

EXAMINING INDETERMINATE GROWTH IN FRESHWATER TURTLES

by

RIA NICOLE TSALIAGOS

(Under the direction of J. Whitfield Gibbons)

ABSTRACT

The assumption that reptiles exhibit indeterminate growth is widely accepted as a form of conventional wisdom, although the supporting evidence is equivocal. Over time, there has been frequent speculation backed by anecdotal evidence for and against continued growth in large, old, individual reptiles. Although documentation of growth in old, mature reptiles has been reported for some turtle species (e.g., *Terrapene ornata*, *Trachemys scripta*), it has been stated as not occurring in others (e.g., *Chelonia mydas*, *Kinosternon subrubrum*, *Emydoidea blandingii*). Definitive evidence of patterns of indeterminate growth in turtles and other reptiles has remained obscure. Several freshwater turtle populations on the Savannah River Site (SRS) in South Carolina contain known-age individuals, many originally captured in the 1960's and 1970's. Since then, over 30,000 turtles have been involved in mark-release-recapture studies. This study investigated whether turtles can continue growing at diminishing rates throughout their lives by using two species of freshwater turtles found on the SRS. Data from both mud turtles (*K. subrubrum*) and slider turtles (*T. scripta*) demonstrate unequivocally that some reptiles have indeterminate growth.

INDEX WORDS: Indeterminate growth, Mud turtle, *Kinosternon subrubrum*, Slider turtle, *Trachemys scripta*

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INTRODUCTION

The assumption that reptiles exhibit indeterminate growth is widely accepted as a form of conventional wisdom, although the supporting evidence is equivocal (Bellairs 1970; Porter 1972; Zug 1993; Pough et al. 2001; see Table 1). Throughout the literature, a variety of organisms are noted for exhibiting indeterminate growth including fish, lizards, snakes, shrimp (Charnov and Berrigan 1991; Heino and Kaitala 1996), trees (Wilson and Loomis 1952), male kangaroos (McFarlane 2002), daphnia (B. Taylor personal communication), clams (Heino and Kaitala 1996), insects (Ernsting et al. 1993), sea anemones (Sebens 1982) and various other types of invertebrates. Lincoln et al. (1982) defines indeterminate growth as “growth that continues throughout the life span of an individual such that body size and age are correlated”, however, variations to this definition have been reported (Sebens 1987). Over time, there has been frequent speculation backed by anecdotal evidence for and against continued growth in large, long-lived, individual reptiles (Flower 1925; Oliver 1955). Although growth in mature reptiles has been reported for some turtle species (e.g., ornate box turtle (*Terrapene ornata*), wood turtle (*Clemmys insculpta*), yellow-bellied slider (*Trachemys scripta*; Legler 1960; Lovich et al. 1989; Dunham and Gibbons 1990) and stated as not occurring in others [green turtle (*Chelonia mydas*), mud turtle (*Kinosternon subrubrum*), Blanding’s turtle (*Emydoidea blandingii*; Bjorndal 1980; Carr and Goodman 1970; Gibbons 1983; Congdon et al. 2001)], definitive evidence of patterns of indeterminate growth in turtles and other reptiles remains obscure.

Table 1. Statements made regarding indeterminate growth in reptiles.

Author	Quote(s)
Flower 1944	“...Reptiles, Amphibians and Fishes, as a rule grow rapidly when young, and then settle down to a period of very slow growth, which in the course of years becomes negligible, and, if the animal lives long enough, eventually ceases.”
Oliver 1955	“At the present time our knowledge of growth in amphibians and reptiles is very incomplete ...in most species we cannot yet say whether growth is determinate or indeterminate.” p. 266
Goode 1967	“It is known that reptiles continue growing throughout their lives, but often mature size is achieved quite early in a long life span.” p. 112
Bellairs 1970	<p>“In reptiles...growth ends less abruptly and may continue for a relatively much longer period after maturity has been reached; a reptile may grow nearly twice as big before it dies as it was at the time of its first successful mating.” p. 458</p> <p>“...one has the impression that many species of reptile, particularly the smaller kinds, show a similar type of limited or determinate growth pattern as the mammals, and that they ultimately stop getting any bigger after a certain age or size has been attained.” p. 458</p>
Jackson 1970	“A typical progressive decline in growth rate accompanies increase in size.” p. 528
Carr and Goodman 1970	“It now appears that some green turtles mature at small, and others at large sizes; and that once they are mature...their growth becomes negligible, as compared with individual variation in maturity-size.” p. 783
Ernst and Barbour 1972	“Growth is rapid in young turtles but slows considerably after maturity is reached. As long as environmental conditions are favorable some growth occurs; probably the ability to grow is never lost.” p. 7
Porter 1972	“Reptiles also appear to be characterized by indeterminate growth so that individuals tend to get bigger as they get older.” p. 433
Heatwole 1976	“In some species growth may occur throughout the entire life span, as exceptionally large, presumably very old, individuals are occasionally found.” p. 112
Bjorndal 1980	“Growth in marine turtles essentially stops once sexual maturity has been reached.” p. 526
Andrews 1982	“...there appears to be good evidence that individuals reach an asymptotic size after which growth is negligible.” p. 276
Duellman and Trueb 1985 (see Halliday and Verrell 1988)	“Amphibians presumably have indeterminate growth.” p. 261
Sebens 1987	“Evidence from growth studies of higher vertebrates, reptiles, birds, and mammals suggests that growth is very determinate...”

Halliday and Verrell 1988	<p>“It is widely assumed that amphibians and reptiles show indeterminate growth...” (Duellman and Trueb 1985) p. 253</p> <p>“...there is rapid growth up to the time of first breeding and that, thereafter, growth is very slow, presumably because of a shift in resource allocation from somatic growth to reproduction.” p. 257</p>
Gibbons 1990	<p>“An additional observation is that indeterminate growth occurs in <i>T. scripta</i>; growth continues in older, larger individuals, although at a low rate and in an inconsistent manner.” p. 139</p> <p>“The data for mud turtles suggest that not all species of turtles continue to grow as adults. Mud turtles apparently increase in size for a few years after maturity is reached but then do not continue to grow.” p. 313</p>
Pough et al. 2001	<p>“Estimating the maximum size of crocodilians is difficult because individuals continue to grow slowly long after they reach maturity. Thus, the oldest crocodilians are the largest ones...” p. 10</p>
Zug et al. 2001	<p>“Growth may or may not continue indefinitely throughout life; data in most cases are inadequate to state whether a species has definite or indefinite growth.” p. 43</p> <p>“Both indeterminate (attenuated) and determinate (asymptotic) growth exist in amphibians and reptiles, but the evidence for one or the other is lacking for most species.” p. 43</p>

For many reptiles growth rate slows considerably at the onset of maturity (Ernst and Barbour 1972; Halliday and Verrell 1988; Pough et al. 2001) in comparison to pre-maturity growth rate. Typically, an individual's juvenile growth rate is much greater than its post-maturity growth rate (Andrews 1982). This phenomenon is attributed to a shift in the allocation of resources from somatic growth to reproduction (Halliday and Verrell 1988). Many reptile species show high variability in body size as adults and several reasons have been given for how indeterminate growth may occur in certain reptiles. From an osteological perspective, the skeletal growth characterized by one layer of bone forming on another due to an absence of epiphyses indicates the possibility of unceasing growth in many reptiles (Haines 1969; Bellairs 1970; Zug 1993). Furthermore, although usually displayed in larger forms (e.g., crocodiles, sea turtles, and pythons) the fact that some individual reptiles may reach sizes of gigantic proportion in comparison to others in the same species could be interpreted as lending evidence to continual growth in their lifetime (Bellairs 1970). Even in some smaller reptiles, a broad disparity exists in the sizes of the largest and smallest adults. For example, the average size (straight-line carapace) of the chicken turtle (*Deirochelys reticularia*) is 10 cm-15.2 cm, while the record size is 25.4 cm (Conant and Collins 1998). Similarly, the snapping turtle (*Chelydra serpentina*) ranges in size from 20.3 cm-36 cm, but a specimen reaching 49.4 cm has been reported (Conant and Collins 1998). Possible reasons why one individual might be a giant or experience an accelerated rate of growth may be influenced by genetics (Tinkle 1967; Oliver 1955; Andrews 1982), environment (Oliver 1955; Legler 1960; Andrews 1982; Avery 1984; Frazer et al. 1991), or age (Porter 1972), the latter explanation being consistent with indeterminate growth. Although individuals of some

species do not reach unusually large sizes compared to others (e.g., *Kinosternon*, *Sternotherus* vs. *Pseudemys*, *Trachemys*) they may still be experiencing indeterminate growth, though at a much slower rate (Bellairs 1970) and with a less dramatic disparity.

Many reptiles have extended longevity (Gibbons 1976; Gibbons 1987), and high variability exists in the maximum body sizes among individuals of different populations (Haines 1969; Andrews 1982). If indeterminate growth occurs in some reptiles, a feasible means of documentation would be to use decades of data collected on individual long-lived reptiles (e.g., turtles; Oliver 1955; Heatwole 1976). Such an approach offers one means of addressing the question: Do some reptiles have the capacity to continue to grow at a diminishing rate throughout their lives and, if so, why? As mentioned earlier, there has been some investigation as to the possibility of indeterminate growth and “how” it might occur, but there has hardly been an examination of “why” it might occur.

Exploration of the realized or potential benefits for an individual that exhibits indeterminate growth is consequential to gaining a complete comprehension of this phenomenon. Unfortunately, few researchers have had the ability to conduct such a study on long-lived species in which the above questions can be adequately addressed. This is in part because many reptiles share similar life history strategies such as delayed maturity and longevity, making it difficult to conduct long-term experiments on them.

Potential causes and consequences of indeterminate growth

Researchers have investigated the relationships between body size and reproduction in various amphibian and reptile species. Much of the data suggests a positive correlation between maternal body size and clutch size (Halliday and Verrell

1988). This relationship has been demonstrated in snakes (Seigel and Fitch 1985), lizards (Abell 1999), as well as several turtle species (Cagle 1950; Gibbons 1970; McPherson and Marion 1981; Tinkle et al. 1981; Georges 1985; Congdon et al. 1987; Steyermark and Spotila 2001). Likewise, larger maternal body size has been linked to increased fecundity in *C. serpentina* (Galbraith et al. 1989). Furthermore, a marine turtle species, *Caretta caretta*, represents this reproductive consanguinity as well (Frazer and Richardson 1985). This correlation has also been demonstrated on the SRS for five species of freshwater turtles (*T. scripta*, *K. subrubrum*, *P. floridana*, *S. odoratus*, *C. serpentina*) with larger females having larger clutch sizes (Gibbons et al. 1982). From a fitness perspective, females exhibiting indeterminate growth may possibly benefit from larger clutch sizes over time, thus potentially increasing overall lifetime fecundity (Stearns and Koella 1986). Nonetheless, indeterminate growth may not be the only potential influence on clutch size. For instance, clutch size variation may respond to environmental effects. Congdon et al. (1987) found inter-annual variability in clutches among *C. serpentina*. However, Frazer and Richardson (1985) found little annual variation in clutch size for the loggerhead sea turtle, a finding that agreed with that of Gibbons (1982) for various species of freshwater turtles.

Certain environmental conditions are among the more obvious and testable factors that may influence reptile growth (Legler 1960; Tinkle 1967; Frazer et al. 1991). Seasonal variation such as temperature has been found to significantly affect growth rate in both juvenile (Williamson et al. 1989) and adult species of turtles as indicated by noticeable differences in growth annuli (Sexton 1965). In general, poikilotherms are capable of responding to minute changes in average temperature such that among

habitats, growth rate or maximum size may be significantly different between populations with slight temperature gradients (Sebens 1987). Indeterminate growth effects on body size may be favorable, such that getting larger may be beneficial for surviving harsh environmental conditions (Sebens 1987). Galbraith et al. (1989) suggested that larger *C. serpentina* may exhibit a greater survival advantage during winter as an effect of body size. Further analysis of long-term growth data in combination with the corresponding meteorological conditions (e.g., drought) for a particular year in a specific habitat may be remarkably informative and provide further insight for understanding the phenomenon of indeterminate growth.

Objectives

The term “indeterminate growth” basically implies that after reaching maturity, individuals of long-lived species (e.g., turtles) exhibit the capacity for continual growth in body length (although such growth may be exhibited intermittently and at a decreased rate) indefinitely throughout the remainder of their lives. Contrast to Lincoln et al. (1987), growth may not necessarily correlate with age since characteristically it can be intermittent. In order to determine longevity more accurately in certain species of reptiles, Legler (1960) suggested the study of populations of marked individuals. When incorporated with measurement data on such individuals, mark-release-recapture methods can also be used to test whether or not an individual reptile’s growth continues well past the point of reaching maturity, even until death. Gibbons (1976) further indicated that given the accessibility to reptiles (e.g., turtles) that can be recaptured, the questions associated with growth and longevity can be more accurately addressed.

Several freshwater turtle populations on the Savannah River Site (SRS) in South Carolina contain known-age individuals, many originally captured in the 1960's and 1970's. Since then, over 30,000 turtles have been involved in mark-release-recapture studies (Gibbons 1970; Gibbons and Coker 1977; Gibbons and Semlitsch 1982; Burke et al. 1995; Gibbons 1990). Thus, the opportunity exists to address questions related to indeterminate growth by using species of freshwater turtles found on the SRS.

I used the two SRS species (mud turtle, *Kinosternon subrubrum*, and slider turtle, *Trachemys scripta*) for which the most recapture data had been collected to investigate the question of whether a significant proportion of individual turtles in a population exhibit indeterminate growth. Although examining this question is imperative in order to gain a better understanding of how such growth potentially affects overall fitness, continued individual growth studies of long-lived organisms are limited by the number of long-term data sets available for analysis. The SRS turtle populations are among the longest such studies in the world.

Oftentimes, conservation planning is impaired by a deficiency of commensurate life history data for long-lived species, resulting in conservation programs that are ineffective (Congdon et al. 1994). Having a thorough knowledge of a species' life history often includes understanding patterns of growth prior to maturity. This directly relates to demographic and other aspects of a species' fitness, such as size at maturity, time to reach maturity, and generation time; all of these can influence management planning (Seminoff et al. 2002). Another important life history strategy could be for individuals within a species to demonstrate continued growth past maturity, throughout their lives. Such indeterminate growth could have substantial impacts on lifetime fitness.

Information on whether a species has the capability for indeterminate growth would also have bearing on conservation planning and management techniques. Congdon and Dunham (1997) wrote: “Data obtained from long-term life history studies of species that are not of direct conservation concern are a resource that can contribute to developing concepts and solving problems related to management and conservation practices”.

To reiterate, knowledge of whether indeterminate growth is indeed a phenomenon in the reptile world remains under debate throughout the literature (see Table 1). Thus, it is critical to examine existing long-term data sets in order to reveal this potential life history strategy of freshwater turtles that has received minimal attention thus far. The purpose of this study was to ascertain if indeterminate growth could be demonstrated in long-lived species of reptiles for which adequate long-term recapture data were available and to investigate possible influences on such growth by addressing the following questions:

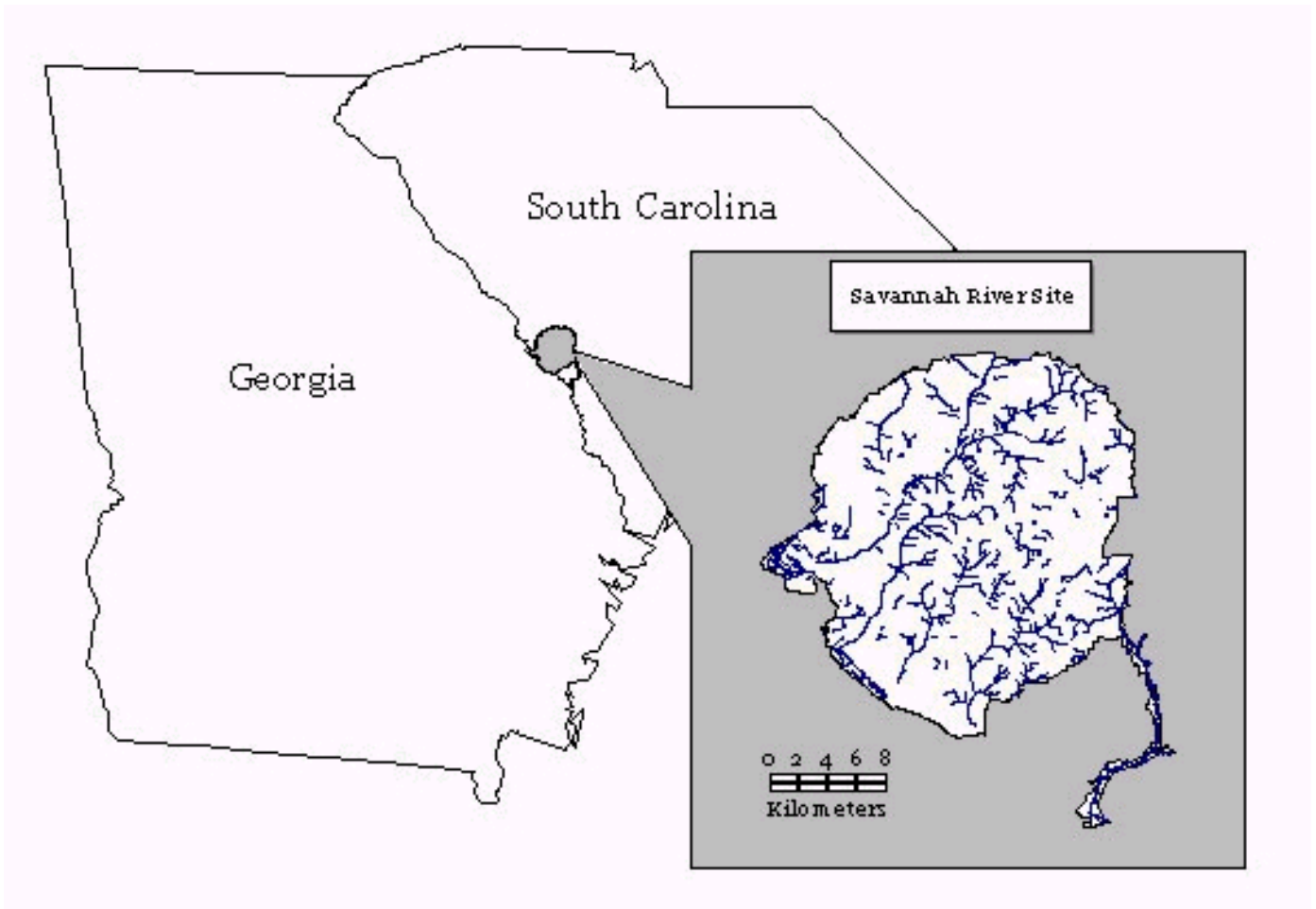
1. Do turtle species vary in their growth patterns after reaching maturity; i.e., can indeterminate growth be demonstrated in some species, but not others?
2. Could indeterminate growth lead to increased fecundity through an appreciable increase in body size?
3. Would indeterminate growth allow turtles to take advantage of intermittent resource opportunities?
4. Are turtles capable of responding to changes in resources by accelerated growth that could lead to possible long-term population consequences from long cycles of high and low temperatures, or even global warming?

MATERIALS AND METHODS

Study site

This study involved selected recaptures of the more than 16,000 original captures of turtles and their corresponding descriptive data collected on the SRS (Gibbons and Coker 1977; Gibbons 1990; Frazer et al. 1991; Burke et al. 1995). The SRS is approximately 750 km² of restricted public access land located in coastal plain habitat south of Aiken, South Carolina (Figure 1). In 1967, the first turtle was marked on the SRS (Gibbons et al. 1983; Gibbons 1990) by researchers at the Savannah River Ecology Laboratory (SREL). Now, more than 35 years later, over 15,000 recaptures have been made in the mark-release-recapture studies (Gibbons and Coker 1977; Frazer et al. 1990; Frazer et al. 1991; Burke et al. 1995). Within the SRS, turtles from three particular areas (Ellenton Bay System, Par Pond System, and the experimental pond) provided most of the data used in the current study. Ellenton Bay System is primarily made up of the bay that bears its name (~10 ha) that being a Carolina bay, which characteristically experiences seasonal fluctuations in water level. Par Pond System is a large (~1, 248 ha) conglomeration of man-made lakes and canals, functioning as a cooling reservoir for the thermal effluent from a plutonium-production reactor that is not currently in operation. The experimental pond (~0.04 ha) is also a man-made body of water located directly behind the Savannah River Ecology Laboratory building. The pond has a sustained water level and is completely enclosed by a fence. Data collected from the Par Pond System

Figure 1. Location and map of the Savannah River Site in South Carolina.



and the experimental pond were analyzed separately from other SRS analyses, unless otherwise noted.

Capture techniques and processing

Over the years, many methods of capturing turtles have been applied. Various techniques include, but are not limited to, collection by hand, basking traps, aquatic traps, dipnetting, shell roundups, terrestrial drift fences with pitfall traps, and incidental captures (Gibbons 1990). Some capture methods prove more effective for collecting certain species of turtles. Nonetheless, although numerous techniques have been used over time to capture turtles, recapture data provide the same vital information for this study; i.e., has an individual experienced growth in body size?

Upon capture (or recapture) of a turtle, the researcher conducts several types of measurements. First, each turtle is marked on the shell marginals or plastron with a unique code distinguishable from all others. An organized process of marking turtles is strictly adhered to and enforced when collecting turtles from the field, thus making an extremely large, reliable, and user friendly data set. Turtles captured in the field are brought into the lab and a variety of descriptive data are gathered from each individual, including ID, plastron length, carapace length and mass. Females are x-rayed for determining the presence of eggs (Gibbons and Greene 1979). If a turtle is not a recapture, an identification code is assigned. Also, distinguishable characteristics (e.g., missing limbs, scars on the shell) are noted, which may aid in identifying recaptured turtles. Similarly, some species may be photocopied (plastron down) as another record of identification, somewhat like taking a “finger-print” (Gibbons 1990).

Data analysis was conducted on turtles discovered in various locations and a variety of SRS habitats (Gibbons 1990). Most turtles were from metapopulations of Ellenton Bay (Burke et al. 1995), Dry Bay, Lost Lake, Par Pond, Pond B, Pond C, Lodge Lake, L-Lake, Risher Pond, Dick's Pond, and Steel Creek (see descriptions of these habitats in Gibbons and Bennett 1974; Semlitsch 1980; Gibbons 1990). No *Kinosternon subrubrum* were captured in either the Par Pond System or the experimental pond.

Statistical analyses

Growth data were examined for two highly contrasting species of freshwater turtles found on the SRS: *Kinosternon subrubrum* and *Trachemys scripta*. To some extent, these species were selected because they provide a comparison between distinct phylogenetic branches within Testudines, so that, if the results were consistent among two independent turtle lines the evidence would be stronger for indeterminate growth. *Kinosternon subrubrum* is a rather small turtle with a carapace length that rarely exceeds 105 mm on the SRS. Their oval shaped carapace lacks a pattern and ranges in color from yellowish to black (Ernst et al. 1994). *T. scripta* is a medium to large turtle. Males and females from the SRS may potentially reach sizes of 220 mm and 280 mm, respectively. Distinguishing features of this turtle include a yellow plastron sometimes with dark blotches on its scutes, as well as the presence of a yellow postorbital stripe on either side of the head (Ernst et al. 1994). Although both species were often collected from the same locations, each has a distinctive morphology and life history strategy, thus the possibility existed that each would demonstrate different patterns of growth past maturity.

For purposes of comparison, each species must be considered separately. For example, plastron length is the most accurate measure of size in *T. scripta* (Frazer et al. 1991; Cagle 1946; Gibbons 1990), whereas size in *K. subrubrum* is best expressed as carapace length, due to the allometric increase of plastron length in males (Gibbons 1983; Frazer et al. 1991). Furthermore, *K. subrubrum* do not exhibit sexual size dimorphism, whereas *T. scripta* do (females get significantly larger than males).

Attainment of maturity may be influenced by age as well as by size in turtles (Cagle 1950; Gibbons 1970; Searns and Koella 1986), however, size is most commonly used as an indicator of maturity (Halliday and Verrell 1988) and is more precise for examining post-maturity growth. Thus, any growth exhibited beyond the reported size at maturity of each sex was considered growth past maturity. Recorded growth measurements (i.e., CL or PL) were analyzed by means of paired *t* tests assuming equal variance. Comparisons were made between the measurements (CL or PL) at the first recorded capture (after maturity was reached) and subsequent recaptures. Using paired *t* tests on mature individuals while selecting for growth during a narrow window of time (e.g., 2 years), gives greater confidence in the results if the findings are significant, as does testing females gravid at first capture, as these individuals are unequivocally mature. Both types of tests were used to ensure that growth was of mature individuals for *K. subrubrum* and *T. scripta*. Average growth past maturity was also measured during varying meteorological conditions. Paired *t* tests were used to measure average growth past maturity during drought periods and non-drought periods. Comparisons of average growth were made for drought vs. non-drought, as well as drought vs. drought using two-sample *t* tests assuming equal variance. Drought and non-drought periods were chosen

for analyses based on historic water levels at Ellenton Bay (see Gibbons et al. 1983; Gibbons 1990). Two different drought periods (1981-1982 and 1987-1988) and one non-drought period (1975-1976) were used based on their dynamics, as well as having sufficient corresponding turtle recapture data during that time.

Both sexes of *K. subrubrum* mature between 70-80 mm CL in this geographic location. Due to expected variation in individual attainment of maturity, I chose the point of maturity to be at or above 80 mm CL for the paired *t* tests as another step to decrease the possibility of including immature individuals in the analyses.

In this part of their geographic range, *T. scripta* males mature at a PL of 100 mm, whereas females usually mature at a much larger PL of 160 mm. For the purposes of the following analyses, maturity criteria were set at >99 mm PL for males and >159 mm PL for females. Females from the Par Pond System, however, mature at around 200 mm PL. Therefore, separate analyses were conducted for Par Pond System females where appropriate.

RESULTS

Mud turtle-*Kinosternon suburbrum*

Growth pattern

Male and female *K. suburbrum* from various locations on the SRS showed significant growth with high variability well past maturity (Tables 2-3; Figures 2a and 2b). In comparing mean CL at first capture (CL > 79 mm) to mean CL at final capture including only those individuals (both sexes) with a time interval of 4 years between captures (N = 132), the mean difference in CL was 2.25 mm and was highly significant (t -value = 7.58; p -value = 2.84×10^{-12}). Male growth (N = 49) was significantly different from zero in CL (2.76 mm; t -value = 5.38; p -value = 1.1×10^{-6}). Females (N = 83) also displayed strong evidence for growth past maturity, with a significant difference in CL (1.95 mm; p -value = 3.13×10^{-7} ; t -value = 5.40).

In addition, individual growth past maturity was apparent for females that were gravid at first capture (Tables 2-3). Gravid females (N = 50) from the Ellenton Bay System (Table 2) had a highly significant mean difference in CL of 2.30 mm; p -value = 2.47×10^{-6} ; t -value = 5.13). Certain gravid females were selected from the data set to display individual variability in growth past maturity (see Table 3).

Comparing growth past maturity for individuals from Ellenton Bay during a drought year and then a non-drought year yielded significant results in one comparison, but not in another (Table 4). Growth was greater during the drought of 1987 than the non-drought of 1975. A paired t test was first used to determine the mean growth in CL

Table 2. Results of paired t test analyses testing for growth past maturity for mature male and female *Kinosternon subrubrum* from the SRS in South Carolina.

	Location	Recapture Interval	N	t-value	p-value	Mean Difference in Carapace Length (mm)
Females	SRS	4 years	83	5.40	3.13E-07	1.95
Males	SRS	4 years	49	5.38	1.1E-06	2.76
Females + Males	SRS	4 years	132	7.58	2.84E-12	2.25
Gravid Females	Ellenton Bay System	varies	50	5.13	2.47E-06	2.30

Table 3. Variability in growth past maturity in post-gravid female *Kinosternon subrubrum* (N=10) captured on the SRS in South Carolina from 1976-1997.

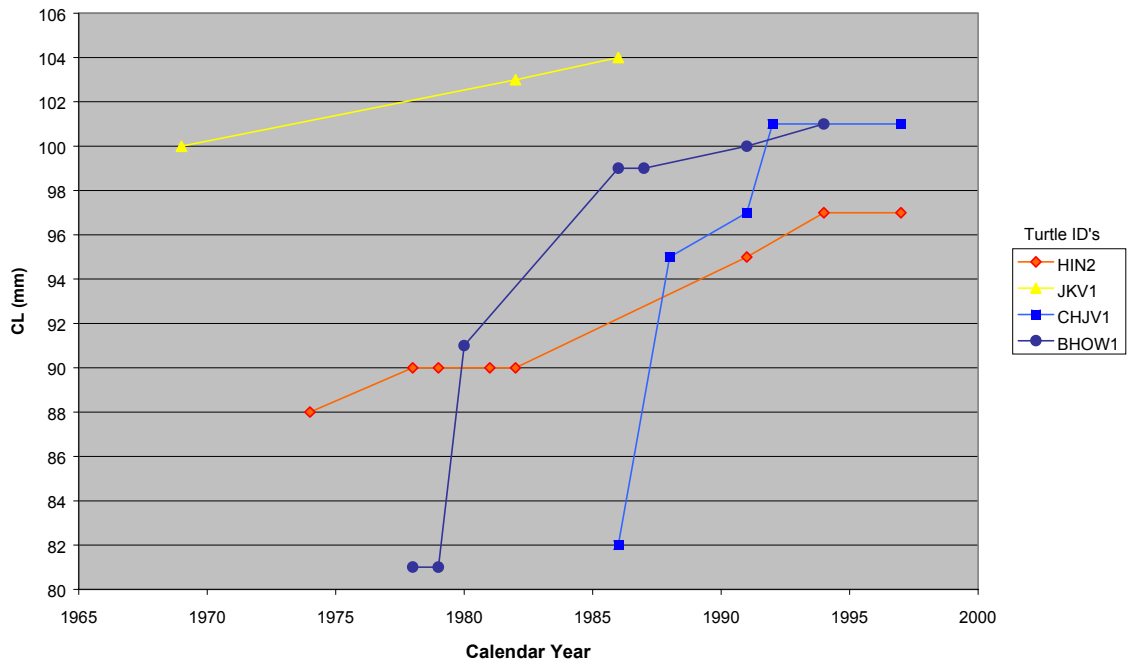
Turtle ID	Carapace Length (mm) @ t_0	Approximate Years Past t_0	Size Increase (mm)
CHJO1	95	3	3
HJL1	92	10	3
ACHM1	97	6	3
KLM1	87	15	3
KLVWX1	90	6	6
NWX1	84	11	6
ABHM1	92	5	6
HIJNO1	79	4	7
HIN2	90	20	7
BKWX1	91	13	13

t_0 = Time of first capture with eggs

Figure 2a. Selected individuals (N=4) of mature female *Kinosternon subrubrum* (CL > 80 mm) from the SRS in South Carolina showing variability in growth past maturity.

Figure 2b. Selected individuals (N=4) of mature male *Kinosternon subrubrum* (CL > 80 mm) from the SRS in South Carolina showing variability in growth past maturity.

a)



b)

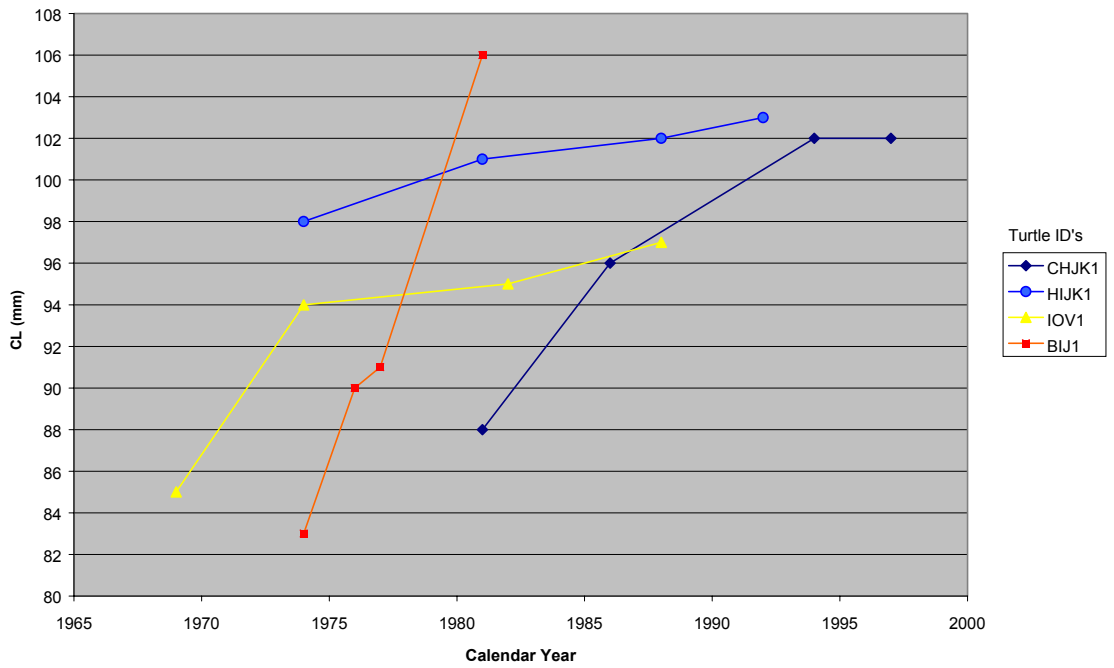


Table 4. Male and female *Kinosternon subrubrum* (>69 mm CL) growth at Ellenton Bay on the SRS in South Carolina during periods of drought and non-drought. Comparisons were made using a two sample *t* test assuming equal variance.

	Years	Recapture Interval	N	<i>t</i>-value	<i>p</i>-value
Non-drought vs. Drought	(1975-76) vs. (1987-88)*	~ 1 year	40	-2.53	0.0078**
Non-drought vs. Drought	(1975-76) vs. (1981-82)	~ 1 year	39	-1.08	0.14
Drought vs. Drought	(1981-82) vs. (1987-88)*	~ 1 year	39	1.72	0.047**

* Indicates the time period in which more growth occurred

** Indicates statistically significant

during the drought period and then for the non-drought period. A two sample t test assuming equal variance was used to compare individuals' drought ($N = 20$) growth to non-drought ($N = 20$) growth. There was a significant difference in growth (t -value = -2.53 ; p -value = 0.0078). On the other hand, individuals' ($N = 19$) growth during the drought period of 1981 compared to that of the previously mentioned ($N = 20$) non-drought of 1975 did not produce significant results. Growth during the drought of 1987 was also compared to individuals' ($N = 19$) growth during the earlier drought of 1981. Growth was significantly greater during the 1987 drought (t -value = 1.72 ; p -value = 0.047).

There existed much variability in growth past maturity in both male and female *K. subrubrum*. Mature males ($N=49$) were divided according to size categories based on CL: Small=80-87 mm, Medium=88-95 mm, and Large=96-102 mm (see Table 5). Average percent growth in 4 years was calculated. The small category grew an average of 5% in 4 years. The medium category grew 3%. The large category had an average percent increase in CL of 1. Certain mature males and females were selected from the data set to show variability in growth past maturity. Individual variation in growth past maturity over time was depicted graphically (see Figures 2a and 2b). In a different analysis, comparisons were made between individual mature male ($N=10$) and female ($N=12$) *K. subrubrum* that were captured in the same year, at the same initial PL, and recaptured within the same time interval (see Tables 6 and 7). Differences in growth over time among individuals varied from as little as 3 mm to as much as 15 mm.

Table 5. Average percent growth over a 4-year recapture interval for mature male *Kinosternon subrubrum* (N=49) from the SRS in South Carolina according to size categories.

CATEGORY	SIZE RANGE OF CARAPACE LENGTH (MM)	% GROWTH
Small	80-87	5
Medium	88-95	3
Large	96-102	1

Table 6. Variable growth past maturity for 10 mature male *Kinosternon subrubrum* (CL > 79 mm) from the SRS in South Carolina. Comparisons were made based on individuals that were captured in the same year, at the same initial CL, and recaptured within the same time interval.

Turtle	Location	Carapace Length (mm)	Recapture Interval	CL₂ (mm)	Size Increase (mm)
1	Ellenton Bay System	89	2 years	94	5
2	Ellenton Bay System			91	2
3	Lost Lake System	80	2 years	92	12
4	Lost Lake System			80	0
5	Ellenton Bay System	89	2 years	95	6
6	Ellenton Bay System			90	1
7	Ellenton Bay System	84	8 years	97	13
8	Ellenton Bay System			92	8
9	Ellenton Bay System	90	10 years	94	4
10	Ellenton Bay System			91	1

Table 7. Variable growth past maturity for 12 mature female *Kinosternon subrubrum* (CL > 79 mm) from the SRS in South Carolina. Comparisons were based on individuals that were captured in the same year, at the same initial CL, and recaptured within the same time interval.

Turtle	Location	Initial Carapace Length (mm)	Recapture Interval	Carapace Length at Recapture (mm)	Size Increase (mm)
1	Ellenton Bay System	92	4 years	99	7
2	Ellenton Bay System			99	7
3	Ellenton Bay System	82	5 years	96	14
4	Ellenton Bay System			92	10
5	Ellenton Bay System	81	2 years	96	15
6	Ellenton Bay System			81	0
7	Ellenton Bay System	87	4 years	93	6
8	Rainbow Bay			88	1
9	Rainbow Bay	82	2 years	86	4
10	Rainbow Bay			82	0
11	Ellenton Bay System	86	10 years	91	5
12	Ellenton Bay System			87	1

Slider turtle-*Trachemys scripta*

Growth pattern

Individuals of both sexes showed significant growth past maturity (Tables 8-9; Figures 3a and 3b). The results for growth during a two-year time interval for male *T. scripta* (N = 217) were highly significant (t -value = 11.80; p -value = 2.0×10^{-25}) with a mean difference in PL of 5.20 mm. Females (N = 151) also showed significant results (t -value = 6.98; p -value = 4.49×10^{-11}) and the mean difference in PL was 4.13 mm. Male and female *T. scripta* growth data combined (N = 368) resulted in significant results as well (t -value = 13.37; p -value = 8.93×10^{-34}) with the mean difference in PL of 4.76 mm.

Growth of gravid female *T. scripta* (N = 92) from various locations on the SRS (at various time intervals) was significantly different from zero and showed a mean difference in PL of 4.17 mm (p -value = 4.47×10^{-8} ; t -value = 5.81). Similarly, growth past maturity was significant for gravid Par Pond System females (N = 16) with a mean difference in PL of 3.94 mm (p -value = 3.65×10^{-3} ; t -value = 3.10). Certain gravid females (N=9) were selected from the data set to display individual variability in growth past maturity (see Table 9).

Comparing growth past maturity for individuals from Ellenton Bay during the drought of 1981 to the non-drought of 1975 did not reveal significant results (Table 10). Comparing individuals' non-drought growth (N = 27) to drought growth (N = 27) using a two sample t test assuming equal variance showed the periods of growth were not significantly different (t -value = -0.985; p -value = 0.165).

Table 8. Results of paired t test analyses testing for growth past maturity for mature male and female *Trachemys scripta* from the SRS in South Carolina.

	Location	Recapture Interval	N	t-value	p-value	Mean Difference in Plastron Length (mm)
Females	SRS*	2 years	151	6.98	4.49E-11	4.13
Females	SRS*	3 years	111	6.09	8.47E-09	4.63
Females	PAR	3 years	23	5.02	2.51E-05	8.30
Males	SRS*	2 years	217	11.80	2.0E-25	5.20
Males	PAR	2 years	25	4.98	2.2E-05	7.32
Females + Males	SRS*	2 years	368	13.37	8.93E-34	4.76
Females + Males	Experiment Ponds	varies	55	4.39	2.64E-05	5.07
Gravid Females	SRS	varies	92	5.81	4.47E-08	4.17

* indicates data from Par Pond System excluded from analysis

Table 9. Variability in growth past maturity in post-gravid female *Trachemys scripta* (N=9) captured on the SRS in South Carolina from 1977-1990.

Turtle ID	Carapace Length (mm) @ t_0	Approximate Years Past t_0	Size Increase (mm)
ABIX1	177	3	0
ABPWX1	184	2	3
ABL2	229	7	3
ACKN3	253	6	4
ABHO1	185	4	6
AHIO2*	246	7	6
AB3	204	4	7
ABV6	209	4	8
ABJK2*	232	6	14

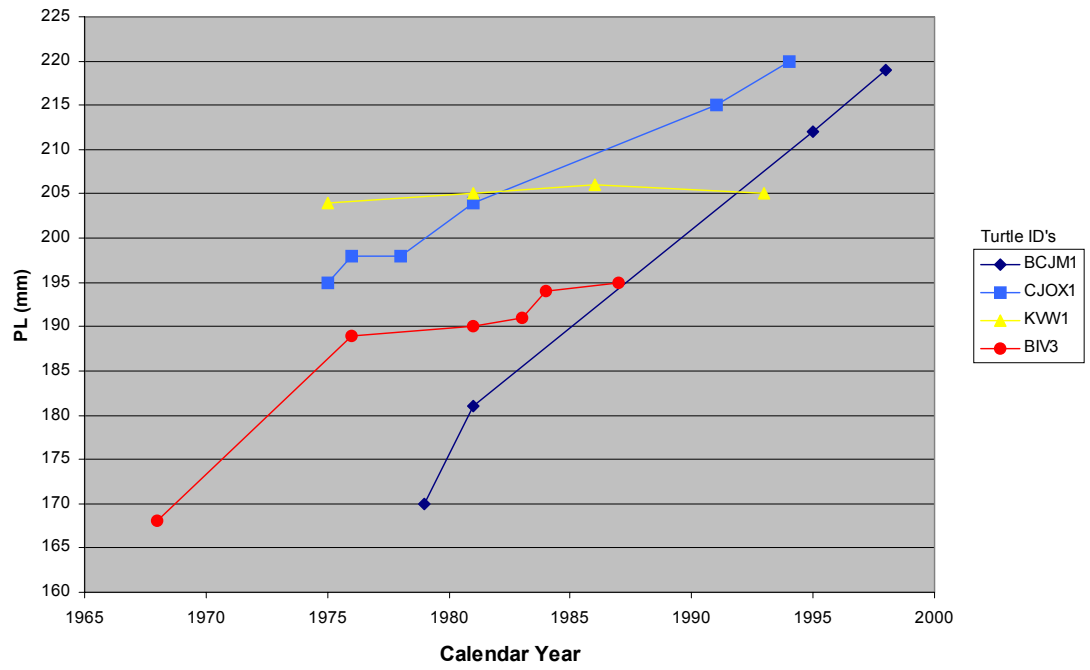
t_0 = Time of first capture with eggs

* = Indicates from Par Pond System

Figure 3a) Selected individuals (N=4) of mature female *Trachemys scripta* (PL > 159 mm) from the SRS in South Carolina showing variability in growth past maturity.

Figure 3b) Selected individuals (N=4) of mature male *Trachemys scripta* (PL > 99 mm) from the SRS in South Carolina showing variability in growth past maturity.

a)



b)

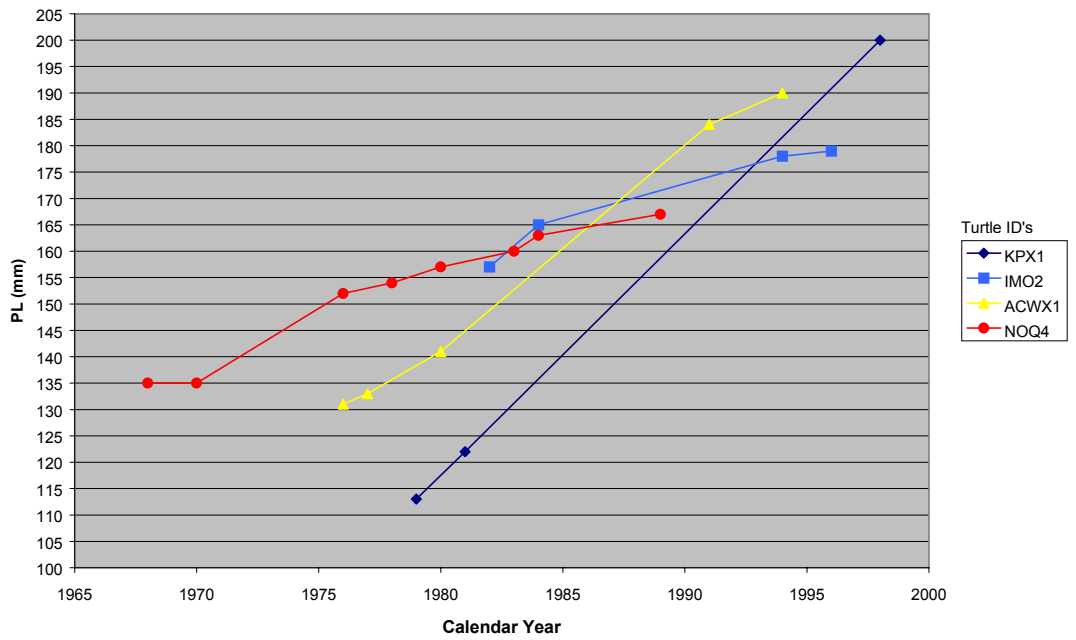


Table 10. Male and female *Trachemys scripta* growth at Ellenton Bay on the SRS in South Carolina during periods of drought and non-drought. Comparisons were made using a two-sample *t* test assuming equal variance.

	Years	Recapture Interval	N	<i>t</i>-value	<i>p</i>-value
Non-drought vs. Drought	(1975-76) vs. (1981-82)	~ 1 year	54	-0.99	0.16

* Indicates the time period in which more growth occurred

** Indicates statistically significant

Growth data for individuals captured in the Par Pond System yielded highly significant results. Female *T. scripta* growth from the Par Pond System (N = 23) during a 3-year time interval had a mean difference in PL of 8.30 mm (t -value = 5.02; p -value = 0.00005). For males from the Par Pond System (N = 25) I used a growth time interval of two years because there were many individuals with that capture interval in common. The mean difference in PL (7.32 mm) was significantly different from zero (t -value = 4.98; p -value = 0.00002).

Individuals living in the experimental pond also displayed evidence for indeterminate growth. Due to a limited amount of data from our experimental ponds, the growth of males and females was combined (N = 55) without a common time interval. Growth was significantly different from zero with a mean change in PL of 5.07 mm (p -value = 2.64×10^{-05} ; t -value = 4.39).

There existed much variability in growth past maturity in both male and female *T. scripta*. Mature males (N=217) were divided according to size categories based on PL: Small=102-142 mm, Medium=143-183 mm, and Large=184-223 mm (see Table 11). Average percent growth in 2 years was calculated. The small category grew an average of 6% in 2 years. The medium category grew 4%. The large category had an average percent increase in PL of 1. Certain mature males and females were selected from the data set to show variability in growth past maturity. Individual variation in growth past maturity over time was depicted graphically (see Figures 3a and 3b). In a different

Table 11. Average percent growth over a 2-year recapture interval for mature male *Trachemys scripta* (N=217) from the SRS* in South Carolina according to size categories.

Category	Size Range of Plastron Length (mm)	% Growth
Small	102-142	6
Medium	143-183	4
Large	184-223	1

* indicates Par Pond System data excluded

analysis, comparisons were made between individual mature male (N=13) and female (N=10) *T. scripta* that were captured in the same year, at the same initial PL, and recaptured within the same time interval (see Tables 12 and 13). Differences in growth among individuals varied from as little as 0 mm to as much as 20 mm.

Table 12. Variable growth past maturity for 13 mature male *Trachemys scripta* (PL > 99 mm) from the SRS in South Carolina. Comparisons were made based on individuals that were captured in the same year, at the same initial plastron length, and recaptured within the same time interval.

Turtle	Location	Initial Plastron Length (mm)	Recapture Interval	Plastron Length at Recapture (mm)	Size Increase (mm)
1	Lost Lake System	158	2 years	169	11
2	Lost Lake System			165	7
3	Lost Lake System	135	2 years	161	26
4	Lost Lake System			151	16
5	Lost Lake System	142	3 years	153	9
6	Lost Lake System			147	5
7	Lost Lake System	120	2 years	127	7
8	Steel Creek			125	5
9	Lost Lake System			122	2
10	Lost Lake System	155	2 years	178	23
11	Lost Lake System			174	19
12	Lost Lake System			165	10
13	Lost Lake System			158	3

Table 13. Variable growth past maturity for 10 mature female *Trachemys scripta* (PL > 159 mm) on the SRS in South Carolina. Comparisons were made based on individuals that were captured in the same year, at the same initial PL, and were later recaptured within the same time interval.

Turtle	Location	Initial Plastron Length (mm)	Recapture Interval	Plastron Length at Recapture (mm)	Size Increase (mm)
1	Lost Lake System	207	2 years	210	0
2	Lost Lake System			210	0
3	Ellenton Bay System	190	3 years	198	8
4	Ellenton Bay System			193	3
5	Ellenton Bay System	186	3 years	191	5
6	Ellenton Bay System			189	3
7	Ellenton Bay System	210	3 years	212	2
8	Ellenton Bay System			220	10
9	Ellenton Bay System	188	3 years	194	6
10	Ellenton Bay System			192	4

DISCUSSION

Throughout the literature, uncertainty exists regarding indeterminate growth in reptiles (Table 1), and supporting, unequivocal evidence has not been reported for reptiles. The results of these analyses indicate that some growth continues well past maturity in both male and female *K. subrubrum* and *T. scripta* from the SRS (Tables 2 and 8) and provides strong evidence that indeterminate growth occurs in two distinct species with different phylogenetic lineages. Because gravidity was also used for determining maturity (rather than presuming maturity based solely on CL/PL), these data provide an indisputable measure of growth past maturity (Tables 3 and 9). The results of my study on freshwater turtles do not agree with Sebens (1987) who stated, “Evidence from growth studies of higher vertebrates, reptiles, birds, and mammals suggests that growth is very determinate”. My results also conflict with Carr and Goodman (1970), Bjorndal (1980), and Congdon et al. (2001) who all concluded that variability in mature sizes of turtles are due to differing juvenile growth rates (pre-maturity) rather than effects of post-maturity growth (indeterminate growth). Likewise, Halliday and Verrell (1988) presumed reptiles attaining sexual maturity at smaller sizes would remain smaller than individuals that matured at larger sizes. My results for *K. subrubrum* and *T. scripta* also differ from Congdon et al. (2001) who reported that old, mature *Emydoidea blandingii* stop growing. Furthermore, Gibbons (1990) indicated growth ceases in older mature individuals of *K. subrubrum*, based on a shorter-term study of the same population used in the present study.

Extended longevity in some reptile species seems to be a key component for indeterminate growth to be exhibited. Due to the nature of indeterminate growth and dependence on sporadic periods of high resource availability (Zug et al. 2001), individuals with more limited generation times seem more likely to concentrate their resources solely on reproduction (once past maturity) in order to maximize lifetime fecundity. Identifying the appropriate cues for when to allocate resources to which action is something for which the individual strives in order to maximize fitness (Perrin et al. 1993). From the onset of maturity for some reptile species with longer life spans, there exists a potentially longer time period for reproduction, thus providing the opportunity for continued growth as well. From one viewpoint, an individual may delay maturity in order to reach a larger body size in a shorter amount of time, which may help to avoid predation. Nonetheless, delaying maturity could decrease potential lifetime fecundity due to the increase in generation time (Stearns and Koella 1986) and the greater likelihood of mortality prior to reproduction (Andrews 1982). Rather, it may be advantageous for an individual to allocate some resources to reproduction as soon as physically possible, resulting in an earlier appreciable decrease in growth rate and hence juvenile growth that potentially makes them more susceptible to predation because of smaller size.

The advantages to female turtles exhibiting indeterminate growth are explicit from a fitness standpoint. On one hand, they may attain maturity at an earlier age, but the increased clutch size that occurs with greater size can also be realized by continued increase in body size later in life. Increased body size that translates to increased fecundity (Day and Taylor 1997, Andrews 1982) depends, in part, on resource availability (Georges 1985; Abell 1999), which may vary considerably over the lifetime

of a long-lived individual. Indeterminate growth allows the individual to reproduce successfully at an early age, while over time, taking advantage of high resource years to continue increasing body size, albeit at a reduced rate.

Conversely, the advantage of being larger and experiencing indeterminate growth for male turtles is not as obvious. Several hypotheses exist as to why it is advantageous for males to have large size. In the case of male-to-male combat, larger size would be selected for because a larger male would be more likely to out-compete a smaller male for an opportunity to mate with a female (Berry and Shine 1980), thus increasing his fitness. This advantage (larger male body size) may also be linked to female preference (Andrews 1982), as demonstrated in some anuran species (Gatz 1981; Howard 1978), which again, would support selection for indeterminate growth in males. Male as well as female turtles with larger body sizes are less susceptible to some forms of predation (Gibbons 1990; Gibbons et al. 1979) and body size can increase chances for survival (Kirkpatrick 1984). Furthermore, males of some species of turtles tend to exhibit more overland travel than their female counterparts (Morreale et al. 1983). Such land travel by males is oftentimes a result of searching for females in land-locked aquatic habitats and may make males more vulnerable to terrestrial predation. A larger body size would provide better protection from terrestrial predators they might encounter. Thus, like female turtles, males of some species may benefit from indeterminate growth because selection favors larger body size, which can be realized through indeterminate growth that permits early reproduction with later opportunities for a continued increase in size.

Growth data of turtles from distinct locations on the SRS (i.e., Ellenton Bay/Ellenton Bay System (EB), Par Pond System (PP), and experimental pond (EP)), made it possible to take a closer look at the potential influence that environment and habitat have on growth. Several severe droughts have occurred on the SRS since the onset of these turtle studies. Different turtle species respond to drought in a variety of ways such that some are more negatively affected than others (Gibbons et al. 1983). Moreover, certain habitat types are affected more drastically than others. For example, turtles living in river systems or stream-fed ponds are less likely to experience a complete drying of aquatic habitat. Conversely, Carolina bays persist on rainfall; thus droughts often dramatically alter such habitat types. For this reason, growth in turtles from EB was selected for analyses.

Unexpectedly, *K. subrubrum* grew significantly more during the drought periods. This may be due to resources becoming more readily available with aquatic prey items such as tadpoles, salamander larvae, invertebrate larvae, etc., becoming more concentrated with shrinking water bodies (J. L. Greene, personal communication), thus decreasing the individual turtle's search time. However, these benefits are temporary. As the drought persists, aquatic prey items should become increasingly scarce, as aquatic habitats with steadily lowering water levels cannot sustain sufficient amounts of prey items for an extended period of time. Remarkably, *K. subrubrum* grew significantly more during the 1987-1988 drought period than the 1981-1982 drought period. This difference in growth may be related to the timing (season), magnitude, and duration of the drought.

In contrast to *K. subrubrum*, *T. scripta* did not show significant differences in mature growth during either the drought or non-drought period from EB. One possible explanation may involve how the two turtle species respond to drought. Gibbons et al. (1983) found that *T. scripta* emigrated from Ellenton Bay during the drought of 1981 with few returning the following year; conversely, *K. subrubrum* did not show an appreciable rate of emigration. Thus, *T. scripta* would not have been present during the period when concentrated resources were available as a consequence of lowered water levels.

Comparing longer or additional periods of drought and non-drought may further reinforce the observed disparity in apparent growth patterns and provide additional evidence for how indeterminate growth can be translated into overall fitness. Furthermore, given sufficient data, comparing growth using the same set of turtles for the drought period and then again for the non-drought period (or drought vs. drought) might eliminate some of the individual variation in growth that was observed.

Analyses conducted on growth data for *T. scripta* captured in PP were considered independently from other areas of the SRS because it is a location that historically served as a cooling reservoir for the thermal effluent from a nuclear reactor. In studies conducted on reactor cooling water effects on turtles, one significant finding was that individual female *T. scripta* from PP attain maturity in the same amount of time as non-PP individuals, but at a much larger PL (>199 mm), while size at maturity in males does not seem to be affected (Gibbons 1970). Hence, males mature at an earlier age. As a result of my study, it was found that PP individuals show greater mean growth past maturity than non-PP individuals for the same recapture interval (i.e., 2 and 3 years). The

mean difference in growth in PL (8.30 mm) between initial capture and recapture of females from thermally affected habitats was nearly twice that of females from the non-thermally affected habitat (4.63 mm) during the same time interval. Furthermore, the mean difference in growth in PL for males from PP (7.32 mm) was larger than that of males living in non-thermally affected habitat (5.20 mm) when tested for the same recapture time interval.

Gibbons (1970) also found that because of increased primary productivity in their thermal habitat, females attained larger body sizes and, thus, a higher reproductive output (clutch size) was also realized in PP *T. scripta*. As for indeterminate growth based on gravidity, the paired *t* test for gravid PP females resulted in a slightly smaller mean difference in growth in PL (3.94 mm) than non-PP gravid females (4.17 mm), but was still significant (p -value = 3.65×10^{-3} ; t -value = 3.10). Without using a common time interval for comparing post-gravid growth (due to a lack of sufficient data), it is unclear as to whether non-PP post-gravid females grow at approximately the same rate or a slightly faster rate past maturity than post-gravid PP females.

T. scripta recaptured from the experimental ponds showed evidence for indeterminate growth. Their habitat is one that is for the most part unchanging. Within the enclosure, predatory levels on adults are presumably lower than in a natural habitat. The water level is constant and turtles are provided with regularly scheduled supplemental feedings. Seemingly, normal activities persist for the turtles. Mating occurs and females nest on the banks within the enclosure. Likewise, mature EP *T. scripta* continue to grow significantly, just as other SRS *T. scripta* do. The mean difference in PL (5.07 mm) for male and female *T. scripta* living in the EP is similar to

those living elsewhere on the SRS (4.76 mm). Due to the small data set for the EP, using a common time interval for growth was not feasible. Hence, the possibility exists that this growth of *T. scripta* may differ from others on the SRS. One way to correct for this (given sufficient data) would be to apply a two-year recapture time interval to the EP turtles, as done for the SRS turtle growth. However, time interval may not influence results. The analysis that yielded a mean difference in growth in PL (4.17 mm) for gravid *T. scripta* (SRS) did not use a common recapture interval, yet the average growth was nearly identical to the mean difference in growth in PL (4.13 mm) for female *T. scripta* (SRS) with a 2-year recapture interval.

Variability in growth past maturity

If the presumption is true that a reptile's growth rate slows proportionately to its increase in size (Jackson 1970; Halliday and Verrell 1988), why do some turtles (that currently are at the same mature size) later grow at differing rates? Just as juvenile growth rates vary in hatchlings of the same size from the same clutch (Jackson 1970), growth rates vary for turtles that are well-past maturity. Certain statements made in the literature suggest that turtles having recently attained maturity may continue to display some growth shortly thereafter, but that such growth will soon cease (Gibbons 1990; Congdon et al. 2001). Classifying SRS growth data for individuals according to size categories has revealed some patterns of growth past maturity for different sizes, as well as different species of turtles (Tables 5 and 11). For male *T. scripta* (Table 11) at sizes ranging from just past maturity (>99 mm PL) to slightly over 140 mm PL, the average percent increase in PL in 2 years was 6%. As PL gets larger (143 mm-183 mm), average

percent increase in PL for the same time interval was 4 %. In the largest size class (184 mm-223 mm) for SRS (excluding Par Pond System individuals) data used, the average percent increase in PL for two years was 1 %. Thus, some of the largest individual *T. scripta* that may be many years past maturity continue to exhibit growth, though at a decreased rate. A similar post-maturity growth pattern was revealed for male *K. subrubrum* (Table 5) from the SRS. As size class increased, average percent growth decreased, but did not cease. The largest mature size class for individuals still exhibited a 1 % average increase in CL.

But how significant can a 1 % increase in body length be for an individual? It can be quite notable when considering the length-weight relationship displayed in turtles. Although the precision of the “cube law relation” (Lagler and Applegate 1943) has been challenged by some (Mosimann and Bider 1960; Dunson 1967), the “law” represents a fairly accurate interpretation of the important relationship that mass increases exponentially relative to length (Lagler and Applegate 1943; Mossimann and Bider 1960; Dunson 1967; Dunham and Gibbons 1990). Body size of an individual has a powerful influence on a variety of life history strategies from attainment of sexual maturity to overall survival (Kirkpatrick 1984). This effect of even a small increase in body length has the potential to result in a disproportionately larger increase in body mass, thus dramatically increasing overall the aspects of body size that are critical in consideration of bioenergetics and reproduction.

Growth data from SRS (Par Pond System data analyzed separately) also show examples of individual variation in mature growth of both male and female *T. scripta* and *K. subrubrum* (Tables 6-7 and 12-13). Comparisons within species were made based on

individuals that were captured in the same year, at the same initial PL or CL, and recaptured within the same time interval. For example, some individual male *T. scripta* (Table 12) that were well past mature size, had identical PL's during the same calendar year and were from the same location. However, when the same individuals were captured three years later, their PL's were substantially different. These data suggest that post-maturity growth rates also vary among individuals just as they do for hatchling or juvenile, pre-maturity growth rates (Jackson 1970; Andrews 1982). Likely, this growth is also influenced by a combination of both genetics and environment, being especially influenced by resource availability, which may differ considerably among individual turtles as a consequence of experience within microhabitats and chance encounters of prey.

Implications for conservation

It is important to have a complete knowledge of a species' life history in order to appropriately assess conservation planning and management techniques.

Sebens (1987) wrote:

The life-history approach is likely to provide the next advance in our understanding of how natural selection controls the characteristics of animals with indeterminate growth. This methodology, combined with better knowledge of growth energetics and energy allocation for particular species, may help explain how such animals deal with changing environments and how this affects their population dynamics and the size structure of populations across environmental gradients.

Growth patterns are one such life history strategy that may ultimately affect lifetime fitness. By using reliable long-term data sets for two long-lived species, the results of

this study have disclosed a particular life history strategy of two freshwater turtles from different phylogenetic lineages that has been under debate for nearly a half-century.

CONCLUSIONS

Turtle species vary in their growth patterns after reaching maturity as demonstrated by higher average linear growth and a faster growth rate both before and after reaching maturity in *T. scripta* than *K. subrubrum*. The differences observed between the two species is not surprising, considering the much larger body size in *T. scripta* at all stages. However, despite the dissimilarities in absolute growth, these two very different species, from two different phylogenetic lineages, both exhibit indeterminate growth. Further studies need to be conducted to verify whether indeterminate growth occurs in other turtle species.

Indeterminate growth may lead to increased fecundity through an appreciable increase in body size. Previous studies have shown a positive relationship with body size (i.e., length) and clutch size for various species of freshwater turtles (Cagle 1950; Gibbons 1970; Steyermark and Spotila 2001). This relationship has been identified in both *K. subrubrum* and *T. scripta*, which were also found to exhibit indeterminate growth in this study. Continued growth, i.e., increased body size would ultimately allow for larger clutch sizes in individuals demonstrating indeterminate growth. Even a small incremental increase in body size could translate into a concomitant, albeit small, increase in clutch or egg size, with a proportional increase in fitness. Consequently, removal of the largest females from a population has the most severe impact on

population recruitment since it is the largest females that can potentially lay the most eggs.

An advantage of indeterminate growth in some turtles is that species living in unpredictable habitats with fluctuating resources can take advantage of intermittent resource opportunities. The effects of drought on growth in *K. subrubrum* showed increased average growth for mature individuals during a period of time following the onset of drought. This may be due to shrinking water bodies resulting in concentration of aquatic prey (Greene pers. comm.), thus decreasing individual search time for food. Gibbons et al. (1983) found *K. subrubrum* responded to drought by remaining in the drying habitat, while *T. scripta* were more likely to emigrate over land to the nearest water body, possibly explaining why average growth during a drought period for *T. scripta* was not significantly different from that of a non-drought year.

The disadvantage of attaining maximum size at maturity is that it requires forecasting of lifetime resource availability, which could possibly result in an unsustainable situation for an individual. However, when individuals are capable of responding to increases in resources by accelerated growth, gradual increases in size, and fitness, can result when opportunities are presented. Such growth may lead to possible long-term population consequences from long cycles of high and low temperatures, or even global warming. *K. subrubrum*'s growth response to drought over time may lead to long-term population consequences such as effects on size structure, though they may be subtle. It is known that turtles have an active season, when feeding and growth occur, as well as, an inactive period (during cooler temperatures) when feeding ceases and as a result, little or no growth occurs (Andrews 1982). Whether the earth is experiencing

global warming may influence a variety of population consequences related to indeterminate growth. Most species of turtles have temperature dependent sex determination (TDSD; Zug et al. 2001). For turtles, warmer incubation temperatures produce females. Such effects could have a dramatic influence on sex ratios of future populations (Spotila et al. 1987; Zug et al. 2001). Theoretically, if indeterminate growth is being selected for in various species of turtles, one long-term population consequence might be larger average adult body size.

Turtles with indeterminate growth have the option of allocating all resources into egg laying, hence not growing in situations where resources are low. Of course, bet hedging, in which reproduction at a smaller size and lower reproductive output is favored over an increase in size would be relative to habitat and resource availability, both of which have tremendous influence on growth (e.g., average mature growth rate as in the PP individuals), thus affecting overall size structure of populations. Frazer et al. (1993) investigated the effects of growing season on attainment of maturity. Male turtles reached maturity earlier during the latter part of the decade during a time when the growing seasons were on average longer and warmer (see also Frazer et al. 1991). This effect on size to maturity, influenced by environment in another way has been demonstrated in PP female *T. scripta*. Such individuals also exhibit increased average growth rate past maturity, likely due to the heated effluent from the nuclear reactor, which caused increased primary productivity in the habitat (Gibbons 1970) and provided a resource base conducive to an increase in body size.

Future Studies

Future studies will analyze other species for which there is sufficient growth data and may include data sets based on populations off of the SRS such as *Malaclemys terrapin* from coastal South Carolina and *Emydoidea blandingii* from southern Michigan. Conceivably, turtle growth patterns will exhibit some variation among species but based on preliminary analyses, some or all are expected to demonstrate indeterminate growth.

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