Exceptional Growth Rates Observed in Immature *Pseudemys* from a Protected Spring System in Florida

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Abstract. The genus *Pseudemys* represents some of the largest emydid turtles in North America. Surprisingly, many in this genus are poorly studied and despite their large size little is known about their growth. Using mark-recapture data we examined extreme growth in two *Pseudemys* species, *Pseudemys peninsularis* and *P. nelsoni* in a protected spring system in central Florida. Ten immature individuals were captured, marked, and recaptured with inter-capture time intervals between 364-1682 days that allowed us to calculate growth rates and determine gender. The *P. peninsularis* individuals showed growth rates that ranged from 30.38 to 74.29 mm/year, representing annual increases in size of 23–104.6%. The *P. nelsoni* individuals grew slower with growth rates that ranged from 19.96 to 42.15 mm/year, representing annual size increases of 14.6–42.2%. Growth within a species was not significantly different between males and females; however, between species the slightly smaller *P. nelsoni* females grew at a slower rate than *P. peninsularis* females. We believe that this extreme growth can be attributed to a combination of several different factors including adaptation to predation, living in a habitat that offers year-round growth conditions, and/or the result of the introduction of an energy rich, non-native food source.

Key words. Annual growth, growth rates, *Pseudemys peninsularis*, *Pseudemys nelsoni*, Florida.

Introduction

In most chelonians, body size is a determining factor in reproductive output such as clutch size in females and mate competition in males (Lovich and Gibbons, 1990; Congdon and Van Loben Sels, 1991). Growth is rapid in young turtles but slows significantly as maturity is attained at approximately 72% of maximum body size (Shine and Iverson, 1995). Many potential explanations exist for this quick initial growth rate; however, the most likely explanations are that quick growth while young can lead to reduced predation and early sexual maturation (Martins and Souza, 2008). Yet growth, due to a turtle’s bony shell, is limited by the need to acquire adequate amounts of calcium and phosphorus (Clark and Gibbons, 1969). How quickly a particular species reaches maturity will have a significant impact on the demographics of that species. Additionally, sexual differences, not only in size but in age at maturity, will also have a significant impact on the demographic profile. Thus, the rate of individual growth can have a direct effect on population size and provide insight into the ability of a population to rebound following a stochastic event, and is directly linked to the quality of the habitat occupied. Despite the importance of growth rates, they have not been measured for many freshwater turtle species (Girondot and Pieau, 1993).

*Pseudemys peninsularis* Carr 1938 and *P. nelsoni* Carr 1938 are two of the largest North American emydid turtles (Meylan, 2006). Both species are residents of various freshwater habitats including rivers, lake systems, and freshwater springs throughout the central regions of Florida (Marchand, 1942; Witzell, 1999; Meylan, 2006). Characteristic of the genus, these species exhibit sexual dimorphism, with females obtaining noticeably larger sizes than males (Ernst and Lovich,
To date there has only been one study examining growth rates in these species (see Bancroft et al., 1983), making our study both timely and much needed. In this note we present novel growth rate data for both species. This is noteworthy information as growth rates have rarely been investigated in wild populations of either species (Bancroft et al., 1983; Ernst and Lovich, 2009) and both species rank among the 10 least studied North American turtles (Lovich and Ennen, 2013).

Materials and Methods

We conducted our study at Wekiwa Springs State Park (WSSP) in Orange and Seminole Counties, Florida, United States (Fig 1). This spring expels approximately 164 million liters of water each day with a constant temperature of 22.0 ± 2°C and runs 0.9 kilometers before it joins the Wekiva River (Hubbs, 1995; Scott et al., 2004). With a crew of 10–20 volunteers we have conducted snorkeling surveys for turtles in this spring system since 1999 (Hrycyshyn, 2006). All turtles were measured with dial calipers or tree calipers. Straight-line measurements of maximum carapace length (CL), maximum plastron length (PL), carapace width (CW), and shell height (SH) were recorded to the nearest mm, weighed to the to the nearest g using Ohaus top-loading scales (Ohaus Corp., New Jersey, USA), and filed with a unique notching pattern which is a variation of the technique described by Cagle (1939), and all captured turtles with a CL length of greater than 70 mm were injected with a passive intergraded transponder (PIT) tag (Biomark, Inc., Boise, Idaho, USA). The PIT tags are inserted under the right bridge of the shell, anterior to the right leg. This area is established as an acceptable site for PIT tag retention (Runyan and Meylan 2005) (methods are described in further detail in Munscher et al. in review). Capture and handling protocols were approved by The Florida Department of Environmental Protection (District III, Orlando) and conform to the ASIH/SSAR animal use guidelines (American Society of Ichthyologists and Herpetologists, the Herpetologists League, and the Society for the Study of Amphibians and Reptiles. 2001. Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research. Available from http://www.asih.org/publications [Accessed 09 February 2015]).

The study area at WSSP includes the public swimming area, main lagoon, and spring run habitat (Fig. 1). The entire study area consists of approximately 2.67 ha of protected water habitats. The area that surrounds the spring boil has been modified with concrete walls and steps to facilitate public recreational use. This small public swimming area (0.20 ha) opens into a much larger natural lagoon (1.67 ha), which flows into the spring run. The lagoon is ca. 6.5 m deep at the deepest spot and much of the bottom is covered with a thick (to 1 m) layer of silt and detritus composed primarily of decaying vegetation from many years of herbicide application to control hydrilla (Hydrilla verticillata). The study area and sampling methods are further described in Munscher et al. (in press). Over the 15 years of this study we captured a number of immature *P. peninsularis* and *P. nelsoni* and here present growth data for 10 immature *P. peninsularis* and 10 immature *P. nelsoni* (five males and five females for each species) with inter-capture time intervals ranging between 364-1682 days from first and subsequent captures that allowed us to calculate growth rates and determine gender based on development of secondary sexual characteristics.
We searched for differences in annual growth rate and annual percent increase among male *P. nelsoni*, female *P. nelsoni*, male *P. peninsularis*, and female *P. peninsularis* with Kruskal-Wallis tests. We conducted post hoc comparisons between pairs with Wilcoxon tests. Data were analyzed with JMP 10.0 (SAS Institute, Inc., Cary, North Carolina, USA) with an alpha set at 0.05.

**Results**

The *P. peninsularis* individuals showed growth rates that ranged from 30.38 to 74.28 mm/year. The average growth rate of the five males was 41.41 mm/year, in comparison to five females which averaged 54.96 mm/year (Table 1). This corresponds to average annual percent growth rates of 53.6 % and 74.4 % for males and females, respectively. The highest annual percent increase in body size for a male was 97.5% (#2). Similarly, a female (#7) had a high annual percent increase in body size of 104.62% (Table 1).

The *P. nelsoni* individuals showed growth rates that ranged from 19.96 to 42.15 mm/year. The average growth rate for the five male *P. nelsoni* was 28.13 mm/year and for the five females was 30.64 mm/year. The males exhibited an average annual percent growth rate of 27.7 % while the females exhibited an average of 30.5 %. The fastest growing male (#11) exhibited an annual percent increase of 44.3 % (Table 2), while the fastest growth in a female (#16) was 42.2 % (Table2). The average annual percent increase that *P. peninsularis* females are exhibiting (74.4%) is almost 2.5 times as much as that of *P. nelsoni* females (30.5%), while the difference between males is almost double (*P. peninsularis* 53.6%, *P. nelsoni* 27.7%).

Kruskal-Wallis results demonstrated significant differences in annual growth rate among all four groups (male *P. nelsoni*, female *P. nelsoni*, male *P. peninsularis*, and female *P. peninsularis*; $X^2 = 10.35$; df = 3; $P = 0.00158$). Post hoc Wilcoxon tests identified significant differences between female *P. nelsoni* and female *P. peninsularis* ($P = 0.0122$), but no differences between sexes of the same species or between male *P. nelsoni* and male *P. peninsularis*. A significant difference was also identified between male *P. nelsoni* and female *P. peninsularis* ($P = 0.0122$). This difference contributed to the Kruskal-Wallis results but is unlikely to be biologically significant. Likewise, Kruskal-Wallis results demonstrated significant differences in annual percent increase among groups ($X^2 = 9.79$; df = 3; $P = 0.00158$). Post hoc Wilcoxon tests identified significant differences between female *P. nelsoni* and female *P. peninsularis* ($P = 0.0122$), but no differences between sexes of the same species or between male *P. nelsoni* and male *P. peninsularis*. A significant difference was also identified between male *P. nelsoni* and female *P. peninsularis* ($P = 0.0122$). Again, this difference contributed to the Kruskal-Wallis results but is unlikely biologically important.
Discussion

The life histories of *P. nelsoni* and *P. peninsularis* are very similar (Meylan, 2006), occupying similar if not the same habitat types, exhibiting similar sexual size dimorphism, yet our data suggests that these two species have quite different growth trajectories. Sexual size dimorphism is more pronounced in *P. nelsoni* than in *P. peninsularis* (Meylan, 2006), which is contrary to what one would expect given the presented growth data, as the males and females of both species appear to grow at a similar rate. It is possible that the rapid growth of *P. peninsularis* females is in part explained by their overall larger size compared to *P. nelsoni* (Fig 2: A-C).

Given our small sample size, we were unable to find statistically significant differences in growth between males and females of each species. We do find the 13.55 mm/yr difference in annual growth rates between male and female *P. peninsularis* noteworthy and biologically interesting in regards to sexual dimorphism (Gibbons and Lovich, 1990), and were further surprised that the annual growth rate difference between the sexes in *P. nelsoni* is minimal (< 3 mm/yr), yet both species exhibit marked sexual size dimorphism. We suspect that these results may be artifacts of our small sample size. Further research into the ecology, habitat use, food selection, and growth of these two sympatric species is clearly warranted as they appear to be exhibiting different growth trajectories which could be indicative of different ecological niches or other population level variables.

There is little work with which to compare our results; however, our turtles are growing faster than those studied by Bancroft et al. (1983), the only other study to our knowledge that examines growth rates in these species. Bancroft et al. (1983) found that *P. nelsoni* was similar to many other species of turtles with relatively small linear growth in straight line carapace length (SCL) for adults (3.58 and 3.72 mm/year for females and males, respectively) and much greater growth in juveniles (Fig 2), 19.29 mm/year. Albeit from a small sample size, growth of two hatchlings averaged 44 mm/year for the first three years, then slowed to an average of 22.8 mm/year during years four and five (Bancroft et al., 1983; Ernst and Lovich, 2009). Although not directly comparable as we do not have age class data, our observed growth rates for *P. nelsoni* are slightly higher in regards to our female averages, but overall comparable to the four individuals that averaged 28.56 mm that was reported by Bancroft et al., (1983). From a larger sample size of *P. peninsularis*, Bancroft et al. (1983) observed significant differences for growth rate between the sexes, a result which we did not observe. During their study, adult female SCL growth rate was 3.09 mm/year, while adult males grew more than twice as fast, 7.8 mm/year, a result which is opposite to our observations. Similar to *P. nelsoni*, immature *P. peninsularis* grew at the fastest rate, 12.3 mm/year. These growth rates for both species result in males reaching maturity at approximately 3–4 years, while females, being larger, taking 7–8 years to

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<th>CL (mm) 2nd Capture</th>
<th>Days Between Captures</th>
<th>Growth Rate (mm/day)</th>
<th>Growth Rate (mm/year)</th>
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Table 2. Growth rates calculated for 10 immature *P. nelsoni* captured during snorkeling surveys conducted at Wekiwa Springs State Park from 1999 until the present (2014). CL = carapace length
attain maturity (Bancroft et al., 1983; Meylan, 2006). Our immature *P. peninsularis* are growing up to 2.5–4.5 times faster than what has previously been reported and warrants discussion.

We propose that the faster growth rates we are observing are results of one, or a combination of, three different factors: (1) an adaptation to reach reproductive age and size more quickly due to feeding pressure by American Alligators (*Alligator mississippiensis*); (2) the results of living in year-round growth conditions provided by the spring; and/or (3) the result of the introduction of an energy rich, non-native food source, Hydrilla (*Hydrilla verticillata*).

A diet study on American Alligators by Delany and Abercrombie (1986) from several lake systems in north central Florida, showed that turtles were a large part of the alligators’ diets. Stomach contents from 350 harvested alligators showed that 23.3% of prey items were reptiles, of which turtles, including *Pseudemys*, represented 83%. It was noted that larger size classes of alligators predominately preyed upon larger turtle species such as *P. peninsularis* and *P. nelsoni*. From our own observations since 2000, we have seen several species of turtles in this system, including large river cooters of both species (*P. peninsularis* and *nelsoni*), with conical puncture holes (both fresh and healed) and large scratches on the carapace and plastron that more than likely had been caused by American Alligators. This predation pressure may be selecting for more rapid growth in *Pseudemys* and other species of turtles to push them towards a size that is relatively safe from Alligator predation.

Another possibility for the fast growth rates we are observing at WSSP could be optimal growth conditions of our study system. Wekiwa Springs has been protected as a private hunting club (The Apopka Sportsman Club) since 1941 and then as a state park beginning in 1969 (Philpott, 2008). The spring has a long-term average flow rate of 20.9 m/s and a constant temperature of 22–23 °C year round (Scott et al., 2004). This constant temperature and flow allows turtles to be active year-round, and for the strongly herbivorous *P. peninsularis* (Meylan, 2006) this also means the plants and algae it eats can grow year-round, providing a constant food source. Several springs in Florida have been shown to produce much larger Snapping Turtles (*Chelydra serpentina*) in comparison to other habitats, and the optimal growth conditions of these springs was identified as the likely cause of their large size (Walde et al., *in review*).

In addition to the year-round warm water growing conditions, there is an invasive plant species in this system that is a high-energy, abundant food source. This plant, Hydrilla, has been present within the study site since...
at least 2002 (Matt Bledsoe, Wekiwa Springs Assistant Park Manager, pers. comm.) and reaches extremely high densities in the lagoon, so much so that WSSP conducts invasive removal events (Fig 3). We have observed on numerous occasions, both _P. peninsularis_ and _P. nelsoni_, grazing on this invasive plant and studies have shown Hydrilla to be an extremely important food source for species of _Pseudemys_ in Florida. Bancroft et al. (1983) documented that _Pseudemys floridana_ from Lake Conway significantly preferred Hydrilla and Eel Grass (_Vallisneria americana_) in comparison to other native plants. Similarly, Bjorndal et al. (1997) conducted a dietary overlap study on three species of _Pseudemys_ ( _P. concinna suwanniensis, P. peninsularis, and P. nelsoni_ ) and found that Hydrilla ranked as a primary food source for all three species. Further adding to the knowledge about the importance of Hydrilla in the diet of these turtles, another study compared diet efficiency between _P. nelsoni_ and _Trachemys scripta scripta_ (Yellow-bellied Slider) fed Hydrilla, and found that _Trachemys_ digested Hydrilla significantly better (Bjorndal and Bolten, 1993). However, the intake of Hydrilla by _P. nelsoni_ (a herbivorous species) was nearly double that of the _T. s. scripta_ (an omnivorous species) and this higher intake resulted in _P. nelsoni_ gaining nearly twice the amount of energy and nitrogen on a daily basis, underscoring the important impact this species of plant can have on _Pseudemys_. In an effort to understand how small herbivorous species meet energy and nutrient intakes, Bjorndal and Bolton (1992) performed a diet efficiency and digestibility study with _P. nelsoni_ hatchings. They found that the young turtles

**Figure 3.** Wekiwa Springs Lagoon showing the dense mats of Hydrilla (_Hydrilla verticillata_) being treated for removal in November 2010 during a time when this invasive species was beginning to choke out other aquatic species. Photo credit Ande Williams.
Exceptional Growth Rates Observed in Immature *Pseudemys* from Florida

preyed on the plants, actively taking small bites. This feeding strategy actually allows for selection of higher quality diet items in comparison to adults whose larger mouth size makes it difficult for selective feeding (Bjorndal, and Bolton, 1992). By selectively feeding on higher energy food types and in taking smaller, easily digestible portions, young turtles can allocate this ingested energy into faster growth.

It is not unheard of for native species to shift their dietary focus to an invasive species and benefit from this dietary shift. During a study on the diet of the endemic and threatened Lake Erie Water Snake (*Nerodia sipedon insularum*), King et al. (2006) found that it completely shifted its dietary focus from native fish and amphibians to the invasive Round Gobie (*Neogobius melanostomus*). The result was that its growth rate dramatically increased due to this prey switch. Another prime example of a native species shifting its dietary focus to include or even prefer an invasive species is the Northern Map Turtle (*Graptemys geographica*). Bulté and Blouin-Demers (2008) demonstrated that invasive Zebra Mussels contributed 0–14% of the diet of male map turtles and 4–36% for female map turtles (Bulté and Blouin-Demers, 2008). This estimate is sexually biased due to the extreme sexual dimorphism expressed in the genus *Graptemys*; females of this particular species obtain sizes 10 times that of adult males. This study estimated that the population of Northern Map Turtles consumes approximately 3,200 kg of invasive Zebra Mussel per annum, which accounts for upwards of 33% of the total energy intake by these turtles (Bulté and Blouin-Demers, 2008). Thus an abundant foreign food source, such as Hydridla, that is high in energy, could facilitate increased growth rates within native species populations (Bjorndal and Bolten, 1993; Bjorndal et al., 1997), and coupled with the warm water and year round activity in this spring system could be what is contributing to our fast growth observations.

Here, we have provided a snap shot of growth data for two species, *Pseudemys peninsularis* and *Pseudemys nelsoni*, showing that in the spring environment at WSSP growth rates are significantly higher for *P. peninsularis* and while slightly higher for *P. nelsoni*, generally comparable to the one previous available study (Bancroft et al., 1983). The limited amount of published growth data signifies a substantial gap in our understanding of the basic life histories of these large, common species. The fact that we know so little about the basic life history parameters of two common species highlights the importance of sustained long-term conservation efforts for long-lived species such as freshwater turtles. Further studies should be conducted on life-history traits of *Pseudemys*, but also on the unique dynamics of these natural spring ecosystems. Additional future studies should investigate growth of these turtles in systems with and without this non-native food source to evaluate the consequences to individual and population growth and fitness.

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