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Front-loading life histories: the enduring influence of juvenile growth on age, size, and reproduction of primiparous female freshwater turtles

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ABSTRACT

Primary questions: (1) How do juvenile growth rates influence age and body size at maturity of females of three species of freshwater turtles? (2) Are the patterns similar among species that occupied the same wetlands over the same three decades? (3) What are the reproductive traits (i.e. clutch size and egg size) of primiparous females (first lifetime reproduction)? (4) Is there evidence that adult growth rates subsequently reduce the initial differences in the body size and reproductive traits of primiparous females?

Secondary questions: We asked several additional questions of Painted Turtles. Are growth rates of older juveniles more similar to growth rates of young juveniles or adults? What is the earliest age at which juvenile growth rate is detectably correlated with age and body size of primiparous females? Sample sizes of the other two species were too small to use for these questions.

Organisms: Three long-lived freshwater turtle species: Painted Turtles (*Chrysemys picta marginata*), Blanding's Turtles (*Emydoidea blandingii*), and Snapping Turtles (*Chelydra serpentina*).

Field site: University of Michigan, E.S. George Reserve, southeastern Michigan, USA.

Methods: We conducted a 33 year mark-recapture study to document juvenile and adult growth rates and age and body size at maturity of females. We used X-radiography to determine clutch size and egg widths of primiparous and older females of all three species.

Conclusions: (1) Juvenile growth rate was the most influential trait determining within-population variation in life-history trait values of primiparous females of all three species of long-lived freshwater turtles, and that variation persisted for many years in older adults. (2) Fast-growing juveniles of all three species matured earlier and at larger (or similar) body sizes than slow-growing juveniles. (3) The relationship between juvenile growth rates and age and size at maturity in Painted Turtles was established by age 4 years. (4) Variation in indeterminate (post-maturation) growth was insufficient to reduce differences in reproductive traits within cohorts of females. (5) Similar results from all three turtle species (families

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Emydidae and Chelydridae) suggest that the relationships between juvenile growth rates and age and size at maturity were established in a common ancestor early in the evolutionary history of turtles.

Keywords: age and size at maturity, freshwater turtles, juvenile growth rates, reproductive traits of primiparous females.

INTRODUCTION

The search for organizing principles of life histories has been challenging, with exceptions for study organisms often being the rule. Early global evolutionary theories were based on single environmental or demographic factors as the operative force shaping the co-evolved trait values that make up life histories [e.g. relative resource availability, *r*- vs. *K*-selection (MacArthur and Wilson, 1967; Pianka, 1970)]. As it became apparent that life histories are too complex to result from any single influence, subsequent models incorporated influences of both demographic and resource availability on single or paired life-history traits, such as clutch size, offspring size, and age and size at maturity (e.g. Smith and Fretwell, 1974; Bernardo, 1996; Day and Rowe, 2002; Reznick *et al.*, 2002), but many species-specific exceptions remained. The combination of classic, demographic life-history traits (e.g. age-specific survivorship and fecundity, age at maturity), resource-based traits (e.g. reproductive output, parental investment, and juvenile and adult growth rates), and biophysical and developmental constraints has improved our understanding of the linkages between individuals and populations (Dunham *et al.*, 1988, 1989; Congdon *et al.*, 2001a).

Williams (1966) posited that juveniles grow rapidly because that reduces the period that they are exposed to high risk of predation. Later studies found that juvenile growth rates influenced the age at maturity and size at maturity of females of a variety of species. Ambient temperature, activity season length, resource availability, and relative mortality rates of juveniles and adults have been implicated as proximate determinants of the life-history trade-offs that influence the age and size at which females mature (Wilbur and Collins, 1973; Stearns and Koella, 1986; Roff, 1992, 2002; Stearns, 1992; Day and Rowe, 2002; Angilletta, 2009). The relationships between juvenile growth rate and age and size at maturity documented by comparative studies suggested a need for within-population studies of how among-individual variation in juvenile and adult growth influence the life-history trait values of adult females.

Turtles live longer and mature later than many other animals (Brooks *et al.*, 1988; Gibbons, 1990; Congdon *et al.*, 2001b), thus long-term field studies of populations are required to obtain the longitudinal data to document trade-offs between life-history traits. However, empirically sufficient data on long-lived organisms have been slow to accumulate because substantial investments of time (i.e. seeking funding, training assistants, conducting studies, and data entry and editing) conflict with personal and academic commitments (Tinkle, 1979; Gibbons, 1990).

Early studies of maturation in turtles concluded that time of maturation depended on a turtle attaining either a minimum age or a minimum body size (Cagle, 1950; Tinkle, 1961; Graham and Doyle, 1977; Gibbons *et al.*, 1981). However, later studies of freshwater and sea turtles found substantial variation in age and size at maturity (Congdon and van Loben Sels, 1993; Congdon *et al.*, 2003), and also that juvenile growth rate influenced an individual turtle's time of maturation (Carr and Goodman, 1970; Ernst and McDonald, 1989; Galbraith *et al.*, 1989; Congdon and van Loben Sels, 1993).

We conducted a 33 year (1975–2007) life-history study of three syntopic species of late-maturing freshwater turtles (Painted Turtles, *Chrysemys picta*; Blanding's Turtles, *Emydoidea blandingii*; and Snapping Turtles, *Chelydra serpentina*) on the University of Michigan's E.S. George Reserve (ESGR) near the town of Hell in southeastern Michigan. We collected longitudinal data on hatchling body size, age-specific body size of juveniles and adults, and the age and reproductive traits of primiparous and older females.

Two gravid female Blanding's Turtles initially marked as adults in the 1950s were recaptured on the ESGR in the 2016 and 2018 field seasons and had minimum ages of 84 and 86 years, respectively (J.D. Congdon, unpublished data), and Painted and Snapping Turtles on the ESGR have estimated longevities of 40 and 70 years, respectively. The oldest females of all three species continued to reproduce. The age at maturity of Female Painted, Blanding's, and Snapping Turtles was 6–12, 14–21, and 11–18 years, respectively, and their extended juvenile periods allow additive differences in juvenile growth rate to accumulate and result in substantially different body sizes at maturity (Table 1).

The primary goals of our study were to determine whether relationships between juvenile growth rate and age and size at maturity occur, and if so, whether the relationships are similar for all three species. We also compared the reproductive traits of primiparous females to their traits as older females to determine the magnitude of increase in reproductive output associated with age and indeterminate growth. Our three secondary goals were to: (1) test the assumption that older juveniles have growth rates that are more similar to younger juveniles than to adults (Stearns and Koella, 1986); (2) determine the earliest age at which juvenile growth rate is significantly correlated with age and size at maturity of Painted Turtles; and (3) determine if there is a trade-off between juvenile growth rates and adult growth rates that would reduce differences in reproductive output associated with fast- and slow-growing juveniles.

MATERIALS AND METHODS

Permanent wetlands on the ESGR include a 7.3 ha complex of Southwest Swamp, Fishhook Marsh, and Crane Pond and an 8.0 ha complex consisting of East Marsh, Hidden Lake, and Cattail Marsh. Turtles were captured in aquatic areas using baited traps, un-baited fyke and drift sets, dip netting and muddling. In terrestrial habitats, we captured turtles by hand, at drift fences, and while females were nesting or when hatchlings were emerging from nests. At first capture, we marked individuals with unique identification codes notched or drilled in the marginal scutes of the carapace (Nagle *et al.*, 2017), and we recorded body size (carapace length, CL) and ages or age categories. We assigned hatchlings and yearlings 'age 1', and juveniles ages based on growth rings of the plastron and carapace scutes. We coded older adults as 'not ageable'. We released all turtles into wetlands near their capture location.

We searched all nesting areas on the ESGR repeatedly every day of each nesting season from 1976 to 2007. A fence that encircled East Marsh was monitored daily during all nesting seasons from 1983 to 2006. Females exiting East Marsh to nest were captured, identified, measured, and X-radiographed (Hinton *et al.*, 1997). The combination of methods resulted in long-term longitudinal data on growth rates of juveniles and adults, age and body size of females at first lifetime reproduction (primiparous females), body size- and age-specific clutch sizes, and egg widths of primiparous and older females. We made 2120 captures of hatchlings, juveniles, and primiparous females of the three species. We used capture histories and reproductive state data (gravid or non-gravid) to identify 290, 34, and 38 primiparous Painted, Blanding's, and Snapping Turtles, respectively. We calculated average overall juvenile growth rate as: (CL of individual primiparous females minus the mean CL of hatchings emerging from nests) / (age at maturity – 1). We calculated adult growth rates as: (CL last capture – CL at first capture) / (capture interval in years).

We used SAS statistical software, v. 9 (SAS, 1998). We assessed relationships between age, body size, clutch size, and egg widths of primiparous females using Spearman rank correlations (r_S), and we calculated linear regressions to obtain estimates of slopes for those relationships. To remove the differences in age-specific growth rates, we plotted juvenile growth rates on primiparous year [years before (–) and years after (+) maturity] so that fast- and slow-growing juveniles were included in each year category (Fig. 1a). We set statistical significance at $P < 0.05$. We present measures of central tendency and dispersion as the mean, minimum–maximum, ± one standard error (SE).

RESULTS

Juvenile growth rates

Mean growth rates of juvenile females (from yearling to the year before maturity) were approximately 10 times those of adult Painted Turtles and Snapping Turtles and 7.5 times the growth rate of adult Blanding's Turtles (Table 1). Average growth rate of juvenile Painted Turtles over the three years prior to maturation (i.e. −4 to −1 years prior to first reproduction) was approximately half the average overall juvenile growth rate, but still about six times the growth rate of young adults during the 10 years following first reproduction (Fig. 1a). The average juvenile growth rate of Painted Turtle females decreased by

Table 1. Traits of juvenile and primiparous females of three turtle species on the E.S. George Reserve, Michigan [data are mean, SE, (minimum–maximum)]

			Primiparous females		
Species	Hatchling carapace length (mm)	Juvenile growth rate (mm/year)	Carapace length (mm/year)	Age at maturity (years)	Adult growth rate (mm/year)
Chrysemys picta [*N* = 290]	25.2, 0.04 (19.0–29.0) [*N* = 1463]	12.3, 0.126 (8.4–21.2)	127.8, 0.32 (111–141)	9.5, 0.08 (6–12)	1.2
Emydoidea blandingii [*N* = 34]	35.1, 0.05 (26.0–39.0) [*N* = 1172]	9.3, 0.26 (6.5–12.8)	187.7, 2.12 (162–215)	17.7, 0.41 (14–21)	1.2
Chelydra serpentina [*N* = 38]	29.5, 0.34 (22.8–33.0) [*N* = 2076]	14.8, 0.421 (9.4–19.9)	220.6, 2.38 (176–251)	14.5, 0.40 (10–17)	1.4

Note: Growth rates of adult females are from Congdon *et al.* (2013).

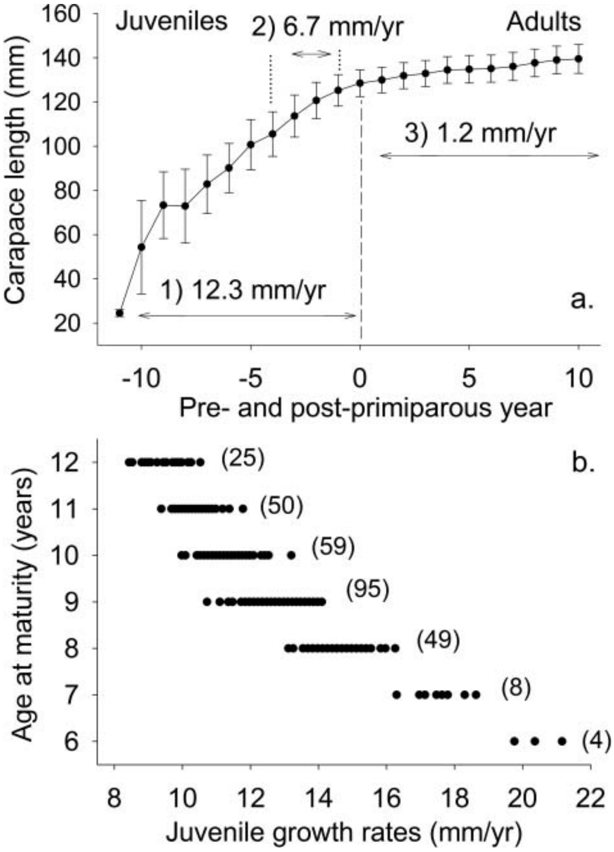

Fig. 1. (a) Body size and growth rates of juvenile female Painted Turtles (*Chrysemys picta*) over 1) all years as juveniles, 2) the 3 years prior to reaching maturity, and 3) the 10 years following first lifetime reproduction. (b) Variation in average juvenile growth rates of primiparous females maturing at different ages, (N).

approximately 1 mm for each age at maturation (Fig. 1b), and fast-growing individuals matured earlier than slow-growing ones.

The body size of Painted Turtles at age 3 years was positively correlated with hatchling size at emergence from nests ($r_S = 0.240$, $P < 0.001$, $N = 120$), but the correlation became non-significant by age 4 years ($N = 106$). At age 4, growth rates of 93 juvenile Painted Turtles were negatively correlated with age ($r_S = -0.46$, $P < 0.001$) and positively correlated with body size ($r_S = 0.33$, $P < 0.001$) of primiparous females. Individually paired growth rates of juveniles and adult females (over the first 10 years post-maturity when indeterminate growth was highest) were not correlated ($r_S = 0.69$, $P = 0.36$, $N = 180$). Individually paired body sizes of primiparous females and at 20–33 years of age were positively correlated ($r_S = 0.720$, $P < 0.0001$, $N = 82$).

Juvenile growth and age and size at maturity

The ranges of average overall juvenile growth rate were 12.3 mm, 9.3 mm, and 14.4 mm per year for Painted, Blanding's, and Snapping Turtles, respectively (Table 1). The ranges of carapace lengths of primiparous females were 33 mm for Painted Turtles, 53 mm for Blanding's Turtles, and 75 mm for Snapping Turtles, whereas the range of ages at maturity was 6–7 years across all three species (Table 1; Fig. 2). Average overall juvenile growth rate was strongly negatively correlated with the age at maturity of females for all three turtle species (Fig. 3a, c, e, respectively), whereas average juvenile growth rate was significantly and positively correlated with the body size of primiparous Painted Turtles and Blanding's Turtles (Fig. 3b, d, respectively) but not Snapping Turtles (Fig. 3f). The combined negative influence of juvenile growth rate on age at maturity and its weaker positive influence on size at maturity resulted in a pattern among individuals of all three species. Slow-growing juveniles of late-maturing (i.e. older-maturing) individuals attained smaller or similar sizes than fast-growing (i.e. early-maturing) juveniles [Patterns 1 and 2, respectively (Stearns and Koella, 1986)].

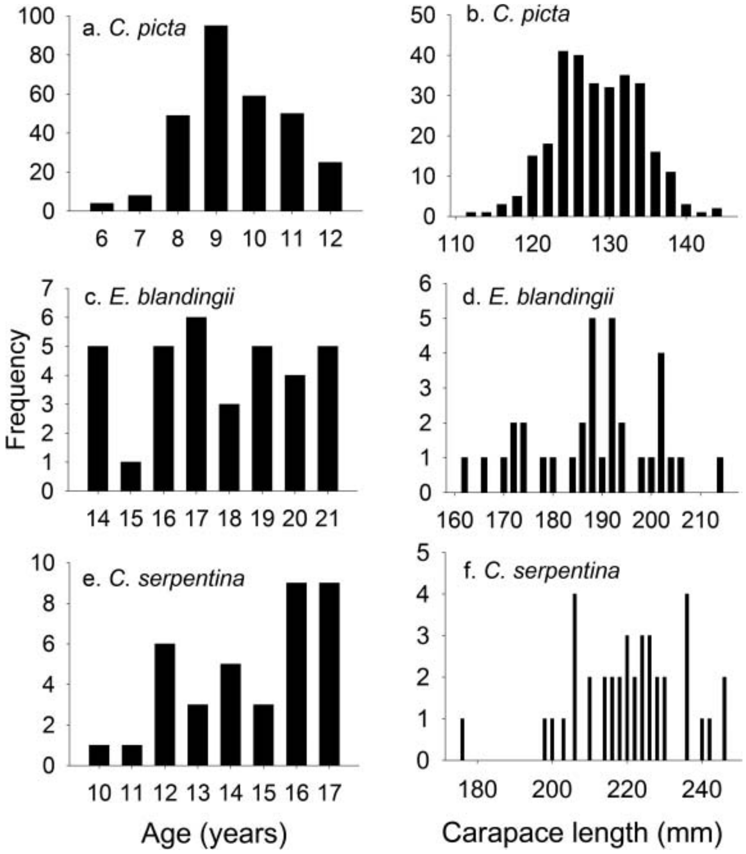

Fig. 2. Frequency distributions of ages and body sizes at maturity, respectively, for (a, b) *Chrysemys picta* ($N = 290$), (c, d) *Emydoidea blandingii* ($N = 34$), and (e, f) *Chelydra serpentina* ($N = 39$) on the E.S. George Reserve.

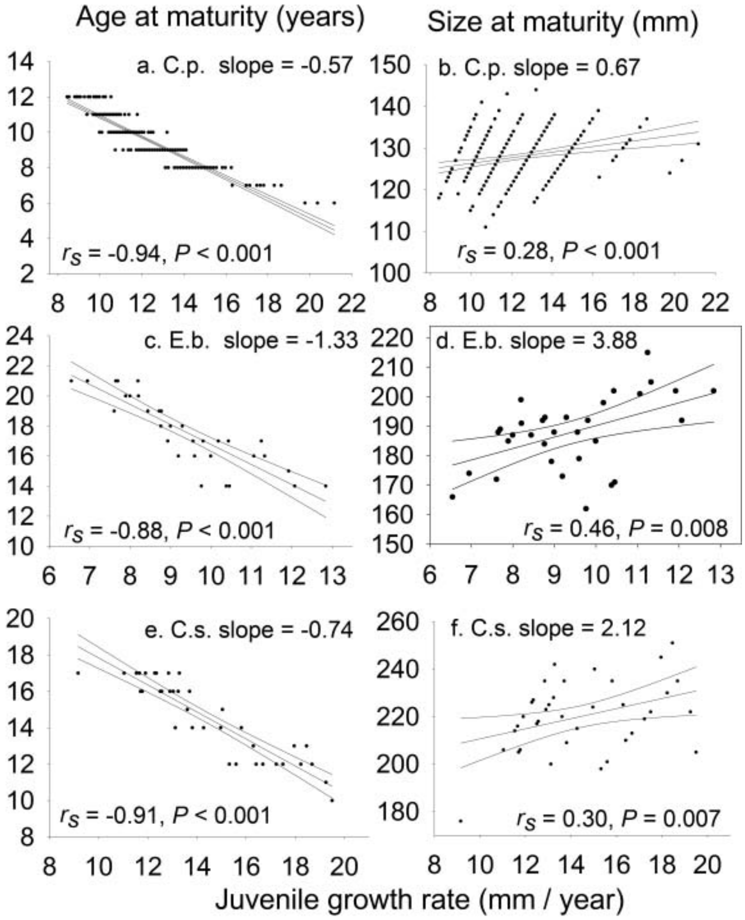

Fig. 3. Spearman rank correlations (r_S) and slopes of linear relationships between juvenile growth rate and age at maturity and carapace length (CL) of primiparous female (a, b) *Chrysemys picta* ($N = 290$), (c, d) *Emydoidea blandingii* ($N = 34$), and (e, f) *Chelydra serpentina* ($N = 39$).

Reproductive traits of primiparous females

Average clutch sizes of older female Painted and Blanding's Turtles were both one egg larger and those of Snapping Turtles eight eggs larger than those of primiparous females (Table 2). Neither clutch size nor egg width of primiparous female Painted Turtles was significantly correlated with juvenile growth rate (clutch size: $r_S = 0.091$, $P = 0.17$; egg width: $r_S = -0.039$, $P = 0.57$), but both were correlated with body size (clutch size: $r_S = 0.192$, $P = 0.003$; egg width: $r_S = 0.310$, $P < 0.0001$). Only egg width was correlated with age of primiparous females ($r_S = 0.151$, $P = 0.03$). Egg widths in first and second clutches of primiparous female Painted Turtles were both significantly smaller than those of older females (Mann-Whitney rank sum tests, all $P < 0.01$).

Table 2. Comparison of reproductive traits of primiparous and older female turtles on the E.S. George Reserve [data are mean, SE, (minimum–maximum)]

	Primiparous		Older females	
Species	Clutch size	X-ray egg width (mm)	Clutch size	X-ray egg width (mm)
Chrysemys picta	**FC:** 6.2, 1.59 (3–10) [*N* = 222]	**FC:** 16.2, 0.05 (13.7–18.3) [*N* = 220]	**FC:** 7.5, 0.07 (3–12) [*N* = 509]	**FC:** 18.3, 0.04 (15.9–22.0) [*N* = 509]
	SC: 5.9, 1.21 (4–8) [*N* = 12]	**SC:** 16.2, 0.35 (15.4–16.7) [*N* = 12]	**SC:** 7.1, 0.10 (4–11) [*N* = 167]	**SC:** 18.1, 0.05 (16.0–20.1) [*N* = 167]
Emydoidea blandingii	9.5, 0.38 (6–15) [*N* = 20]	23.5, 0.34 (20.9–27.1) [*N* = 28]	10.0, 1.19 (2–16) [*N* = 315]	24.6, 0.06 (21.6–28.1) [*N* = 315]
Chelydra serpentina	19.0, 0.93 (7–27) [*N* = 27]	26.6, 0.19 (24.7–28.6) [*N* = 29]	27.0, 1.3 (11–44) [*N* = 188]	29.2, 1.32 (26.2–32.2) [*N* = 188]

Note: FC = first clutch, SC = second clutch. Ages of older females are 20–29 years for Painted Turtles and 25–34 years for Blanding's and Snapping Turtles (*N* = number of clutches of primiparous or older females).

DISCUSSION

Early growth rates of juvenile Painted Turtles

Correlations between juvenile growth rate and age and size at maturity were strong enough by 3 years of age to predict whether female juvenile Painted Turtles would fall into the general categories of large and young, or small and old, primiparous females. Establishment of the relationships between juvenile growth rate and age and size at maturity early in life suggests that conditions driving the variation in growth rates influence both slow- and fast-growing juveniles similarly throughout the remaining years of juvenile growth. That is, individuals remain relatively slow or fast growing despite the fact that years vary between good and poor environmental conditions.

An important assumption of the model of Stearns and Koella (1986) is that growth rates of older juveniles during the period of delayed maturity remain most similar to those of young juveniles, rather than to those of adults. Growth rates of juvenile Painted Turtles support that assumption (Fig. 1a, b) and delaying maturity by one year achieves a six-fold increase in linear growth compared with primiparous females.

Juvenile growth rate and age and size at maturity

In all three turtle species (families Emydidae and Chelydridae), the correlation between juvenile growth rate and age at maturity was strongly negative, and that between juvenile growth rate and size at maturity was weakly positive (Fig. 3). The divergence in body size began in young juveniles and continued in older juveniles as they approached maturity. Captive juvenile Green Sea Turtles (family Cheloniidae) raised in controlled conditions and fed high-quality diets (Bjorndal *et al.*, 2013) had substantial variation in juvenile growth rate that led to fast-growing juveniles maturing earlier and at larger body sizes than slow-growing individuals. That is the same pattern we found in the three freshwater turtle species. Such similar results in marine and freshwater turtles suggest that phenotypic plasticity is not the only determinant of variation in juvenile growth rate, and that the relationships between juvenile growth rate and age and size at maturity were established in a common ancestor quite early in the history of turtles (Crawford *et al.*, 2015).

Reproductive characteristics of primiparous and older females

Reproductive traits such as clutch size, egg size, and reproductive frequency increase with body size of female turtles, within and among populations of many species (Congdon and Gibbons, 1985; Gibbons and Greene, 1990; Moll and Iverson, 2008; Nagle and Congdon, 2016). The shells of many turtles probably limit maximum clutch volume of each reproductive bout, and if mortality increases with reproductive output or reproductive frequency, single clutches should be more frequent in the longest-lived turtle species. Primiparous and older Blanding's and Snapping Turtle females produce a maximum of one clutch annually, whereas shorter-lived Painted Turtles produce two and occasionally three clutches of eggs in a single season. Females of all three species skip reproduction in some years (Congdon *et al.*, 1983, 2003, 2008).

Although clutch size and egg width increase with age and body size of females for all three species (Congdon *et al.*, 2001b, 2003, 2008; McGuire *et al.*, 2015), these relationships are more pronounced in Painted Turtles. The largest gain in reproductive output in Painted Turtles results from an increase in the proportion of second (within season) clutches produced by larger and older females (Congdon *et al.*, 2003). Only 5% of primiparous female Painted Turtles produced second within-season clutches, whereas an average of 25% (minimum–maximum = 7–50%, $N = 123$) of older females produced second clutches (Congdon *et al.*, 2003; McGuire *et al.*, 2014).

Larger primiparous and older multiparous female Painted Turtles produced larger clutches of larger eggs, whereas such correlations were not evident in the smaller samples of primiparous female Blanding's and Snapping Turtles. Based on age at maturity, average clutch sizes, and clutch frequencies of 1.0, the earliest-maturing females have the potential to produce many more eggs than the oldest-maturing individuals. For example, the earliest-maturing Painted Turtle can produce 36 eggs over six years, Blanding's Turtle 63 eggs over seven years, and the Snapping Turtle 114 eggs over six years (in each case, the number of years before the latest-maturing females of each species reach maturity). Compared to slow-growing juveniles of all three species, faster juvenile growth rates appear to produce winner-take-all scenarios for primiparous and older female turtles.

Variation in body sizes and reproductive traits of primiparous female turtles of all three species persist on the ESGR over many years because juvenile growth rates are not correlated with adult growth rates and because indeterminate growth is low and slows or ceases with increased age (Congdon *et al.*, 2013). Indeterminate growth thus has minimal influence on the variation in adult body sizes that is established among cohorts of primiparous females and their subsequent, size-dependent reproductive traits. For example, at the average adult growth rates of Painted, Blanding's, and Snapping turtles, respectively, it would take approximately 50, 93, and 74 years to increase body size enough to add one egg to a clutch (Congdon *et al.*, 2013). Low indeterminate growth rates and the lack of correlation of juvenile and adult growth rates indicate that small-bodied, late-maturing females are unable to increase body size enough to compensate for differences in the higher reproductive output that is characteristic of large-bodied, early-maturing females.

CONCLUSIONS

In long-lived turtles, the relationships between juvenile growth rate and age and size at maturity are established early in life. The combined effects of differences in juvenile growth rate and age at maturity result in fast-growing juveniles of all three species of turtles maturing earlier and at the same or larger body sizes compared with slow-growing juveniles. We found no evidence of the expected life-history trade-off in the reproductive output of early- vs. late-maturing primiparous females. Combined results from the three freshwater species on the ESGR and those from Green Sea Turtles (Bjorndal *et al.*, 2013) indicate that juvenile growth rate is one of the most influential traits shaping fundamental and long-lasting variation in the suites of life-history trait values within cohorts of long-lived female turtles. We hypothesize that such relationships may be common in populations of other long-lived ectotherm vertebrates.

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