EFFECT OF DIET ON GROWTH IN CAPTIVE *PODOCNEMIS UNIFILIS*: ASSESSING OPTIMAL DIETS FOR TURTLES IN HEAD-STARTING PROGRAMS

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ABSTRACT

Because turtles have come under increasing pressures from habitat loss and over-exploitation as food sources and traditional medicine, efforts have focused on options for conservation, including head-starting programs. Success of head-starting programs depends on establishing economical means of rearing hatchlings over relatively short time frames to sizes resistant to predation. We examined effects of three different diets on growth of a clutch of captive Yellow-spotted Amazon River Turtles (*Podocnemis unifilis*) over a two-year period in a Florida zoo. Rates of growth differed among the three treatment groups; relationships between morphological variables were not affected by diet. Results indicate that turtles fed on a commercial gel diet may exceed growth rates of animals fed on a more natural, vegetarian diet by more than 15% as measured by straight-line carapace length, or by more than 50% in body mass. Use of a vegetarian diet reduced costs to less than 10% of the cost of a commercial gel diet. Choice of diets for turtles in head-starting programs is a variable that should be weighed against other conservation objectives such as captive duration and intended sizes attained.

Key words: *Podocnemis unifilis*, ontogeny, growth, head-starting, conservation, diet, river turtle.

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INTRODUCTION

Turtles have historically served as a prime source of protein for local communities, but are under severe pressures due to increasing economic growth, loss of natural habitat, human population growth, and prevalence of a growing international trade (Fachin-Teran et al., 2004; Bell et al., 2005; Schneider et al., 2011). Turtle consumption is deeply ingrained in many cultures, particularly in Asia and South America (Gong et al., 2009; Haitao, 2008; Hoffman and Cawthorn, 2012). Due to a growing human population paired with income growth, consumption of turtle meat is now more prevalent than in the past (Schneider et al., 2011). Human consumption of turtle meat and eggs accounts for 46% of the decline in Chelonian taxa (Caputo et al., 2005). As a result, many governments have recognized the need to regulate turtle collecting; however, there are usually insufficient funds to enforce such regulations (Schneider et al., 2011). Despite development of commercial farms to support the turtle industry, extraction of turtles from the wild by local peoples remains a cheaper alternative (Fachin-Teran et al., 2004; Haitao et al., 2008), strongly suggesting the need for replenishment of wild stocks as a means of conservation.

Podocnemis unifilis (Yellow-spotted Amazon River Turtle) is one of the largest species of South American river turtles second only to *P. expansa* in female body size (Thorbjarnarson et al., 1993). It is native to the Amazon and Orinoco river systems of South America (Venezuela, E. Colombia, E. Ecuador, northeast Peru, Guyana, Brazil, and north Bolivia) and occurs in calm waters of flooded forests, swamps, or riverbeds during the dry season (Foote, 1978; Fantin, 2007). After sharp decline of *Podocnemis expansa* populations, *P. unifilis* populations have become increasingly exploited. A substantial black market exists due to a lack of enforcement in rural riverine villages and uncontrolled smuggling by middlemen. Riverine communities employ various hunting techniques from gill nets to spears, and are able to use their knowledge of the land to extract many turtles species and individuals in short time periods (Fachin-Teran et al., 2004). Hunting has affected several species of *Podocnemis* in recent years (Pantoja-Lima et al., 2014). High juvenile mortality and relatively late sexual maturity make it difficult to estimate appropriate extraction quotas and amount of support to sustainable turtle meat industries (Schneider et al., 2011). That said, *P. unifilis* seems to be primarily affected by opportunistic exploitation rather than systematic efforts directed at it specifically (Norris and Michalski, 2013). *Podocnemis unifilis* is a species of interest for conservation and management efforts due to known population declines in the Amazon basin (Thorbjarnarson et al., 2000).

Although the utility of head-starting programs has recently been criticized (Páez et al., 2015), such conservation efforts have been suggested as a way to enhance over-exploited, wild turtle populations (Bell et al., 2005). A head-starting program was started by the Brazilian government in the late 1970s to enhance natural populations of *P. expansa* (Cantarelli, 1997). Two million hatchlings have reportedly been released into the wild each year, although unfortunately there are no data on the impacts of this program (Fachin-Teran et al., 2004). In Venezuela, however, a head-starting program for *P. expansa* has been in place since 1992 (Hernández et al., 1998) with recent results indicating that the number of juvenile turtles in the wild is higher today due to this program (Peñaloza et al., 2015). Similarly, studies on head-start programs for *Chelonia mydas* (Green Sea Turtle) demonstrated decreases in natural mortality rates with head-started individuals reaching sexual maturity earlier than hatchlings released immediately into the wild. Earlier attainment of sexual maturity has been attributed to increased growth and size of individuals released as yearlings (Bell et al., 2005).

Understanding the effects of captivity on growth in turtles is central to the success of head-starting programs that seek to release individuals of greater size for their age than would be found in nature (Bell et al., 2005; Dodd and Dreslik, 2008). Accelerated growth rates are well known in captive animals and may be a product of differences in diet, environmental conditions, or other factors

(Swingle et al., 2005). Páez and colleagues (2009), for example, documented maternal effects on growth rates of hatchlings over the first month post-hatching, although it is unclear if effects observed during that time period would have long term effects on growth. Protein content of diets affects growth rates early in turtle ontogeny, with experimental animals receiving more protein typically achieving greater body mass over experimental periods than those either not receiving protein or receiving comparatively less (Avery et al., 1993; Páez and Bock, 2004).

We examined effects of three different diets on growth of turtles from a single clutch by a captive female *Podocnemis unifilis* over two years. Females of large and small turtle species often reach sexual maturity as a function size, rather than age (Shine and Iverson, 1995), suggesting that growth rates may be a valuable indicator of health and influence on sexual maturity, both important components of conservation efforts. We predicted that a diet with high protein levels would have a more positive effect than diets without added protein.

MATERIAL AND METHODS

In late April 2003, a female *P. unifilis* laid 37 eggs in the aquatic habitat at Lowry Park Zoo (LPZ; Tampa, Florida). We successfully retrieved 24 eggs and incubated them at 30.2°−30.4° C. Within this clutch, 21 of 24 eggs hatched between 17 June and 21 June. Of these, we retained 18 for growth analysis at LPZ. Although paternal tests were not performed, maternal effects, temperature, and genetic variation were minimized by use of a single clutch of eggs and uniform incubation and housing in this study.

We divided individuals randomly into three dietary treatment groups (n = 6 animals each) reared following standard husbandry practices of the institution. We housed Individuals in each group together in a single tank with approximately three quarts of water and 10% basking area. We reared turtles on identical diets (herbivore pellets and aquatic gel diet) for the first six months. Subsequently, we segregated treatment groups into three Rubbermaid 150 gallon stock tanks with terrestrial substrate available, basking lights on a 12-h schedule, and regular enclosure cleaning and maintenance. We increased water volume from 40 to 80 gallons as turtles grew. Basking area was constant in experimental tanks at 825 cm^2. In addition, a regular diet schedule included removing and replenishing food sources daily. We housed all three of the treatment groups in the same indoor facility at the zoological institution and maintained at identical water (approximately 27° C) and air temperatures (23–29° C). The zoological staff was responsible for daily feeding and care. Although temperatures in the facility were influenced slightly by fluctuating ambient conditions, all treatment groups experienced the same temperature variables.

Three dietary treatments were designed by zoological keeper staff with veterinary approval and each reared on the following diets: Group 1: MAZURI gel diet (Aquatic Gel Diet #5M7N a powder based diet containing not less than 55% crude protein, not less than 15.0% fat, and not more than 2.0% crude fiber). Group 2: Vegetable diet consisting of widely available foods including romaine, kale, apples, oranges, and small amounts of Mazuri® herbivore pellet (ADF 25; not less than 14% crude protein, not less than 3% fat, not more than 23% crude fiber and 25% detergent fiber). Group 3: Omnivorous diet (vegetable diet identical to above making up 33% of food provided by mass and 66% protein made-up of arthropods and insect larvae). Each treatment group was allowed to feed *ad libitum*, with excess food removed daily prior to fresh food provision. We changed water weekly throughout the study period.

Data collection occurred monthly over a period of 24 months. Data collection frequency was reduced beginning in year two of the study in order to reduce costs and allow the study to reach our desired end-date of two years from initiation. Data collection was limited to a minimum of three personnel in order to minimize measurement errors. We made replicas of each turtle carapace by molding each individual in fast-setting commercial silicone molding compounds, typically curing in about ten min (Fig. 1; AtoZ Knead-a-Mold or

Figure 1. Making a mold of the carapace of a juvenile specimen with silicone molding compound.

Smooth-On Body Double compounds both for use in the art industry were used in this study), and subsequently casting the molds in resin (Smooth-On Smooth-Cast 300/Q). This methodology had the advantage of creating permanent, three-dimensional replicas of each turtle carapace and minimizing restraint time. As turtles increased in size, fiberglass orthopedic cast tape was used to reinforce molds and minimize deformation, although this was rarely necessary. We then digitized resin casts using a Microscribe® 3DLX and Rhinoceros® 5.0 computer graphics package to measure straight-line carapace length (SCL) in each individual. We weighed each individual to the nearest gram beginning in the month seven of carapace replication (May, 2005). Average body mass (BM) and SCL were calculated monthly for each group, allowing comparison of growth across the three treatments.

We examined effects of diet on growth using one-way and repeated measures ANOVAs. We used one-way ANOVAs for SCL and BM analyses of monthly growth rates across groups, and repeated measures ANOVAs (RM ANOVA) for sequential measurements of individuals. We examined relationships between ln-body mass and ln-straight carapace length with least-squares regression analysis. All analyses were conducted using IBM SPSS® Statistics Version 24 (IBM Corp., 2016). Means are followed by one standard deviation.

RESULTS

Measurements of SCL began in November 2003 (population mean = 48.95 ± 0.66 mm). RM ANOVA revealed a significant time-diet interaction during the first year of growth (November 2003–November 2004) (F = 4.81, P <0.005). Results for the second year of growth (November 2004–November 2005) were comparable to the first year of monthly SCL measurements (F = 18.84, P <0.0005). The commercial gel diet treatment group yielded the highest rate of average monthly growth rate throughout the study (Table 1: mean = 3.96 ± 0.51 mm/month over 1 year and 4.58 ± 0.24 mm/month over 2 years) while the omnivorous treatment produced the lowest rate (Table 1: mean = 1.87 ± 0.66 mm over 1 year and 2.71 ± 0.32 mm over 2 years). The vegetarian treatment yielded a rate most similar to the population average monthly growth rate (mean = 3.02 ± 0.41 mm over 1 year and 3.69 ± 0.13 mm over 2 yr).

Differences in growth rate were well-established by the end of the first year after hatching (Fig. 2), with monthly rates differing by more than a factor of two among the study groups. Commercial gel diet animals exhibited the highest growth rate and the omnivorous diet the slowest (Table 1; ANOVA, Year 1: $F_{(2,17)} = 21.18$, $P < 0.0005$; Year 2: $F_{(2,14)} = 77.54$, $P < 0.0005$).

Body mass recording began several months after hatching due to lack of equipment prior to the

Table 1. Comparisons of straight-line carapace length (SCL) and body mass (BM) across treatments over the two-year growth study of captive juvenile *Podocnemis unifilis*. Group n = 6 in all cases; values are mean±one standard deviation.

	Treatment Groups					
	Commercial Gel		Vegetarian		Omnivorous	
Observation	SCL (mm)	BM (g)	SCL (mm)	BM (g)	SCL (mm)	BM (g)
11/2003	49.04±2.66	n/a	48.95±1.34	n/a	50.13±1.12	n/a
05/2004	70.20±1.56	64.0±11.4	68.19±2.50	56.7±4.13	63.60±3.55	48.5±4.97
11/2004	101.08±3.56	168.2±28.0	88.56±3.89	117.3±12.8	75.66±9.49	76.5±21.5
05/2005	125.75±2.87	438.7±38.0	107.15±3.24	292.7±22.0	85.05±12.13	125.7±43.7
11/2005	159.96±4.55	654.3±58.9	137.63±2.60	420.3±28.3	115.40±8.77	208.4±73.3

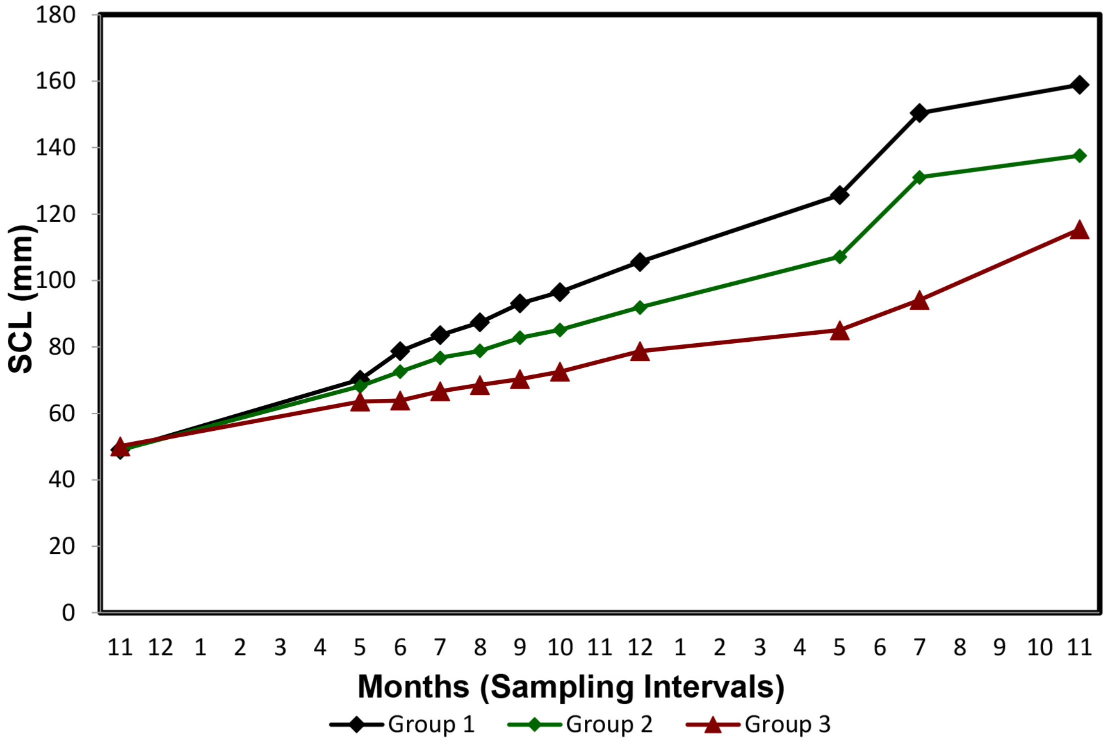

Figure 2. Comparison of straight carapace lengths (SCL) for each treatment over the length of the study (November 2003-November 2005).

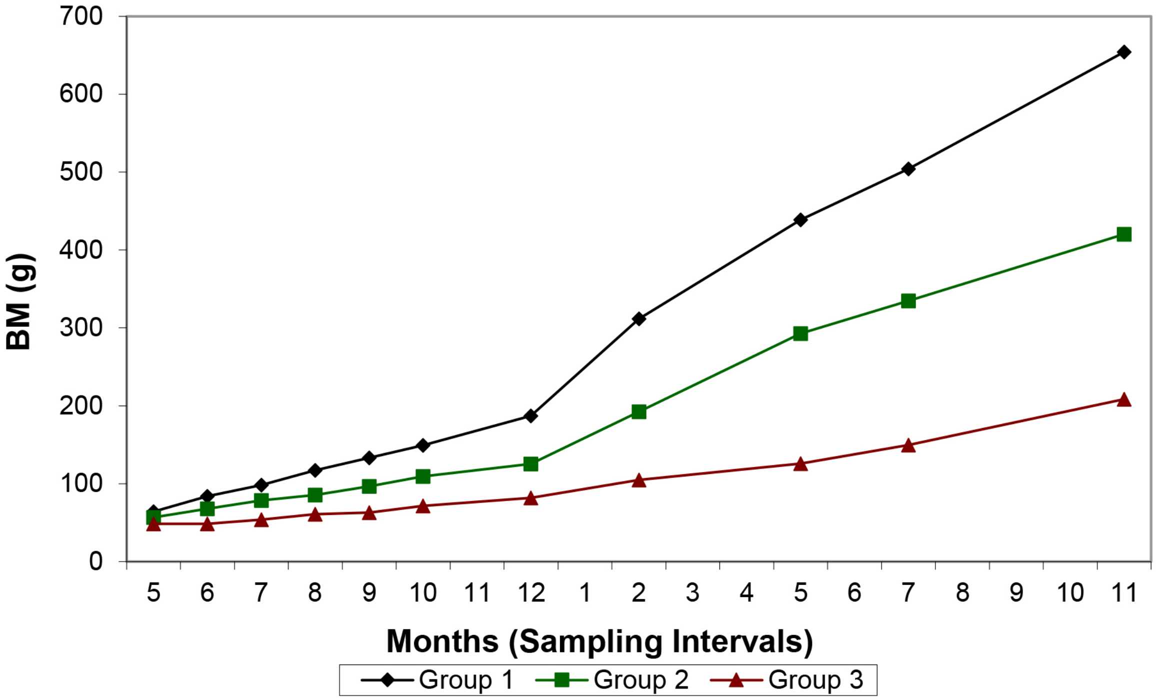

Figure 3. Comparison of body mass (BM) in grams for each treatment over 18 months of the study (May 2003-November 2005).

acquisition of funding for the project. Nonetheless, results are consistent with SCL data, with the greatest gain in mass among the commercial gel diet group (32.8 g/month over the course of data collection) and the slowest rate of mass gain among the omnivorous diet group (8.9 g/month; see Table 1; ANOVA, $F_{(2,16)} = 90.50$, $P < 0.0005$). An RM ANOVA using monthly BM data from May 2004 to November 2005 revealed a significant time*diet interaction ($F = 97.33$, $P <0.0005$). Mean BM differed among the three groups by more than two-fold (Fig. 3). The relationship between BM and SCL was consistent and linear across treatment groups (Fig. 4).

The commercial gel diet was a powder-based food for turtles that was transformed into a gel for consumption and had the highest cost per unit (mean = $0.0684/gram). Average cost for a variety of fruits and vegetables provided by the U.S. Drug Administration (Agricultural Marketing Service 2015) yielded a mean price per unit for the vegetarian diet in 2015 of $0.006349/gram. Price per unit for an omnivorous diet (mean = $0.020106/gram) was calculated by using total prices of the 33% vegetarian components and 66% insect larvae as sourced from vendors in the U.S.

DISCUSSION

Our experimental study of the effects of diet on carapace growth in a single clutch of *P. unifilis* raised in a zoological institution demonstrated significant differences in growth rates among treatment groups. Although relationships between body size and sexual maturity has been shown to be complex in some turtles (Congdon and van Loben Sels, 1993), size may be the primary determinant of the timing of sexual maturation (Blueweiss et al., 1978; Trembath, 2005; Mogollones et al., 2010). Results of our study suggest that previously reported variability of size relative to age in the closely related *P. expansa* (Mogollones et al., 2010) may be due to post-hatching nutrition. Although numerous factors may affect growth in captive facilities, our results show that achieving exceptional growth in relatively short time periods is possible. Rapid growth and early sexual maturation occurs in other captive turtles (Swingle et al., 1993). Early onset of sexual maturation is an important goal for head-

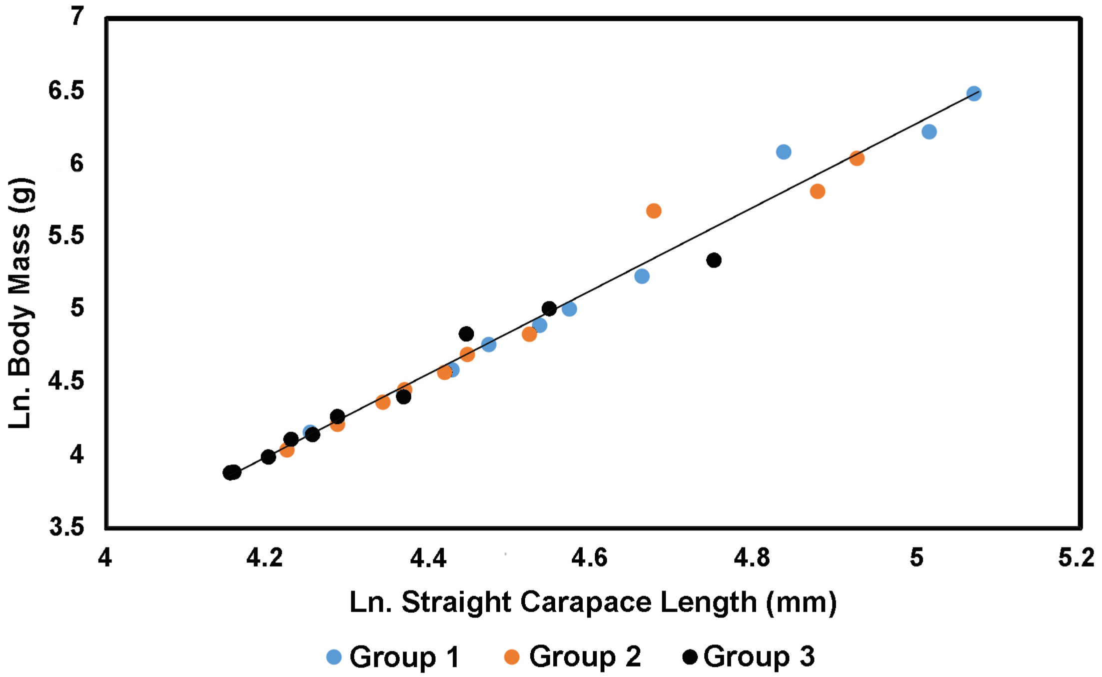

Figure 4. Body Mass relative to Straight Carapace Length. The relationship between body mass and carapace length is consistent across treatment groups ($y = 2.8465x – 7.9617$; $r^2 = 0.9805$).

starting programs with depleted local populations (Bell et al., 2005).

In order for management programs to enhance the reproductive health of the population, these turtles must survive, behave normally, and reach sexual maturity at the same time or earlier than their wild counterparts (Bell et al., 2005). Turtles experience delayed sexual maturity relative to most tetrapods, so size is one feature that can be used to determine if individuals are sexually mature (Caputo et al., 2005).

The minimum size (SCL) for sexual maturity for *P. unifilis* is 270 mm (Foote, 1987). Vanzolini (1977) suggested a slightly larger size, 313 mm. In our study, the commercial gel diet group reached an average SCL of nearly 160 mm in two years, roughly half the size of sexually mature individuals, with the vegetarian group lagging behind by the equivalent of six months' growth and the omnivore diet group nearly a year's growth behind. Given that plant material is the primary food source for *P. unifilis* in nature, representing 89.5% of the volume of stomach contents in studies of wild animals (Belensiefer 2006; Fachin-Teran et al. 1995), natural growth over this time frame is best approximated by our vegetarian diet experimental group, particularly as diet shifts away from consumption of meat proteins with increasing size (Fachin-Teran et al., 1995). This suggests that animals head-started on commercial gel diets optimized for growth could reach sexual maturity well ahead of annual cohorts once released into the wild, a worthwhile goal of head-starting programs. Our results suggest that even after a single year's growth, the differences in SCL are significant between each of the three treatment groups (RM ANOVA, $F = 4.81$, $P < 0.005$).

In the wild, *P. unifilis* exhibits sex differences in diet, with females consuming more fruit and seeds while males consume more shoots and stems (Fachin-Teran et al., 1995). Our study did not examine individual consumption, and gender was not controlled in the study. It is possible that our commercial gel diet group consisted primarily of females. Because protein content results in accelerated growth in other species of chelonians (Avery et al., 1993; Páez and Bock, 2004), this could have affected our results. Because eggs from this clutch were incubated at a uniform temperature of 30.2º–30.4º C, we expected a male biased sex ratio (approximately 80%) from the clutch based on known constant temperature incubation studies of this species (de Souza and Vogt, 1994), reducing the odds of such a bias in the present case.

Head-starting conservation efforts for river turtles such as *P. unifilis* should weigh the conflicting demands of resources and time when planning diets for captive-reared animals. The vegetarian treatment group provided the middle growth rate of the three treatment groups, but the lowest cost per unit ($0.0006 per gram compared to $0.07 per gram for the commercial gel diet). Consequently, a vegetarian diet plan for a head-starting program would be efficient and economical for this species where urgency of increasing the reproductive population is not severe. The similarity of this diet to a more natural diet could provide a simplified transition from captivity to the wild as food acquisition would be more similar, and growth rates would likely reflect local wild populations.

For those head-starting programs augmenting a severely depleted local reproductive population, it is worth considering additional factors in rearing methods. An optimal incubation temperature of 32° C has shown to rear equal numbers of male and female individuals, as well as support greater growth rates by the end of the first year of life (Páez and Bock, 2004). Given the ability to determine sex through incubation temperatures, head-starting programs with limited funding can pair the optimal incubation temperature with a vegetarian diet, forgoing the more expensive commercial gel diet, but maintaining healthy, increased growth rates.

Timing of release of head-started individuals is also an important consideration and, although a year of growth can produce viable and healthy cohorts (Bell et al., 2005), rearing individuals for three to four years may allow attainment of sizes suggested to decrease vulnerability to predation (Páez and Bock, 2004). Our study builds on the shorter-term study by Páez and Bock (2004) that indicated growth rates are affected by diet in the period prior to the dietary divergence in our study. Together, the two studies suggest that we might have seen even greater differentiation among dietary treatment groups with an earlier separation of our groups. Páez and Bock (2004) clearly demonstrated a growth advantage for turtles reared with meat in their diets. Previous studies have found small amounts of meat (bivalves, fish, and crustaceans) in stomach contents of *P. unifilis* (Fachin-Teran et al., 1995; Balensiefer and Vogt, 2006). In contrast, our vegetarian treatment group grew at a faster rate than our omnivorous group that was provided with meat in the form of arthropods, suggesting difficulty digesting these protein sources or an unwillingness to feed on them in captivity.

The onset of accelerated growth rates observed in body mass in the present study differed from that in carapace length by five months, suggesting a decoupling between gain in body mass and subsequent gain in carapace length. Growth spurts of this sort are known for sea turtles at later ages (Balazs and Chaloupka, 2004). Results of our study appear to be the first evidence that rapid gains in body mass may precede increased growth rate in skeletal structure. Similar outcomes have been suggested for mammalian growth spurts associated with puberty (e.g., Cadogan et al., 1998; Jackowski et al., 2009).

The apparent homogeneity of relationship between body mass and straight carapace length is somewhat unexpected given the known and theoretical effects of heterochronic acceleration in growth rate on morphology (Gould, 1977; Cole, 1992; Richtsmeier et al., 1993; Werneburg and Sánchez-Villagra, 2015). Growth rate can affect morphology in one of two ways. First, shape can be size-specific; shape is predictable based on size regardless of chronological age of the animal. Second, shape may be independent of size in which case modifications of growth rate may yield unpredictable allometric relationships (Forsman, 1996). Our results support the former model for these important Amazon river turtles. Given that variation in carapacial morphology indicates variable hydrodynamic environments throughout a species' range (Rivera, 2008), relatively constrained relationships may indicate comparatively homogeneous hydrodynamic environments inhabited by this species.

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