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# Testing hypotheses of aging in long-lived painted turtles (*Chrysemys picta*)

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## Abstract

For 38 of the past 50 years, Painted Turtles were studied on the University of Michigan's E.S. George Reserve in southeastern Michigan. We compared age specific body sizes, reproductive traits and survival of Painted Turtles ranging from 9 to 61 years of age to test contrasting predictions of the Relative Reproductive Rate and Senescence Hypotheses of aging. Indeterminate growth (i.e. continued body growth of adults) was important in increasing reproductive output of older turtles; however, growth rate of the oldest age-group was reduced compared to that of younger adults. Although clutch size and among year reproductive frequency did not increase with age, within year reproductive frequency (production of second clutches), egg size, and hatchling size did. Nest predation rates and the proportion of surviving nests that produced hatchlings were similar among age groups, and embryo mortality in nests was not related to age. Survivorship of males was less than that of females, and survivorship of the oldest group of females was not statistically different from that of a younger group of females. No decline in reproductive output or survivorship was detected in the oldest females as predicted by the Senescence Hypothesis. Thus, the majority of data on reproductive traits and survivorship support the Relative Reproductive Rate Hypothesis. We also compared Painted Turtles to Blanding's Turtles, another species studied on the E.S. George Reserve. That Painted Turtles exhibit indeterminate growth whereas Blanding's Turtles do not, appears to be a primary mechanism for some differences between species in the relationships between reproductive traits and age. An important mechanism for increasing reproductive output in both species was increased reproductive frequency in older females. Painted Turtles also increased offspring quality (egg and hatchling size) with age, whereas Blanding's Turtles did not. Compared to younger individuals, there was no reduction in survivorship in the oldest Painted Turtles and survivorship increased in the oldest Blanding's Turtles.
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*Keywords:* Aging; *Chrysemys picta*; Longevity; Painted turtle; Reproduction; Senescence

## 1. Introduction

Age related changes occur in all organisms and such changes in older individuals are thought to result in deterioration in performance traits that impact reproductive ability directly, or indirectly through reduced survivorship (i.e. senescence, Medawar, 1946, 1952; Williams, 1957; Hamilton, 1966). Senescent changes have been known to occur in a wide range of animals (Comfort, 1979; Finch, 1990; Rose, 1991; Finch and Austad, 2001), and have been reported in natural populations of long-lived turtles (Cagle, 1944; Legler, 1960; Gibbons, 1969). However, the importance of senescence (Gibbons, 1976), its presence or absence (Congdon et al., 2001; Miller, 2001) in natural populations of reptiles remains to be demonstrated.

Two evolutionary hypotheses make contrasting predictions about changes associated with aging, particularly in the oldest individuals. The Relative Reproductive Rate Hypothesis predicts that, particularly in long-lived organisms, older individuals should have traits that enhance reproductive success directly (clutch size, clutch frequency, egg and offspring size) or indirectly through increased

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reproductive life (i.e. survivorship) compared to younger individuals (Williams, 1957, 1966; Congdon et al., 2001). In contrast, the Senescence Hypothesis predicts that in the oldest individuals in a population, reproductive output or survivorship will decline compared to younger individuals (i.e. the oldest individuals will exhibit negative effects associated with aging; Williams, 1957; Hamilton, 1966).

Evidence for senescence in turtles is weak. Senescent ovaries were reported in three species of turtles: Chicken Turtles (*Deirochelys reticularia*; Gibbons, 1969), Ornate Box Turtles (*Terrapene ornata*; Legler, 1960), and Slider Turtles (*Trachemys scripta*; Cagle, 1944). However, observations of senescence were made on large females and the authors apparently assumed that large adult body sizes were indicative of old age. In addition, more extensive observations on female chicken turtles indicated that those that initially appeared to be reproductively senescent, reproduced in later years (Gibbons and Greene, 1978).

Two recent studies indicate that, if it occurs, detecting senescence in turtles may be difficult, and that older female turtles have traits that increase the proportion of late-versus early-births. For example, female Blanding's turtles (*Emydoidea blandingii*) greater than 60 years of age had higher survivorship and increased reproductive output (larger clutches and higher reproductive frequency) than did younger females (Congdon et al., 2001). In another study, Three Toed Box turtles (*Terrapene carolina triunguis*) older than 60 years of age were still reproductive and had clutch sizes similar to those of younger females (Miller, 2001).

Because age-specific traits related to reproduction and survival form the conceptual and theoretical focus of life history evolution (Williams, 1966), a central goal of life history studies is documenting changes in trait values associated with aging. Data from long-term studies of age-specific traits are required to test differences predicted by the Relative Reproductive Rate and Senescence Hypotheses. Tinkle (1979) discussed why long-term life history studies are rare, and the following statement certainly describes studies of turtles 'in the larger forms the life-cycle is so easily modified by diapause, diet, temperature, and the like that individuals probably age at rates so different as to be beyond the access of actuarial statistics except in an experiment of intolerable length'. (Comfort, 1979).

For 38 of the past 50 years (1953–2002) Painted Turtles have been studied on the University of Michigan's E.S. George Reserve (ESGR). Some individuals marked between 1953 and 1957 (Owen Sexton) remain in the population and are now >55 years old, and some marked between 1968 and 1973 (Henry Wilbur) are >35 years old. The majority of turtles marked during the present study (1975–2002) are of known age. We combined data from all years (Table 1) to test predictions based on the Relative Reproductive Rate

Table 1
Summary of data on Painted Turtles used for the present study

| Total individuals marked | Individuals of known age | Recaptures | Hatchlings | X-radiographs | Nests |
| --- | --- | --- | --- | --- | --- |
| 5749 | 3116 | 21,466 | 1028 | 2881 | 2204 |

and Senescence Hypotheses. Specifically, we compared survivorship and reproduction (clutch size, egg size, hatchling size, and reproductive frequency) among ages and age groups. In addition, because adult body growth was shown to be negligible in adult Blanding's Turtles (Congdon and van Loben Sels 1991; Pappas et al., 2000), we examined whether indeterminate growth is a mechanism for increasing reproductive output in older Painted Turtles. We also compared survivorship and reproductive traits of Painted and Blanding's Turtles (Congdon et al., 2001) for similarities and contrasts in patterns of aging.

## 2. Materials and methods

### 2.1. Midland painted turtle (Chyrsemys picta marginata)

Collectively, the four subspecies of Painted Turtles (family Emydidae) are broadly distributed across North America. The range of the Midland Painted Turtles (those found on the ESGR) is restricted to south central Canada and north-central United States as far south as Tennessee. Females reach sexual maturity from 7 to 13 years of age and males mature in 4–5 years at body sizes smaller than females. Females generally produce a maximum of two clutches of 2–12 eggs each year, and the sex of embryos is determined by incubation temperatures in nests (Schwarzkopf and Brooks, 1985). After emerging from eggs hatchlings overwinter in nests (Breitenbach et al., 1984; Nagle et al., 2000) and emerge in spring. Annual survivorship of adults is high.

Some other ecological studies of Painted turtles include those on: reproduction (Gibbons, 1968a; Iverson and Smith, 1993), nesting activity (Cagle, 1937; Ernst, 1971; Tinkle et al., 1981; Mitchell, 1988; Congdon and Gatten, 1989), and population biology and demography (Sexton, 1959; Gibbons, 1968b; Wilbur, 1975; Zweifel, 1989; Frazer et al., 1991).

### 2.2. Study site

The ESGR encompasses 650 ha of woodlands, old fields, and wetlands with human access restricted by a 4 m high fence and locked gates that provide the security critical for conducting research on natural populations. Descriptions of

the aquatic and terrestrial habitats of the ESGR have been published previously (Cantrall, 1943; Sexton, 1959; Wilbur, 1975; Congdon and Gibbons, 1996).

### 2.3. Life history study

The population of adult Painted turtles had remained essentially stable at approximately 1100 adults between 1975 and 1994 (Congdon and Gibbons, 1996). Intensive aquatic trapping was carried out during most years (see Congdon and Gibbons, 1996 for details on capture methods). Between 1953 and 2002, 5749 Painted turtles were marked and over 21,466 recaptures were made (Table 1). Of the individuals marked, 1028 were hatchlings marked at nests or terrestrial drift fences. Upon first capture, all juvenile and adult turtles were individually marked by notching margins of the carapace. Hatchlings were assigned an age of one, and, when possible ages of juveniles were determined by counting growth rings on the plastron. We measured body mass and straight line carapace length (CL), then released all individuals close to their point of capture.

Between 1978 and 1999, 2881 X-radiographs were taken of all females captured during the reproductive season to determine clutch size and egg size (Gibbons and Greene, 1979; Hinton et al., 1997). We also recorded timing and duration of terrestrial activities, observations on nesting behavior, nest predation, and in nests escaping predation, egg failure and embryo survivorship. Data from 2204 natural nests, X-radiographs of gravid females, and hatchlings marked at nests (associated with known females) provide data on reproductive output and success of individual females.

Prior to capture of the first gravid female each year, all drift fences were activated and searches of nesting areas were made each day. After the first gravid female was captured, frequent systematic searches of all nesting areas were initiated, and drift fences were checked approximately every 30 min (usually between 0600 and 2000 h or cessation of turtle activity). Searches of nesting areas were conducted on all days that females were active on land throughout nesting seasons (all years = 15 May–early July). We recorded each female's identification and the location of her nest was marked with a stake placed 2 m from the nest or with flagging tied to nearby vegetation.

Observed nests were monitored daily until they were destroyed by predators. Surviving nests were monitored daily until the end of the nesting season, and weekly throughout summers when field work was ongoing. In late fall, surviving nests were encircled with a 0.3 m aluminum fence buried to a depth of 15 cm. Fenced nests were monitored in the spring and emerging hatchlings were captured, measured, weighed, and then marked and released. In some years, nests were excavated in late

March before hatchling emergence and data on hatchlings and embryo mortality were recorded.

### 2.4. Analyses

When sample sizes were adequate, analyses were made on age specific traits of individuals (adult body growth, clutch size, clutch frequency); when sample sizes were not adequate, analyses were made on non-overlapping age-groups (adult suvivorships, nest survival). Embryo failure was calculated as the difference between clutch size determined from X-radiographs and the number of hatchlings emerging from nests that produced at least one hatchling. Parametric statistical tests were used when variables were continuous and assumptions of the tests were met. Otherwise, non-parametric Wilcoxon tests were used (SAS, 1993). Levels of significance were set at alpha $< 0.05$ and measures of central tendency and dispersion are presented as the mean $\pm$ one standard error. Adult survivorships between sexes and two age groups were compared over approximately the same 25 years to minimize differences in environment. Survivorship curves were determined using PROC LIFETEST (Allison, 1995) for adults that were initially marked prior to 1973 (i.e. sampling period 1973–2002 with right censored survivorship period of 3 years).

## 3. Results

### 3.1. Body size of adults

Ages of females ranged from 9 to 61 years and body sizes ranged from 111–169 mm CL. Body size of adult females (Fig. 1a) and adult males (Fig. 1b) increased more rapidly at youngest ages than at later ages. Among age groups, body size (CL) of adult females increased with age ($F_{2,718} = 159.39$, $P < 0001$; Table 2). Growth rate was three times higher between youngest and middle-age group ($\sim 1.0$ mm year), than that between middle-age and old-age group (0.3 mm year).

### 3.2. Relationships of reproductive output to body size and age

Clutch size (Fig. 2a), egg width (Fig. 2b), and hatchling size (Fig. 2c) all increased with body size of females. Egg width (Fig. 3a) and hatchling body size (Fig. 3b) also increased with age of females, but clutch size did not.

The proportion of second clutches increased from 0.1 to 0.5 among six age-groups (except the oldest; Fig. 4a), and older females tended to nest earlier in the season than did younger turtles (Fig. 4b). Annual reproductive rate (the proportion of females captured each year were reproductive) averaged 97% across all age groups and was not related to age.
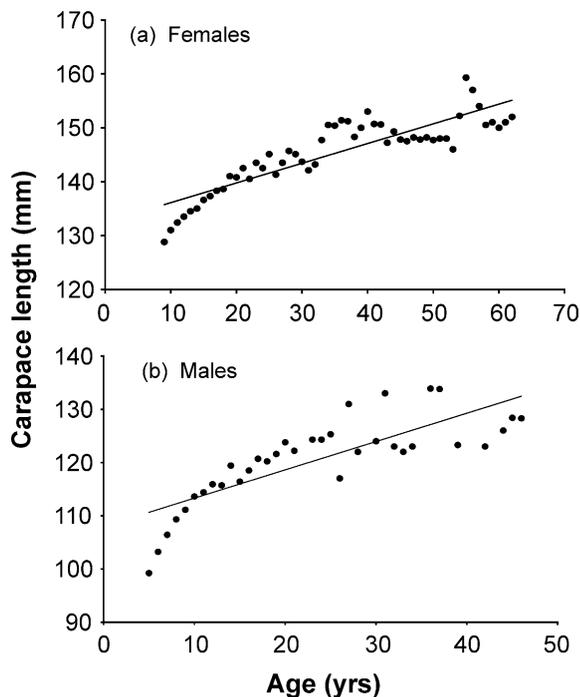
Fig. 1. Age specific body size (carapace length) of a) females, and b) males. Linear regression lines through all data highlight the difference between early and later growth of adult turtles.

### 3.3. Nest and hatchling success among age groups

Predation rates of nests among age-groups were similar (Table 3). The percent of nests surviving predation that subsequently produced hatchlings were not significantly different between age-groups (Paired comparisons all, Gadj., $P > 0.05$; Table 3). The proportion of embryo deaths (or infertile eggs) in surviving nests was not related to age of females (Fig. 4c).

### 3.4. Survivorship of males and females

Survivorship of adult males was significantly lower than that of females (Fig. 5) over early portion (Wilcoxon Test $= 11.51$, $P = 0.0007$) and later portion (Log-Rank Test $= 22.15$, $P < 0001$) of the 25-year sampling period. Over the same period, survivorship of the oldest females was consistently greater than that of females from the middle aged group, but not significantly so (Wilcoxon $= 1.827$, $P > 0.17$; Log-Rank $= 3.900$,

Table 2
Characteristics of Painted Turtle Age Groups ($N/n =$ number of individuals/number of captures; data are mean, (minimum–maximum)

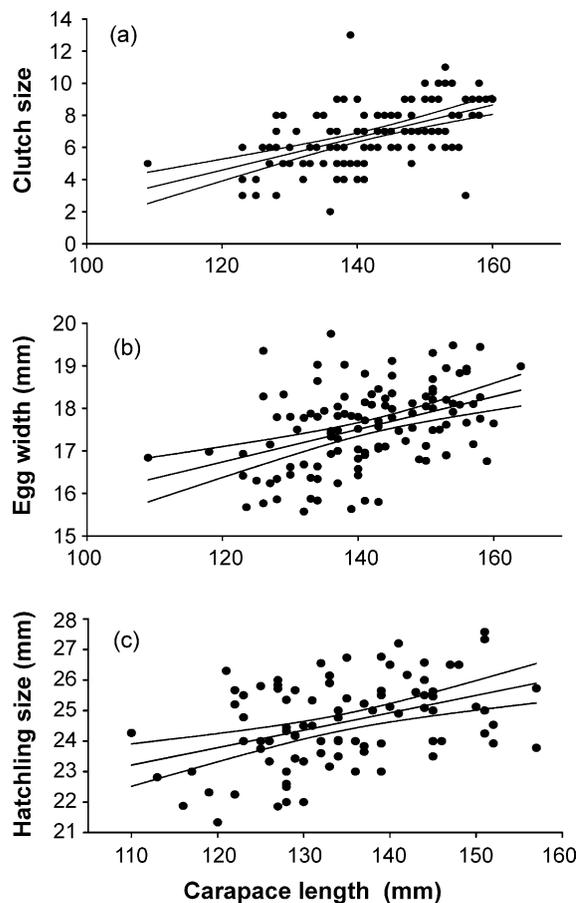| Age category | $N/n$ | Age (years) | Carapace length (mm) |
|---|---|---|---|
| Oldest | 20/103 | 41.5, (30–61) | 149, (139–169) |
| Middle | 115/409 | 22.8, (20–29) | 144, (125–165) |
| Youngest | 585/2,207 | 13.4, (9–19) | 135, (111–164) |



Fig. 2. Relationships of (a) clutch size (intercept $= -7.58$, slope $= 0.10$, $r^2 = 0.29$) and (b) egg width (intercept $= 12.14$, slope $= 0.04$, $r^2 = 0.18$), and (c) hatchling body size (carapace length; intercept $= 16.94$, slope $= 0.06$, $r^2 = 0.17$) to body size of female Painted Turtles Included are linear regression lines and 95% confidence intervals.

$P = 0.06$). Lack of statistical difference may be due to the small sample size of the old age group; (Fig. 5).

## 4. Discussion

### 4.1. Indeterminate growth and body size of adults

Body sizes of adults increased with age (Fig. 1a and b), and with age-group of females (Table 2), but growth rates slowed from approximately 1 mm per year in the youngest individuals to 0.3 mm per year in older individuals. In contrast, adult Blanding's Turtles do not exhibit indeterminate growth (Congdon et al., 2001; Pappas et al., 2000). Reduction in growth rates of older adults could be interpreted as support for the Senescence Hypothesis; however, diverting resource allocation of younger turtles from growth to reproduction as they become older would be interpreted as support the Relative Reproductive Rate Hypothesis. Within the family Emydidae, the relationship between body size and age of adults, that is often assumed to exist as a mechanism for promoting late vs. early births in
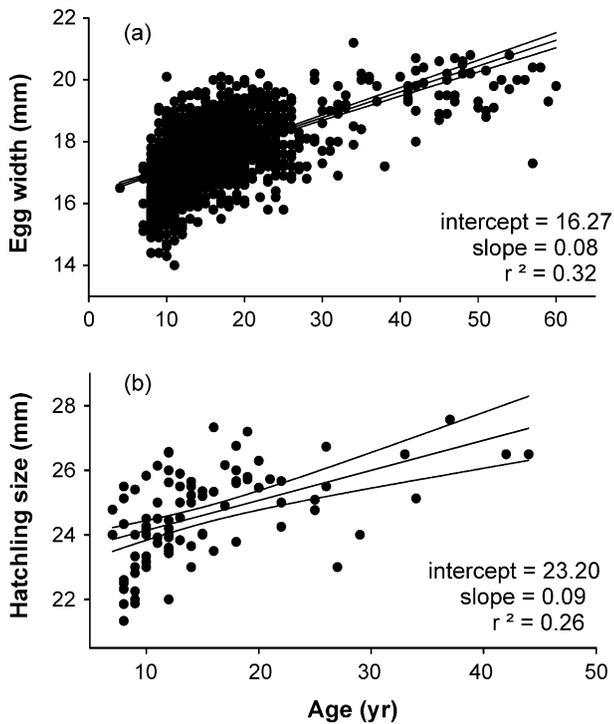
Fig. 3. Relationships of (a) egg width and b) hatchling body size (carapace length) to age of females. Iincluded are linear regression lines and 95% confidence intervals.

turtles, is present in Painted Turtles, but absent in Blanding's turtles.

## 4.2. Reproductive output

In Painted Turtles approximately half of the increase in reproductive output associated with body size is due to increased clutch size and the other half due to increased egg size (Congdon and Gibbons, 1987). That clutch size increased with body size (Fig. 2a) but not with age of females is puzzling given that adult females continue to grow. In contrast, actual egg widths (as an index of egg size) increased with body size (Fig. 2b) as did egg widths (from X-radiographs) with age (Fig. 3a). Some portion of the increase in egg widths from X-radiographs is attributable to slight magnification of egg images because actual eggs are suspended in the body above the film (Graham and Petokas, 1989). However, hatchling body size also increased with body size (Fig. 2c) and age (Fig. 3b) of females, and hatchling size is determined primarily by egg size in Painted Turtles. Egg width in painted turtles is thought to be constrained by the size of the pelvic aperture, a constraint that is relaxed in larger and older turtles (Tucker et al., 1978; Congdon and Gibbons, 1987). Why the relationships between body size and age were different for clutch size, but not for egg width is not apparent. However, clutch size relationships were based on data (body sizes, ages, and clutch sizes)
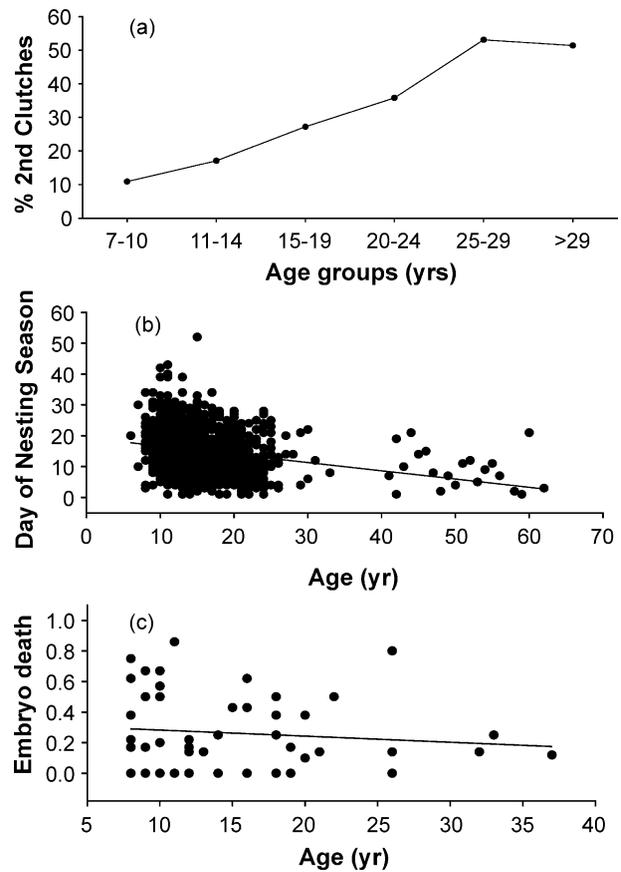


Fig. 4. Relationships of the following traits to age of female Painted Turtles: (a) percent of second clutch production (among 6 age groups), (b) day of nesting season when first nests first nesting occurred, and (c) the proportion of embryo mortality in nests. Slopes of linear regression lines in figures (b) and (c) are not significantly different from zero.

from the same females, whereas actual egg sizes were obtained from a different sample of females than were X-radiograph data on egg widths. Also, total variation in adult body size in the population is a combination of variation in body size at sexual maturity (Carr and Goodman, 1970) and variation due to indeterminate growth. The way these two categories of variation interact may have differentially affected patterns of association among clutch size, egg size, and age. In comparison, clutch size increased with age in Blanding's Turtles, but egg size did not (Congdon et al., 2001).

Table 3
Nesting success among age groups of Painted Turtles

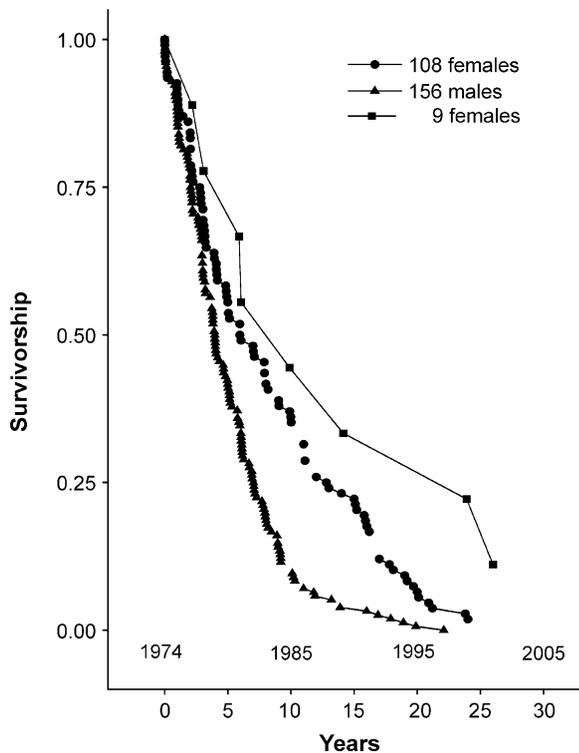| Age category | # Nests | % Destroyed | # Surviving | # Produced hatchlings | % Produced hatchlings |
|---|---|---|---|---|---|
| Oldest | 51 | 78 | 11 | 8 | 72 |
| Middle | 232 | 82 | 41 | 36 | 87 |
| Youngest | 895 | 76 | 213 | 175 | 82 |

Fig. 5. Survivorship of 108 females and 156 males (>9 and >5 years old, respectively) compared to 9 females (>20 years old) at the beginning of the time period. Survivorship for all groups determined over the same 25 years.

## 4.3. Reproductive frequency

Reproductive frequency is difficult to determine in the field, but is probably the most important component of variation in lifetime reproductive output among female turtles. We limited the analysis of second clutch production to East Marsh only because it is completely encircled with a fence that is continually monitored during the nesting season. Therefore, almost all females leaving the marsh to nest are captured. Among six age groups, the oldest females produced second clutches within a nesting season at five times the rate of the youngest females (Fig. 4a). In conjunction with the increased reproductive frequency, older females tended to begin nesting earlier in the season than do younger females (Fig. 4b). The frequency of reproduction by individuals among years was high (average = 97% across all age groups) and not related to age. Older Painted Turtle females produced more frequently within a nesting season, but not among years. Because Blanding's turtles do not produce more than one clutch per year (and females occasionally skip years), increased reproductive frequency of the oldest Blanding's turtle females was among years (Congdon et al., 2001).

## 4.4. Nest and embryo mortality

That females have limited opportunities to assess potential predator activity on a nesting area, may be the reason that nest predation rates were similar among age groups. A female's encounter with a predator in a nesting area is often fatal, and depredation of nests usually occurs after the females has departed. Females appear to select nest sites primarily on the basis of influence on incubation of eggs (i.e. exposure to sunlight, vegetation cover, and soil types). Senescence could be expressed as developmental problems with embryos; however, success of nests that survived predation, and the proportion of infertile eggs or embryos that failed to develop were not related to age of females (Fig. 4c) nor to body size of females. In Blanding's turtles, nests of the oldest females may have suffered higher predation and embryo mortality rates; however, nests were scattered through time and space, and sample sizes for comparisons of embryo mortality rates were small (Congdon et al., 2001).

## 4.5. Survivorship of males and females

Survivorship of adult females was greater than that of adult males, and survivorship of middle-age group and oldest-age group females was not significantly different (Fig. 5). Compared to females, males mature at earlier ages and at smaller body sizes. In general, male turtles tend to move among wetlands more frequently than do females (Morreale et al., 1984), and such movements probably expose them to higher risk of mortality. Comparison of survivorships of the younger and oldest-age groups of females (Fig. 5). indicates that senescence does not contribute to mortality rate.

## 4.6. Comparison Blanding's turtle

That Painted Turtles exhibit indeterminate growth, whereas Blanding's Turtles do not, appears to be a primary mechanism contributing to other differences between the species in relationships between reproductive traits and age. An important mechanism for increasing reproductive output in both species is increased reproductive frequency in the older females (increases in

Table 4
Comparison of traits of Painted and Blanding's Turtles supporting the Relative reproductive rate (RRR) and senescence (SEN) Hypotheses of aging (~ indicates a result that had potential sample bias)

| Traits | Painted Turtles | | Blanding's Turtles | |
|---|---|---|---|---|
| | RRR | SEN | RRR | SEN |
| Growth as adults | YES | NO | NO | NO |
| Adult body size | YES | NO | NO | NO |
| Clutch size | NO | NO | YES | NO |
| Egg size | YES | NO | NO | NO |
| Reproductive frequency | YES | NO | YES | NO |
| Nest destruction | NO | NO | ~YES | NO |
| Embryo mortality | YES | NO | NO | ~YES |
| Adult survivorship | YES | NO | YES | NO |

production of second clutches within a season in Painted Turtles and increases in reproduction among years in Blanding's Turtles). Painted Turtles also increased off-spring quality (egg and hatchling size) with age, whereas Blanding's Turtles did not. For both species, no reduction in survivorship was found in the oldest individuals compared to younger individuals (Table 4).

## 5. Conclusions

The oldest age Painted Turtles and Blanding's Turtles on the ESGR are respectively, now more than 55 and 65 years old. Compared to younger individuals in the populations, the majority of reproductive traits of the oldest females support predictions made by the Relative Reproductive Rate Hypothesis. Older females apparently support some of the increased allocation of resources to reproduction by reducing body growth rates; however, that reduction does not seem adequate to explain the total increase in reproductive allocation. In addition, older Blanding's turtle females also have increased reproductive output compared to younger females, and they do not exhibit indeterminate growth. Lifetime reproductive output of older Painted and Blanding's Turtles was also indirectly enhanced through their prolonged reproductive longevity. Traits that increase the proportion of late versus early births in Painted and Blanding's Turtles remain detectable in the oldest females in the population, and will probably remain detectable until the female dies.

## Acknowledgements

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