diets, and Protocol

Juvenile yellow-bellied slider turtles were obtained as hatchlings from a commercial turtle farm in Port Mayaca, Florida, in mid-June 2000. These turtles were the offspring of breeding adults collected from northern Florida, Georgia, and South Carolina. Sex of these turtles was unknown. Adult turtles were collected in May 2001 from Kathwood Ponds, located in the Audubon Society's Silver Bluff Sanctuary in Aiken County, South Carolina. All adult turtles used in this trial were males. All research conducted with these animals was approved by the Institutional Animal Care and Use Committee at the University of Florida (project Z012).

The plant diet was duckweed, *Lemna valdiviana*, collected from a pond in Gainesville, Florida. Duckweed is a small, floating aquatic plant consumed by adult *Trachemys scripta* throughout much of its range (Parmenter and Avery 1990). The animal diet was freshwater grass shrimp, *Palaemontes paludosus*, purchased from a bait shop that obtained the shrimp from Gainesville-area lakes. Pretrial observations indicated juveniles tended not to eat the most anterior portion of the shrimp containing the eyes and antennae or the posterior portion containing the caudal fin. To ensure that all animals consumed the same diet, these parts were removed before shrimp were fed to juveniles and adults. Nutrient composition of each diet is described in Table 1. Because adult and juvenile trials were not conducted simultaneously, composition of duckweed varied between the trials. The difference resulted in juveniles receiving a higher quality diet (lower in fiber and higher in nitrogen and energy). Therefore, if juveniles performed poorly on the duckweed diet relative to adults, it could not be attributed to differences in diet quality between age classes.

Juveniles were housed individually in square Rubbermaid containers (18 cm × 18 cm), with four containers placed within a larger Nalgene tank (45 cm × 60 cm). Each day, juveniles were rotated between Nalgene tanks to avoid a tank effect. Each Nalgene tank was equipped with a 75-W floodlight and a 20-W full-spectrum natural light fluorescent bulb. Adults were housed individually in the same Nalgene tanks. All turtles ex-

Table 1: Nutrient composition of duckweed and shrimp diets fed to juvenile and adult turtles *Trachemys scripta*

	Duckweed Diet		Shrimp Diet	
	Juveniles	Adults	Juveniles	Adults
Organic matter (%)	86.4	85.5	88.0	87.1
Fiber (%):[a]				
NDF	41.2	45.2		
ADF	19.7	21.4	6.4	4.8
Nitrogen (%)	5.0	4.1	12.6	12.6
Energy (kJ g dry matter^{-1})	18.49	17.35	21.75	20.91
Calcium (%)	.8		2.2	

Note. All values except energy are presented on a dry matter percentage basis. Note that shrimp values are for shrimp with anterior and posterior portions removed.

[a] Neutral detergent fiber (NDF) represents cellulose, hemicellulose, lignin, and cutin, whereas acid detergent fiber (ADF) represents cellulose, lignin, and cutin of duckweed. ADF represents the chitin component of shrimp.

perienced a 12L : 12D photoperiod and temperatures between 25° and 26°C.

Turtles were fed either duckweed (juveniles, $n = 7$; adults, $n = 7$) or shrimp (juveniles, $n = 7$; adults, $n = 5$) diet. Both juvenile and adult feeding trials lasted 5 wk and consisted of a 2-wk acclimation period followed by a 3-wk experimental period during which daily food intake and feces production were quantified. The juvenile trial was conducted from August 29 to October 2, 2000, and the adult trial from May 30 to July 2, 2001. Before the juvenile trial began, adult feces were introduced into tanks so juveniles could acquire microbial gut symbionts (Troyer 1984*a*). At the onset of the juvenile trial, turtles had an average mass of 11.6 g (range 9.4–16.6 g). At the onset of the adult trial, turtles had an average mass of 995.4 g (range 375.2–1,451.1 g), with average masses in the duckweed and shrimp treatments of 956.2 g (range 375.3–1,280.2 g) and 1,081.1 g (range 912.0–1,251.1 g), respectively. Mean mass of the adult groups did not differ if the two smallest turtles were omitted from the duckweed group, and results did not differ when these turtles were excluded from analyses.

To determine digestibility, all feces were collected during the experimental periods in water balloons (juveniles) or condoms (adults), using techniques modified from Avery et al. (1993) and Bjorndal (1991). See Bouchard (2004) for a detailed description of fecal collection devices.

During both trials, water was drained from tanks every morning at 0800 hours so all turtles could bask for the same amount of time each day and differential thermoregulation among turtles could be controlled. At 1000 hours, feces were collected, and tanks were refilled with water. At 1100 hours, turtles were fed a known mass of either duckweed or shrimp. Enough food was provided to ensure turtles fed ad lib. Turtles fed for 6 h until 1700 hours, when orts (remaining food) were collected and weighed. At 1800 hours, feces were collected from adults a second time to prevent overfilling of condoms.

Nutrient Analyses and Digestive Processing Calculations

During the experimental periods, samples of duckweed and shrimp diets were collected daily. Daily diet, ort, and fecal samples were dried overnight at 60°C. Daily diet samples, as well as daily ort and fecal samples for each turtle, were combined to obtain a composite sample of each across the 3-wk period. All samples, except juvenile fecal samples, were ground to pass through a 1-mm screen in either a Wiley mill or a coffee grinder. Juvenile fecal samples were not ground because (1) sample quantities were so small that grinding would have resulted in loss of a significant percentage of sample, and (2) the entire fecal sample for each turtle was dried and combusted for analysis of dry matter and organic matter.

Diet samples were analyzed for dry matter, organic matter, neutral detergent fiber (NDF), acid detergent fiber (ADF), nitrogen, and energy content. Fecal samples were analyzed for dry and organic matter because juveniles produced insufficient quantities for further analyses. Duckweed orts and shrimp orts were analyzed for nitrogen and energy content to determine if turtles fed selectively.

Dry matter and ash (mineral) content were determined by drying subsamples overnight at 105°C and then combusting them at 500°C for 3 h. The difference between these two measures represents the organic matter component of the sample. NDF and ADF were determined by sequentially refluxing samples with neutral detergent and acid detergent solutions (Goering and Van Soest 1970) in an Ankom 200 Fiber Analyzer according to the guidelines supplied with the equipment (Ankom Technology 1998, 1999). NDF represents the cell-wall component of the plant diet (cellulose, hemicellulose, lignin, and cutin), and ADF represents the ligno-cellulose and cutin component. The ADF component of the shrimp diet represents the exoskeleton (primarily chitin) fraction of the diet (Stelmock et al. 1985). Nitrogen content of the samples was determined using a Carlo Erba elemental

Table 2: Growth and nutrient composition of juvenile turtles *Trachemys scripta* fed duckweed or shrimp

	Duckweed Diet	Shrimp Diet	*t*	*P*
Growth rate (mg wk^{-1})	**195.0 ± 54.6**	**616.2 ± 126.6**	**3.056**	**.015**
Composition:				
Body water (%)	**83.8 ± .3**	**75.5 ± .7**	**10.987**	**<.001**
Organic matter (%)[a]	84.6 ± .9	84.1 ± .4	.685	.507
Nitrogen (%)[a]	**12.5 ± .1**	**11.4 ± .1**	**6.220**	**<.001**
Nitrogen, lipid-free basis (%)	**17.4 ± .4**	**16.4 ± .3**	**2.289**	**.043**
Lipid (%)[a]	28.2 ± 1.5	30.6 ± .9	1.401	.189
Energy (kJ g^{-1})[a]	21.23 ± .39	21.70 ± .22	1.087	.300
Minerals (%)[a]	15.4 ± .9	15.9 ± .4	.203	.843
Calcium (%)[a]	3.26 ± .27	3.67 ± .37	.885	.410
Sodium (%)[a]	**1.08 ± .03**	**.74 ± .07**	**4.158**	**.002**
Potassium (%)[a]	.63 ± .14	.49 ± .06	1.016	.331
Magnesium (%)[a]	.11 ± .01	.09 ± .01	1.473	.169

Note. Values are means ± SE, and boldface indicates significant differences (*t*-tests) between treatments.
[a] Dry matter percentage basis.

analyzer. Energy content was determined with a Parr bomb calorimeter (Parr Instrument Company 1960).

To determine if juvenile turtles experienced an advantage of small bite size, we counted the number of duckweed fronds that passed through the gut intact in subsamples of feces from juvenile and adult turtles. If juveniles experienced an advantage of small bite size, they would have significantly fewer intact duckweed fronds in their feces.

Intake of dry and organic matter was calculated as the difference between the quantities of food offered and orts remaining each day multiplied by the fraction of dry matter and organic matter in the diet. Because nutrient composition of the orts was similar to that of the diet, no adjustments were necessary to account for selective feeding. Digestibility was determined using the equation (intake − feces)/intake, where intake is total grams of dry matter or organic matter consumed during the trial and feces is grams of dry matter or organic matter in the feces produced during the trial. Note that this equation calculates apparent digestibility because it does not correct for the introduction of nutrients into digesta from endogenous sources of the turtle or from the microbial symbionts. Daily digestible intake was calculated by multiplying daily intake and digestibility. For adults eating shrimp, digestible dry matter intakes were less than digestible organic matter intakes, suggesting that either the quantity of ash in the diet was underestimated or the quantity in the feces was overestimated. Because of this discrepancy, only organic matter digestibilities and digestible intakes are presented. Because of unequal variances, differences in all digestive parameters between treatments were evaluated with Kruskal-Wallis tests and post hoc analyses according to Conover (1980). Using the Statistical Package for Social Sciences (SPSS), we ran linear regressions on log-transformed data to determine the allometric slope between turtle body mass and dry matter intake of shrimp and duckweed; 95% confidence intervals (CIs) around these estimates were calculated.

Juvenile Growth and Composition

Juvenile turtles were weighed once a week during the 5-wk trial to determine growth rate. At the conclusion of 5 wk, turtles were killed with sodium pentobarbital. Carcasses without digestive tract contents were dried to constant mass at 60°C and ground in a Wiley mill to pass through a 1-mm screen. Juveniles were analyzed for dry matter, organic matter, nitrogen, lipid, energy, and mineral (calcium, sodium, potassium, magnesium) content. Methodologies were the same as for diet samples, except a Gentry-Wiegert Phillipson microbomb calorimeter (Gentry Instruments) controlled by a data logger (21 ×, Campbell Scientific) was used for energy analysis. Mineral composition was determined by solubilizing samples in a hydrochloric acid solution and analyzing filtrate with a Perkin-Elmer Model 5000 Atomic Absorption Spectrophotometer (Hesse 1972). Nonpolar lipid content was determined by extraction for 8 h in a Soxhlet extractor, with diethyl ether and petroleum ether as the solvent. Differences in nutrient content between juveniles were compared using *t*-tests. All percentage data were arcsin transformed before analysis.

Results

Juveniles fed shrimp grew 3.2 times faster than juveniles fed duckweed ($P = 0.015$; Table 2). Body composition of juveniles fed shrimp was 10% lower in body water ($P < 0.001$), 9% lower in nitrogen ($P < 0.001$), and 31% lower in sodium ($P = 0.002$; Table 2).

Mass-specific intake varied significantly between treatments for dry matter ($P = 0.002$), organic matter ($P = 0.002$), energy ($P < 0.001$), and nitrogen ($P < 0.001$; Table 3). For both juveniles and adults, mass-specific intake of dry matter was higher on the shrimp diet than on the duckweed diet, and this difference was more extreme for the juveniles. Organic matter digestibility differed significantly between diets ($P < 0.001$), with shrimp being more digestible than duckweed in both age classes (juveniles, 97.2% vs. 65.7%; adults, 89.4% vs. 68.6%). Mass-specific digestible organic matter intake also varied significantly with treatment ($P < 0.001$); turtles fed shrimp consumed more digestible organic matter on a mass-specific basis than those fed duckweed (5.3 times more for juveniles, 1.8 times more for adults).

On the shrimp diet, mass-specific intakes of dry matter, organic matter, energy, and nitrogen were three times higher in juveniles than in adults (Table 3). Dry matter intake of shrimp scaled to body mass with an allometric slope of 0.815 ± 0.166 (95% CI; $F_{1,10} = 119.21$, $P < 0.001$). Juvenile shrimp digestibility was significantly higher than that of adults (97.2% vs. 89.4%). Although mass-specific digestible organic matter intake was not significantly different, it tended it be higher in juveniles (8.0 vs. 2.3 mg g turtle^{-1} d^{-1}), and this trend approached significance (t_{critical} of Conover [1980] post hoc test = 5.0, $t_{\text{calculated}} = 4.7$).

On the duckweed diet, mass-specific intakes of dry and organic matter as well as energy were not significantly different between juveniles and adults (Table 3). Dry matter intake scaled to body mass with an allometric slope of 0.948 ± 0.071 (95% CI; $F_{1,12} = 836.54$, $P < 0.001$). Both age classes achieved equivalent digestibilities and consumed similar quantities of digestible organic matter, on a mass-specific basis, on this diet. Additionally, juveniles had significantly fewer intact duckweed fronds in their feces (median = 38%, range = 33%–47%) than did adults (median = 49%, range = 37%–61%; one-tailed Mann-Whitney U-test: $U = 7.00$, $P = 0.039$).

Discussion

Juvenile Growth and Composition

Ultimately, the value of a diet to juvenile turtles is best reflected in the growth and condition of individuals feeding on that diet. Juveniles fed shrimp grew 3.2 times faster than those fed duckweed. Such dramatic variation in growth probably resulted from differences in energy and nitrogen gains from each diet. Juveniles fed shrimp consumed 4.2 times more energy and 9.1 times more nitrogen than did juveniles fed duckweed. Although diet composition does not equal availability per gram of diet, juveniles fed shrimp probably assimilated substantially more energy and nitrogen than did those fed duckweed. Although juveniles fed duckweed did increase in mass over the course of the trial, their tissues contained 11% more water than did tissues of turtles fed shrimp. Therefore, the mass gained may indicate more a gain in water than in new tissue. Juveniles fed duckweed gained an average of 994.3 mg wet mass during the trial, whereas those fed shrimp gained 3,142.9 mg. Assuming the mass gained during the trial had the same water content as the tissue at the end of the trial, juveniles fed duckweed gained only 161.1 mg of dry matter compared to 770.0 mg for those fed shrimp.

Table 3: Digestive processing of duckweed and shrimp diets fed to juvenile and adult turtles *Trachemys scripta*

	Duckweed Diet		Shrimp Diet			
	Juveniles ($n = 7$)	Adults ($n = 7$)	Juveniles ($n = 7$)	Adults ($n = 5$)	H	P
Intake (mg g turtle^{-1} d^{-1}):						
Dry matter	2.6 (1.6–2.9)^{AC}	2.0 (1.3–3.2)^{A}	9.5 (3.1–16.9)^{B}	3.2 (2.0–4.7)^{C}	14.676	.002
Organic matter	2.3 (1.4–2.5)^{AC}	1.8 (1.1–2.8)^{A}	8.3 (2.7–14.9)^{B}	2.8 (1.8–4.1)^{C}	15.338	.002
Energy (kJ g turtle^{-1} d^{-1})	48.4 (29.3–53.1)	34.3 (23.4–54.0)^{A}	206.1 (66.7–367.7)^{B}	66.0 (42.6–97.7)^{C}	18.359	<.001
Nitrogen	.13 (.08–.14)^{A}	.07 (.06–.11)^{B}	1.19 (.39–2.13)^{C}	.40 (.26–.59)^{D}	21.570	<.001
Organic matter digestibility (%)	65.7 (61.3–71.0)^{A}	68.6 (63.2–77.6)^{A}	97.2 (96.1–99.0)^{B}	89.4 (84.9–93.4)^{C}	21.000	<.001
Organic matter digestible intake (mg g turtle^{-1} d^{-1})	1.5 (.8–1.7)^{A}	1.3 (.8–1.8)^{A}	8.0 (2.7–14.4)^{B}	2.3 (1.6–3.6)^{B}	18.406	<.001

Note. Comparisons between groups were made with Kruskal-Wallis tests and post hoc tests according to Conover (1980). Values are medians with ranges in parentheses, and different superscripts across rows indicate significant differences between treatments.

Such differences in juvenile growth have important implications for *Trachemys scripta* survival and reproduction. Because juvenile turtles have higher mortality than adults (Frazer et al. 1990; Bodie and Semlitsch 2000), rapid growth allows juveniles to pass through a vulnerable life stage more quickly. Additionally, male *T. scripta* mature on reaching a certain size, whereas females tend to mature at a certain age regardless of size (Gibbons et al. 1981). Faster juvenile growth therefore decreases age at maturity for males and increases size at maturity for females. Early maturation is advantageous for males because it allows males to obtain more matings over their lifetime. Large size at maturity is advantageous for females because growth slows significantly at maturity, and both reproductive output and survivorship of nesting females are positively correlated with size (Congdon and Gibbons 1983; Tucker et al. 1999).

Clark and Gibbons (1969) hypothesized that juvenile turtles may be carnivorous in order to obtain sufficient calcium for shell hardening after hatching. However, no difference was found in calcium percentage of juvenile tissue between diets. Turtles fed shrimp were, however, significantly lower in nitrogen percentage than those fed duckweed. This result is surprising and difficult to explain, given that nitrogen intake was higher on the shrimp diet. However, when nitrogen percentage was examined on a lipid-free basis, the difference approached nonsignificance.

Digestive Processing

Digestive physiology plays an important role in the ontogenetic diet shift of *T. scripta*. Juveniles, which consume a carnivorous diet in the wild, were extremely efficient on the shrimp diet. They had high mass-specific intakes relative to adults, as would be expected based on metabolic demands, and remarkably high digestibilities. Although juvenile mass-specific digestible organic matter intake was not significantly higher than that of adults, there was a strong trend. The lack of statistical significance probably stemmed from low statistical power associated with small sample size.

In carnivorous reptiles, dry matter intake scales to body mass with an allometric slope of 0.963 (Nagy 2001). Dry matter intake of shrimp in *T. scripta* scaled to body mass with an allometric slope of 0.815. Confidence intervals of 95% around the *T. scripta* estimate included the allometric slope for carnivorous reptiles as well as the allometric slope for the interspecific relationship between chelonian metabolic rate and body mass (0.86; Bennett and Dawson 1976). The fact that *T. scripta* dry matter intake scaled with body mass similarly to these other scaling relationships suggests that juveniles easily met their metabolic demands on the shrimp diet.

Juveniles were also able to digest shrimp to a greater extent than were adults. Similar results were found with spiny-tailed iguanas, *Ctenosaura pectinata*, a species that also shifts diet ontogenetically from carnivory to herbivory (Durtsche 2004). Although digestibilities were not as high as those of juvenile *T. scripta* (organic matter digestibility: 82.9% vs. 97.2%), juvenile *C. pectinata* assimilated 20%–25% more energy and nutrients from insect larvae than did adults. Such differences in the abilities of juveniles and adults to digest animal material may be attributed to ontogenetic shifts in enzyme production or in the densities and types of nutrient transporters (Buddington 1992).

Juvenile *T. scripta* did not fare nearly as well on the duckweed diet as on the shrimp diet, despite the fact that duckweed is a preferred food item of adults (Parmenter and Avery 1990). Although juveniles were able to digest duckweed as well as adults, juveniles did not have higher mass-specific intakes. Dry matter intake of duckweed scaled to body mass with an allometric slope of 0.948. The 95% CIs around this estimate include neither the allometric slope for the interspecific relationship between dry matter intake and body mass in herbivorous reptiles (0.717; Nagy 2001) nor the allometric slope for the relationship between chelonian metabolic rate and body mass. Assuming that adult turtles were able to eat enough to meet metabolic demands, these results suggest that juvenile intake was constrained on the duckweed diet and that juveniles had difficulty meeting their growth potential.

Juvenile and adult duckweed intake patterns contrast with those of a previous study in which juvenile *T. scripta* fed a gelatin-based diet had higher mass-specific intake than did adults (McCauley and Bjorndal 1999). The results of these studies may differ because microbial fermentation was probably not required to digest the gelatin-based diet, whereas it may have been to digest the duckweed. Although fiber digestion was not measured in this study, juvenile *T. scripta* fed duckweed in another study had short-chain fatty acid concentrations in their large intestines indicative of active fermentation (Bouchard 2004). If juveniles rely on this fermentation to meet a significant percentage of their energy requirements, then juvenile intake of plant material may have been limited by a minimum gut residence time required for adequate fermentation of the diet. Juveniles fed the gelatin-based diet were able to consume higher mass-specific quantities relative to adults because passage rate of the diet was not constrained by fermentation.

Insight into the digestive processing of *T. scripta* provides support for Pough's (1973, 1983) hypothesis that ontogenetic diet shifts occur in reptiles because small gut capacity limits the ability of juveniles to meet their high mass-specific metabolic rates on plant diets. This contrasts markedly with other herbivorous reptiles that do not support the hypothesis, including the green iguana, *Iguana iguana* (Troyer 1984*b*), desert iguana, *Dipsosaurus dorsalis* (Mautz and Nagy 1987), marine iguana, *Amblyrhynchus cristatus* (Wikelski et al. 1993), and red-bellied turtle, *Pseudemys nelsoni* (Bjorndal and Bolten 1992). Unlike *T. scripta*, juveniles of these species can maintain higher mass-specific intakes compared with adults. The difference between *T. scripta* and these species may be related to differences

in their gastrointestinal tracts. Iguanas possess either spiral valves or transverse folds in the large intestine, which slow the passage of digesta and increase the surface area for absorption (Iverson 1980). Red-bellied turtles lack such valves, but the fermentation chamber in this turtle has expanded to include the small as well as large intestine (Bjorndal and Bolten 1990). The fact that *T. scripta* gastrointestinal tracts do not have these or any other obvious modifications for herbivory (Bouchard 2004) may explain the differences between species. Interspecific comparisons with juveniles would reveal if juvenile *T. scripta* are less efficient herbivores than juveniles of other species. Additionally, future studies that use other plant diets and allow for variable temperature regulation would be valuable to assess variability in *T. scripta* juvenile digestive performance on plant diets.

In conclusion, this study provides an energetic explanation for the carnivorous diet of juvenile *T. scripta*. The question remains, however, why turtles switch to an herbivorous diet as they mature, despite the fact that they can easily process animal material. Possible explanations may relate to costs associated with the pursuit and capture of animal prey by adults. Because they are larger, adults have greater absolute metabolic demands and greater locomotory costs than do juveniles. Consequently, even without the digestive differences measured in this study, the net gain from a given animal prey item is less for adults than for juveniles (Parmenter and Avery 1990). Additionally, larger adults may have more difficulty foraging for animal prey than do juveniles because of maneuverability constraints in the littoral zone, where animal prey is presumably most abundant (Hart 1983). Our understanding of the ontogenetic diet shift of *T. scripta* will not be complete until studies exploring these potential costs associated with prey acquisition by adults are evaluated. Additional research is also necessary to elucidate the physiological mechanisms underlying the chelonian ontogenetic shift and to understand why some small reptiles are herbivorous, but others are not.

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