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Growth, Reproduction, and Survivorship in the Red-Eared Turtle, *Trachemys scripta elegans*, in Illinois, with Conservation Implications

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ABSTRACT. – **Recaptures of nesting female turtles, *Trachemys scripta elegans*, in Illinois marked more than 20 years ago demonstrate a minimum adult survivorship of 85.2% per year. Age estimates based on plastron length were not reliable. Slow growth of some individuals of known age resulted in 50% underestimates of age. Mean clutch size was identical in known-age turtles and females of unknown age. Recaptured known-age turtles and larger newly marked turtles produced both more and larger eggs than did smaller newly marked turtles. Increased adult mortality of larger turtles whose reproductive output is positively correlated with female size may lead to reduction in number, size, and survivability of hatchlings per female produced in the population because the remaining females are smaller. Programs to compensate for adult losses by head starting hatchlings or otherwise artificially decreasing hatchling mortality may not be as effective in mitigating population decline as programs to prevent adult losses.**

KEY WORDS. – **Reptilia; Testudines; Emydidae; *Trachemys scripta*; turtle; ecology; long-lived vertebrates; survivorship; egg size; hatchling size; reproduction; growth; conservation; Illinois; USA**

Turtles are among the longest lived vertebrates (Gibbons, 1987). However, since few long-term mark and recapture studies have been conducted on chelonians, demographic patterns are known in detail for only six species: *Kinosternon subrubrum*, *Trachemys scripta scripta*, and *Deirochelys reticularia* (Gibbons, 1987; Frazer et al., 1991a); *Chrysemys picta* (Frazer et al., 1991b); *Emydoidea blandingii* (Congdon et al., 1993; Herman et al., 1994); and *Chelydra serpentina* (Galbraith and Brooks, 1987; Congdon et al., 1994). Congdon et al. (1993, 1994) pointed out some of the implications such studies have for the conservation biology of chelonian species. Because increased loss of reproducing adults can only be compensated for by an increase in the relatively high juvenile survival rate in aquatic habitats (e.g., Frazer et al., 1990; Congdon et al., 1993), increases in chronic or acute adult mortality can cause populations to become unstable (Congdon et al., 1993, 1994; Herman et al., 1994).

Because so few long-term studies of survivorship have been published, we report on survivorship, reproduction, and long-term growth of females of the red-eared turtle (*Trachemys scripta elegans*) from west-central Illinois originally marked in the 1970s and recaptured some 20 years later. We suggest that differential loss of larger or older adult females could lead to lowered survivorship of hatchlings produced by the remaining smaller or younger turtles.

MATERIALS AND METHODS

Turtles were collected in or near Stump Lake, a backwater of the Illinois River (Jersey County, Illinois, 39°18'04"N, 90°29'42"W). Turtles were originally collected by D. Moll in the 1970s with baited hoop traps (Legler, 1960) and marked by marginal notching (Cagle, 1939). Plastron length (PL, to 1 mm) was measured, the sex was recorded if possible, and maturity (i.e., adult or subadult) estimated. Turtles were recaptured by J.K. Tucker in 1994 and 1995 at a nesting area near Stump Lake. Because all recaptures were of turtles judged to be adult or subadult females in the 1970s, we did not include the number of juveniles nor the number of males in the total number of turtles available to be recaptured in the 1994–95 collections.

Juvenile and female turtles were also collected in 1994 by J.K. Tucker to determine growth pattern. These turtles were collected in Stump Lake with baited hoop traps, unbaited minnow fyke nets, and unbaited Wisconsin-style fyke nets. Trap bait consisted of dead fish, primarily gizzard shad (*Dorosoma cepedianum*) or canned sardines (Ernst, 1965). We determined age for turtles trapped in 1994 using counts of plastron annuli on the right abdominal scute (Tucker et al., 1995a). Measurements (to 0.1 mm) were limited to annuli that represented a full season's growth (i.e., partial growth in the 1994 season itself was not recorded). No evidence of year-to-year variation in growth was found among females in age classes 3–6 where sufficient turtles were available to test for such variation (Tucker et al., 1995b). Because most males at the study area matured in their third or fourth full season of growth (Tucker et al., 1995a), age classes 1–3 contained all juveniles not identifiable as males based on secondary sexual characteristics.

Original ages at initial capture of 1970s females were estimated by assigning each turtle to the currently determined age class (Table 1) whose mean PL most closely approached the PL at initial capture of that turtle, an adaptation of Sexton's (1959) method. The estimated present age of each turtle then equalled the assigned age class plus the number of years between initial and recent recapture. This method is conservative because it tends to underestimate the age of a particular female (Frazer et al., 1990), in that age is not necessarily directly size-related and larger turtles may be younger than smaller ones.

To investigate the effect of size and possibly age on reproduction, we divided the sample of newly captured turtles into those with PL less than 211 mm (the approximate asymptote of plastral growth) and those greater than 211 mm. We presumed that small newly captured turtles would include most of the younger turtles, whereas large newly captured turtles would include mostly older turtles more comparable to the recaptured turtles. However, some error is certain as 3 of 9 recaptured turtles known to be at least 20 yrs old were less than 211 mm in PL. We compared reproductive output of the resulting three classes of turtles overall: small newly captured turtles ($n = 68$), large newly captured turtles ($n = 94$), and small and large recaptured turtles ($n = 9$).

We determined egg and hatchling mass (to 0.01 g) with a Sartorius electronic balance. Egg length and width and hatchling carapace length (CL) and width were measured with vernier calipers (to 0.1 mm). Eggs were incubated in various sized plastic boxes. We did not control incubation temperature but recorded it daily with minimum–maximum thermometers placed next to the boxes. Estimated mean incubation temperature ranged from 26.2 to 29.9°C using the method of Godfrey and Mrosovsky (1994).

In 1994 eggs were incubated on moist perlite ranging in water potential from –60 to –189 kPa, with most at –92 kPa as determined by psychrometry. In 1995 eggs were incubated on moist vermiculite of either –150 or –950 kPa, with most on the wettest substrate. Because some of these eggs were used in experiments that caused mortality we did not compare hatching rates. In both years eggs were obtained by inducing oviposition with oxytocin (Ewert and Legler, 1978).

Because two turtles were recaptured nesting in successive years, sample size is 11 for clutch, egg, and hatchling parameters, whereas it is 9 for female parameters based on the most recent recapture. We combined data from 1994 and 1995 recaptures for comparison to combined data for 175 clutches from 162 newly captured female turtles caught nesting at the same site in 1994 ($n = 48$) and 1995 ($n = 127$, including 13 recaptured from 1994).

We used SAS (SAS Institute, 1988) to analyze our data. Statistical analysis for hatchling and egg parameters were of the means for clutches from individual turtles. Because some data classes were not normally distributed, we used Spearman's rank correlation and the NPAR1WAY procedure with the Wilcoxon option (SAS Institute, 1988) to perform Kruskal-Wallis tests (= KW with degrees of freedom shown as a subscript) to compare means. In most cases variables were correlated to plastron length of the turtle. However, we did not use analysis of covariance to remove the effect of female body size because our purpose was not to characterize relative reproductive output but to evaluate the actual nature of the eggs and resulting hatchlings produced by the recaptured turtles.

The sequential Bonferroni method was employed to avoid overall type I errors for multiple comparisons (Rice, 1989). In the text means are accompanied by ± one standard deviation followed by the range in parentheses.

Table 1. Plastron length by age class determined by annuli counts from juvenile and female *Trachemys scripta elegans* trapped in Stump Lake, Illinois, in 1994.

Year Class	Mean Plastron Length	Range	n
1	49.1	42-55	12
2	70.4	60-89	16
3	103.4	88-118	24
4	130.2	106-151	24
5	152.1	130-181	16
6	167.8	151-186	9
7	186.4	173-205	7
8	199.5	180-212	4
9	206.3	198-214	3
10	215.0	208-222	2
11	218.6	218.6	1
12	225.6	225.6	1

RESULTS

Nine of 306 turtles (2.9%) classified as adult or subadult females when initially marked in 1972, 1974, and 1975 were recaptured in 1994 ($n = 5$) and 1995 ($n = 6$) while attempting to nest. We estimated survivorship by back-calculating the survivorship rate required to have 9 turtles remaining from the original cohort of 306 turtles marked in the 1970s. Because we were not able to separate mortality from emigration and because the interval from initial capture to recapture was long, the resulting 85.2% per year survivorship represented an estimate of mimimum adult survivorship.

We estimated long-term growth rates for the 9 recaptured turtles. When initially marked in the 1970s, the 9 recaptured turtles had a mean PL of 181.6 ± 22.6 mm (150–205 mm). When recaptured, they had increased in PL by a mean of 34 ± 18.7 mm (7–68 mm) to a mean PL of 215.5 ± 8.8 mm (204–229 mm) (Table 2). The mean estimated age for the 9 recaptured turtles was 29.1 ± 1.7 yrs (26–32 yrs), whereas the mean interval between initial capture and most recent recapture was 21.7 ± 1.4 yrs (20–23 yrs). During these 21.7 yrs, the PL of the 9 turtles increased at an estimated rate of 1.6 ± 0.8 mm/yr (0.3–3.0 mm/yr).

Recaptured turtles did not differ from newly captured turtles (Table 2) in PL ($KW_1 = 0.59$, $p = 0.4441$) or body mass ($KW_1 = 0.76$, $p = 0.3846$). Clutch size ($KW_1 = 0.59$, $p = 0.4419$) and egg size (mass, $KW_1 = 2.29$, $p = 0.1303$; length, $KW_1 = 0.51$, $p = 0.4739$; width, $KW_1 = 3.51$, $p = 0.0609$) of recaptured and newly captured turtles also did not differ nor did hatchling size (mass, $KW_1 = 0.32$, $p = 0.5726$; CL, $KW_1 = 0.64$, $p = 0.4238$, carapace width, $KW_1 = 0.45$, $p = 0.5017$). The recaptured turtles were representative of the population as a whole in both size and reproductive characteristics.

However, female PL was correlated with clutch size ($r = 0.31$, $p < 0.0001$), mean egg mass ($r = 0.51$, $p < 0.0001$), mean egg length ($r = 0.38$, $p < 0.0001$), mean egg width ($r = 0.48$, $p < 0.0001$), mean hatchling mass ($r = 0.43$, $p < 0.0001$), mean hatchling CL ($r = 0.44$, $p < 0.0001$), and mean hatchling carapace width ($r = 0.39$, $p < 0.0001$). Conse-

Table 2. Reproductive parameters of *Trachemys scripta elegans* in Illinois in 1994–95 for 11 clutches from 9 recaptured females compared to 175 clutches from 162 newly captured females with larger and smaller turtle cohorts from the newly captured turtles. Sample sizes for eggs and hatchlings are numbers of clutches produced and hatched, respectively. PL = plastron length, CL = carapace length, CW = carapace width.

		Females	Clutch	Eggs			Hatchlings		
Capture Status		PL (mm)	Size (eggs)	Mass (g)	Length (mm)	Width (mm)	Mass (g)	CL (mm)	CW (mm)
Recaptures	mean	215.5	15.1	11.39	36.0	23.0	7.92	30.6	28.8
	SD	8.8	2.5	1.42	2.3	0.7	1.13	1.3	1.5
	range	204-229	12-20	9.52-13.55	32.2-39.6	22.1-24.2	5.96-9.92	28.3-33.1	26.6-31.9
	n	9	11	11	11	11	11	11	11
All New	mean	213.5	14.5	10.55	35.4	22.3	7.63	30.0	28.4
	SD	14.0	3.9	1.60	2.0	1.4	1.17	1.7	1.6
	range	167-240	6-27	6.04-13.45	28.4-39.8	18.0-25.4	3.37-10.02	22.5-33.8	21.8-31.5
	n	162	175	175	175	175	145	145	145
Small New	mean	199.7	12.9	9.61	34.5	21.5	7.09	29.3	27.7
	SD	9.8	3.2	1.69	2.2	1.9	1.30	1.9	1.7
	range	167-210	6-18	6.04-12.88	28.4-38.7	18.0-25.4	3.37-10.02	22.5-33.8	21.8-31.3
	n	68	68	68	68	68	58	58	58
Large New	mean	222.4	15.6	11.15	36.0	22.8	7.99	30.5	28.8
	SD	7.9	3.9	1.21	1.6	1.0	0.92	1.2	1.2
	range	211-240	7-27	8.04-13.45	32.6-39.8	19.3-25.3	5.87-9.84	27.3-32.6	25.4-31.5
	n	94	107	107	107	107	87	87	87

quently, smaller and possibly younger newly captured turtles may have differed from the recaptured turtles, which were known to be more than 20 yrs old.

In accord with the significant correlations between female size and reproductive output, we found that smaller newly captured turtles produced fewer eggs per clutch ($KW_2 = 18.19$, $p < 0.0001$) than did larger newly captured turtles and the recaptured turtles. Eggs of newly captured small turtles were also smaller (mass, $KW_2 = 36.17$, $p < 0.0001$; length, $KW_2 = 20.69$, $p < 0.0001$; width, $KW_2 = 34.53$, $p < 0.0001$) than those of newly captured larger turtles and recaptured turtles. Moreover, the hatchlings from eggs laid by newly captured smaller turtles were smaller than those of newly captured larger turtles and recaptured turtles (hatchling mass, $KW_2 = 17.73$, $p < 0.0001$; hatchling CL, $KW_2 = 18.87$, $p < 0.0001$; hatchling carapace width, $KW_2 = 16.97$, $p < 0.0002$). Clutches, eggs, and hatchlings of larger newly captured turtles and the recaptured turtles (Table 2) did not differ from each other (all KW_1 with $p > 0.05$).

DISCUSSION

While we cannot compute a life table for the turtles in the study area, the 85.2% per year adult survivorship rate for *Trachemys scripta elegans* from Illinois is similar to the 81.7% per year computed for *T. s. scripta* from South Carolina by Frazer et al. (1990) and 83% per year for *Chrysemys picta* from Michigan by Frazer et al. (1991b), but different from those published for *Emydoidea blandingii* (Congdon et al., 1993; 93.5%) and *Chelydra serpentina* (Galbraith and Brooks, 1987, and Congdon et al., 1994; 97%). This is interesting in that the lentic habitats occupied by *T. s. scripta* in South Carolina and the marsh habitat of Michigan *C. picta* differ considerably from the large river backwater habitat of the Illinois *T. s. elegans*. Of course, ours is a minimum estimate of survivorship because we cannot distinguish between the effects of mortality and emigration. However, this was also largely true for the survivorship determinations made by Frazer et al. (1990).

Our data also have a bearing on studies of growth in this and possibly other turtle species. We found some recaptured turtles with a minimum age of 20 yrs to be as small as 204 mm in PL. However, our growth data (by annuli) suggest that the age of such small turtles could also be on the order of 9 yrs (Table 1). Clearly, growth rates constructed from plastral annuli counts are not reliable tools to estimate the age of turtles once they are more than a few years old (Jones and Hartfield, 1995). Furthermore, the error introduced by use of growth rates can be large and would have exceeded 50% in 3 of 9 turtles we recaptured. We suggest that only long-term mark and recapture studies can be used to accurately establish ages for turtles without clearly defined annuli.

Like other studies of known-age turtles (e.g., Congdon et al., 1993, 1994; Herman et al., 1994), we found no evidence of reproductive senescence among the 9 females from which we examined clutches, contrary to the findings of Cagle (1950). Clutch, egg, and hatchling sizes from recaptured turtles were statistically equivalent to the entire sample of turtles. Moreover, they were higher than those observed for smaller turtles, which is consistent with the underlying size correlations.

Our study suggests that the fallacy of a "sustainable harvest of long-lived organisms," so aptly pointed out by Congdon et al. (1993), may be especially true for species such as *T. scripta* where larger turtles produce not only more eggs but larger ones as well. Removal of larger females can only be compensated for by artificially increasing hatchling and juvenile survivorship with head-starting or predator removal programs, but such programs may be minimally effective since juvenile survivorship in aquatic habitats is often already high in most species (Congdon et al., 1993, 1994).

Removal of larger (and possibly older) adult females might have additional effects not previously pointed out in other studies. First, the number of hatchlings may be reduced because smaller females lay fewer eggs per clutch. Second, because smaller females also lay smaller eggs, hatchling size may decline. The size of hatchlings may directly affect their survival once they leave the nest and grow (e.g., Miller et al., 1987; Brooks et al., 1991; Janzen, 1993a, 1993b; Miller, 1993). In addition, smaller eggs may be less likely to hatch, particularly when incubation conditions are not optimal (Gutzke and Packard, 1985), further reducing recruitment. Thus, both lower recruitment and reduced survivability of hatchlings may occur as a result of differential mortality on large adults in species whose egg size is related to female size. Artificial efforts to increase the number of hatchlings entering the system may be partially compromised if differential adult mortality leads to a reduction in average female size.

The additional effects that we noted are not necessarily limited to *T. scripta*. Positive correlations between one or more egg parameters and female size have been reported for a number of other species and in other studies of *T. scripta* (e.g., Congdon and Gibbons, 1983; Gibbons and Greene, 1990; Mitchell and Pague, 1990). Other species of turtles for which a correlation between female size and one or more egg size parameters has been reported include *Chrysemys picta* (Tucker et al., 1978; Congdon and Tinkle, 1982; Schwarzkopf and Brooks, 1986; Congdon and Gibbons, 1985, 1987; Mitchell, 1985a; Iverson and Smith, 1993; Rowe, 1994, 1995); *Clemmys guttata* (Ernst, 1970) and *C. insculpta* (Brooks et al., 1992); *Deirochelys reticularia* (Congdon et al., 1983; Congdon and Gibbons, 1987); *Graptemys pseudogeographica* and *G. ouachitensis* (Vogt, 1980); *Malaclemys terrapin* (Montevecchi and Burger, 1975); *Chelydra serpentina* (Yntema, 1970); *Gopherus polyphemus* (Landers et al., 1980); *Mauremys leprosa* (Da Silva, 1995); *Testudo hermanni* (Swingland and Stubbs, 1985; Hailey and Loumbourdis, 1988) and *T. graeca* (Hailey and Loumbourdis, 1988); *Sternotherus odoratus* (Risley, 1933; Tinkle, 1961; Mitchell, 1985b) and *S. minor* (Cox and Marion, 1978); and *Kinosternon sonoriense* (Hulse, 1982), *K. subrubrum* (Congdon and Gibbons, 1985), *K. flavescens* (Long, 1986; Iverson, 1991), and *K. hirtipes* (Iverson et al., 1991; Ernst et al., 1994). Although this relationship is better established in some of these species than in others, it seems particularly common among smaller emydid and kinosternid turtles. Several species in these two families are endangered or threatened in parts or all of their ranges. Reduction of large adult mortality, not improvement of hatchling numbers, may be particularly important in designing conservation programs for such species.

Although *Trachemys scripta* is a widely distributed species in North America (Ernst et al., 1994), our findings bear directly on the possible impact of the international trade in this species. As many as 100,000 adult *T. s. elegans* may be collected annually from the wild for "breeding" operations (these "farms" are not closed-end operations, thus the quotes) that supply hatchlings to the international pet market (Warwick, 1986; Warwick et al., 1990). A further 765,000 adults are taken annually for export for human consumption (Warwick et al., 1990). The turtles most in demand for human exploitation, large adult females, are the ones that most populations can least afford to lose if they are to remain stable.

Removal of adult females by artificial or natural means (e.g., Turner et al., 1984; Peterson, 1994) is the functional equivalent of complete clutch failure for the year that the particular female was removed and in all subsequent years. Clutch failure has been shown to lead to lower heterozygosity, higher inbreeding, and greater degrees of co-ancestry in *Chrysemys picta* (Scribner et al., 1993). Consequently, removal of females may also directly impact the genetic base of the population or species which may further slow recovery if exploitation is reduced or regulated.

We suggest that removal of large breeding females may make it more difficult for a population to recover even when exploitation is regulated. Although growth of subadults and small adults into large turtles might ameliorate this loss, it may still take up to 20 years to replace the larger females which we found produced larger hatchlings. Even when such hatchlings are produced, fewer than 2% may survive to an age of 20 yrs (Frazer et al., 1990). Sufficient information is available on the demographics of long-lived vertebrates and the importance of maintaining population age structure and genetic diversity to justify conserving the life-stage segments critical to their continued existence.

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