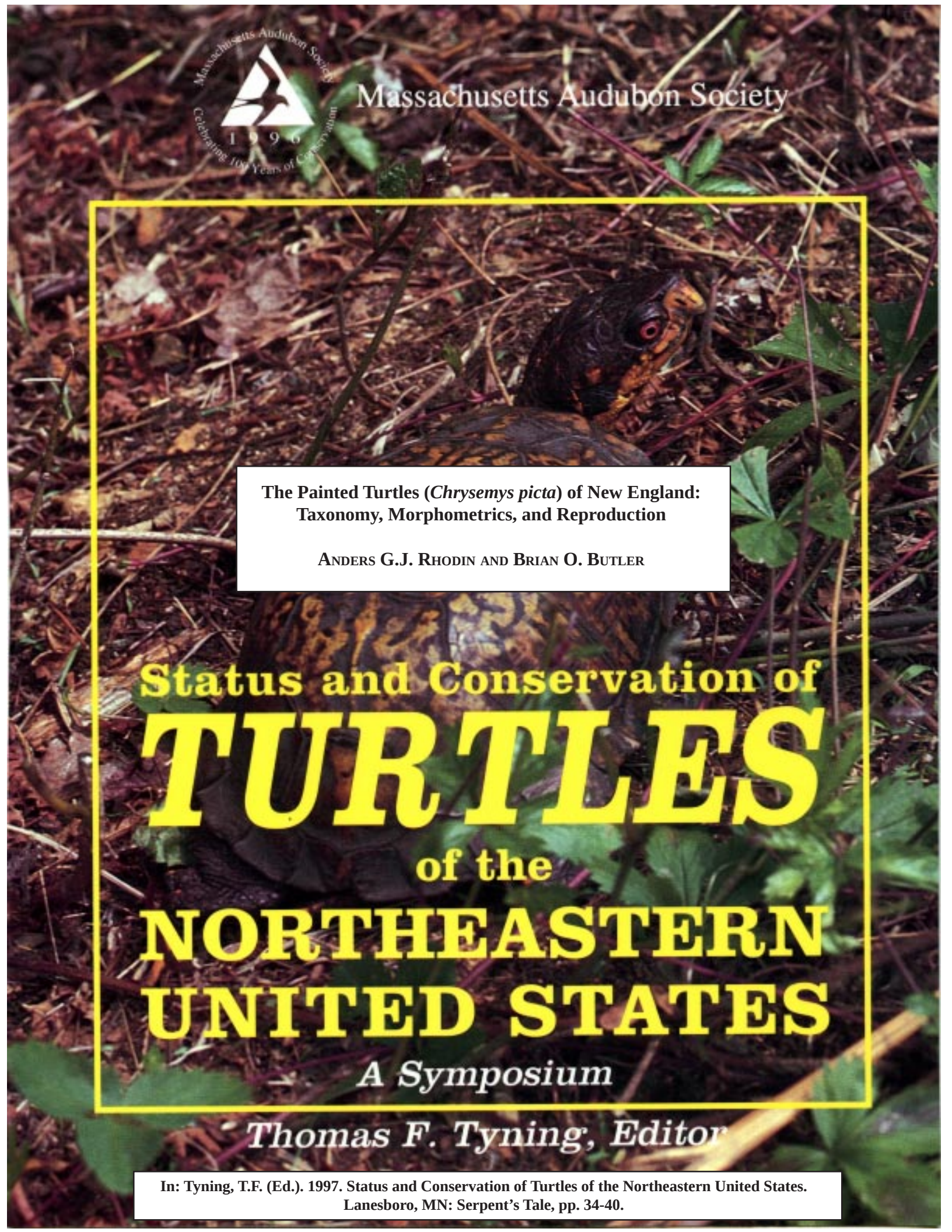

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The Painted Turtles (*Chrysemys picta*) of New England: Taxonomy, Morphometrics, and Reproduction

ANDERS G.J. RHODIN AND BRIAN O. BUTLER

Status and Conservation of TURTLES of the NORTHEASTERN UNITED STATES

A Symposium

Thomas F. Tyning, Editor

In: Tyning, T.F. (Ed.). 1997. Status and Conservation of Turtles of the Northeastern United States. Lanesboro, MN: Serpent's Tale, pp. 34-40.

THE PAINTED TURTLES (*CHRYSEMYS PICTA*) OF NEW ENGLAND: TAXONOMY, MORPHOMETRICS, AND REPRODUCTION

Anders G. J. Rhodin, Chelonian Research Foundation, 168 Goodrich St., Lunenburg, MA 01462 and **Brian O. Butler**, Oxbow Wetlands Assoc. Box 1734, Lunenburg, MA 01462

The painted turtle (*Chrysemys picta*) is certainly neither endangered nor threatened in Massachusetts and New England but instead is our most common and visible turtle species. This small, colorful turtle of the family Emydidae occurs throughout most of northern and eastern North America, ranging from Nova Scotia in the northeast to British Columbia in the northwest, and extending southward to Louisiana in the southwest and Georgia in the southeast. Four subspecies are currently recognized, with two of those occurring in New England: the midland painted turtle (*C. p. marginata*) and the eastern painted turtle (*C. p. picta*).

The painted turtles in this region were first "discovered" about 5,000 to 6,000 thousand years ago by prehistoric Native Americans who used all local turtle species for food. Midden finds of painted turtle bones confirm that they were extensively utilized by people as food, and numerous prehistoric sites in eastern New England have yielded remains of painted turtles (Rhodin 1992).

The first European to describe the painted turtle was Albert Seba, an 18th-century Dutch pharmacist with a large natural history collection. In 1734, Seba published a thesaurus of his natural history observations, in which he illustrated the different species of turtles in his collection. One of these was clearly the eastern painted turtle, described by Seba as *Testudo ex Nova Hispaniae*, the "turtle from New Spain" (Fig. 1). Seba's work, however, preceded the establishment of our modern system of taxonomic nomenclature, created in 1758 by the Swedish naturalist Carl Linnaeus. Linnaeus did not recognize Seba's turtle names, and the name "New Spain turtle" receded into the historic dustbin of pre-Linnaean nomenclature. In 1783, the German turtle specialist Johan Schneider finally recognized the species as distinct and named it *Testudo picta*, the "painted turtle," but mistakenly thought that it came from England. Over the next 70 years, it became clear that the painted turtle was actually from "New England," and a widespread North American species. During this time the species was first reassigned to the genus *Emys* and then finally to its present genus, *Chrysemys*.

In 1857, Louis Agassiz, the Swiss naturalist who emigrated to this country and established the Agassiz Museum of Comparative Zoology at Harvard University in Cambridge, recognized that there was extensive geographic variation in the widespread species *Chrysemys picta*, and described the new species *Chrysemys marginata* from the Midwest, restricting *C. picta* to the East Coast. Finally, in 1931, Bishop and Schmidt in Chicago recognized that all painted turtles were actually subspecies of each other, and our modern view of these animals was established. They showed that the midland painted turtle, *C. p. marginata*, had staggered vertebral-costal sutures, a narrow costal bar, and a prominent plastral figure, whereas the eastern painted turtle, *C. p. picta*, had aligned vertebral-costal sutures, a wide costal bar, and an immaculate plastron without a figure.

The geographic ranges of the two subspecies both extend into the New England region, with midland painted turtles in general occupying a few western and northern ar-

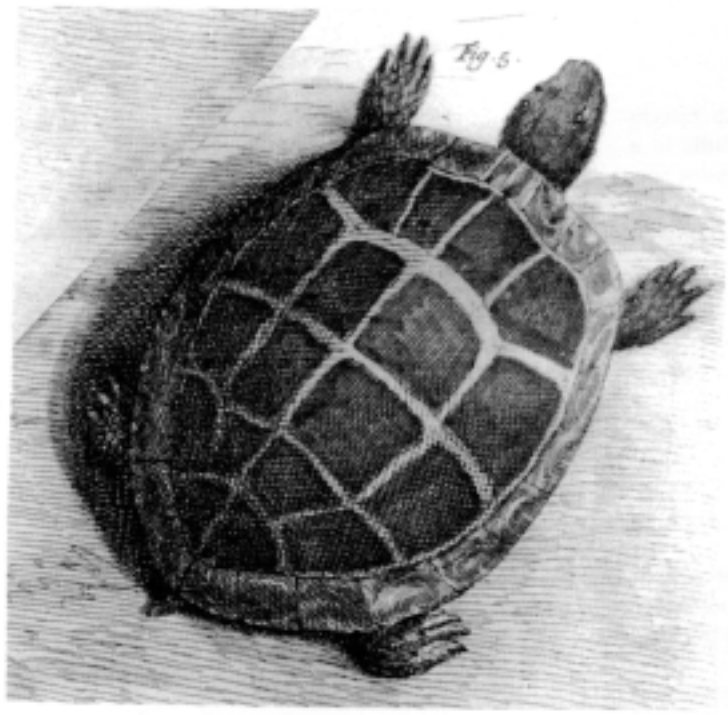

Figure 1. Illustration of *Chrysemys picta picta* from Seba (1734; Plate 80, Fig. 5), showing typical subspecific features of vertebral-costal scute alignment (0% costal disalignment) and broad costal bars.

eas and eastern painted turtles occupying most of the southern and eastern areas. A broad zone of hybridization occurs where these two subspecies intergrade in the New England region. The location, extent, and nature of this zone of hybridization has been the source of long-standing and significant confusion, with varying views presented by different researchers.

In 1958, Hartman devised a method of measuring the degree of vertebral-costal scute disalignment as a way of distinguishing *C. p. marginata* from *C. p. picta*, and of quantifying the amount of *marginata-picta* intergradation in any individual population. By this method, *marginata* has costal disalignment approaching 100 percent, whereas *picta* has disalignment approaching 0 percent. What this means is that *marginata* has staggered vertebral-costal scutes, whereas *picta* has aligned scutes.

This analysis method was applied by Waters in 1964 to the painted turtles of Nantucket Island, Massachusetts, where he noted that these animals had a high degree of *marginata* features, including a high costal disalignment percentage and the occasional presence of large plastral figures (midland painted turtles all have plastral figures, eastern painted turtles have none). No painted turtles with such pronounced *marginata* features had ever been recorded so far east and south in New England, and Waters concluded that they represented a relictual population of *marginata-picta* intergrades.

Table 1. Morphometrics of 883 *Chrysemys picta* from central Massachusetts. Males (n = 511), females (n = 287), and hatchlings (n = 85). No data provided on juveniles (carapace lengths 28 – 94 mm). Lengths in mm, mass in g.

	x	S.D.	Range
Carapace length			
males	120.8	10.4	95.0 – 147.0
females	135.1	13.8	98.2 – 169.6
hatchlings	25.5	1.4	21.0 – 27.2
Body mass			
males	198	46	105 – 340
females	320	91	125 – 555
hatchlings	4.5	0.6	3.0 – 5.4

As a result of his observations, Waters advanced the hypothesis that painted turtles dispersed into New England in several stages. During the last glaciation circa 12,000 years ago, when most of New England was ice covered, eastern painted turtles were isolated in a refugium along the southern emergent continental shelf east of the Appalachians, possibly down around Georgia, and midland painted turtles were isolated in their own refugium west of the Appalachians in the southern Mississippi valley (Fig. 2A). As the glaciers receded and the climate warmed, both subspecies began to disperse northward, with midland painteds coming up the Mississippi and Ohio River valleys, reaching the Great Lakes region, and then extending eastward into eastern Canada and northern New England. At the same time, eastern painteds were expanding their range up the eastern seaboard and exposed continental shelf. Present distributional patterns for the two subspecies demonstrate that midland painted turtles are much more cold tolerant than eastern painteds, and are less limited by extremely cold conditions. Therefore, it is reasonable to postulate that midland turtles would have successfully invaded the colder climatic regions of New England prior to eastern painted turtles (Fig. 2B). As the climate in New England continued to improve over the millennia, eastern painted turtles also began to disperse into the region, now coming into contact with and intergrading with the resident population of midland painted turtles. This led to a broad zone of intergradation between the two subspecies, with the intergrade range including those coastal areas that at the time were exposed due to glacially induced sea level recession and postglacial coastal rebound (Fig. 2C). Over the next several thousand years, sea levels rose again, and many coastal peninsular regions became islands, thereby isolating their resident populations of intergrade painted turtles. At the same time, the climate had continued to improve in New England, and an ever-increasing influx of eastern painted turtles from the south had begun to genetically swamp out the remaining mainland populations of midland-eastern intergrades. Gradually, the mainland populations began to lose their midland painted characteristics and became more and more typically eastern painted in appearance. The zone of subspecies intergradation gradually receded toward western and northern New England as eastern painteds made their way up the coastal plain, leaving a few relictual populations of higher-degree *marginata* intergrades on Nantucket and other coastal islands (Fig. 2D).

Table 2. Reproductive data on female *Chrysemys picta* from central Massachusetts. Data based on measured females with eggs (n = 104), counted clutches (n = 105), measured clutches (n = 23), counted eggs (n = 709), and measured eggs (n = 143). Lengths in mm, mass in g. Relative clutch mass (n = 22) expressed as percent of spent body mass (= gravid body mass – clutch mass).

	x	S.D.	Range
carapace length	142.2	7.7	118.5 – 158.0
plastron length	134.8	7.5	113.0 – 152.0
gravid body mass	384	58	220 – 510
clutch size	6.75	1.3	4 – 10
clutch mass	38.2	6.4	23 – 48
mean clutch egg mass	5.7	0.5	4.5 – 6.5
mean clutch egg length	30.4	1.2	28.2 – 33.5
mean clutch egg width	17.6	0.6	16.4 – 18.5
relative clutch mass %	11.2	2.0	6.6 – 15.1

Figure 2. Rough approximations of the postglacial dispersal patterns of painted turtles in the New England region. The theoretical background is based on work by Waters (1964), but the current hypothesis reflects our own preliminary conclusions. **A**. Early postglacial (ca. 10,000 yrs ago) refugia for *Chrysemys picta marginata* (shaded) and *C. p. picta* (lined). Heavy line represents exposed continental shelf margin. Numbers refer to study populations of painted turtles: 1. Mount Desert Island (Rhodin, 1993); 2. Westminster; 3. Fort Devens; 4. Sudbury; 5. Nantucket (Waters, 1964); 6. Long Island (Pough and Pough, 1968); 7. northwestern New Jersey (Pough and Pough, 1968). **B**. Later postglacial (ca. 8,000 yrs ago) dispersal, with cold-tolerant *C. p. marginata* invading New England and exposed continental shelf margins prior to *C. p. picta*. **C**. Late postglacial (ca. 5,000 yrs ago) zone of high-degree hybridization between the subspecies as *C. p. picta* continued to invade from the south. **D**. Present hypothetical distribution of painted turtles in New England, with relictual populations of high-grade hybrids (significant *marginata*-influence) on islands and western mainland areas and low-degree hybrids (only slight *marginata*-influence) in most eastern mainland areas.

If this hypothesis of dispersal is correct, then one would expect to find an increased degree of *marginata-picta* intergradation in the isolated island populations of painted turtles along the entire coast of New England. Further, one would also predict that those islands isolated earlier in the postglacial period might have a higher degree of *marginata* influence than those islands isolated more recently. Additionally, those islands located farther north along the coast would be expected to have had a higher degree of *marginata* influence for a longer time before the wave of dispersing *picta* reached them from the south.

The Waters dispersal theory was challenged in 1968 by Pough and Pough, who also analyzed painted turtle populations from New England and could find no significant evidence of increased *marginata* intergrade influence in island populations as compared to mainland populations. They concluded that all New England painted turtles simply represented highly variable members of a hybrid swarm of the two intergrading subspecies. However, their study populations were small, with their main sample from Long Island, New York, numbering 72 animals, their mainland northwestern New Jersey sample numbering 26, the comparative Waters sample from Nantucket numbering 25 animals, and all other analyzed mainland

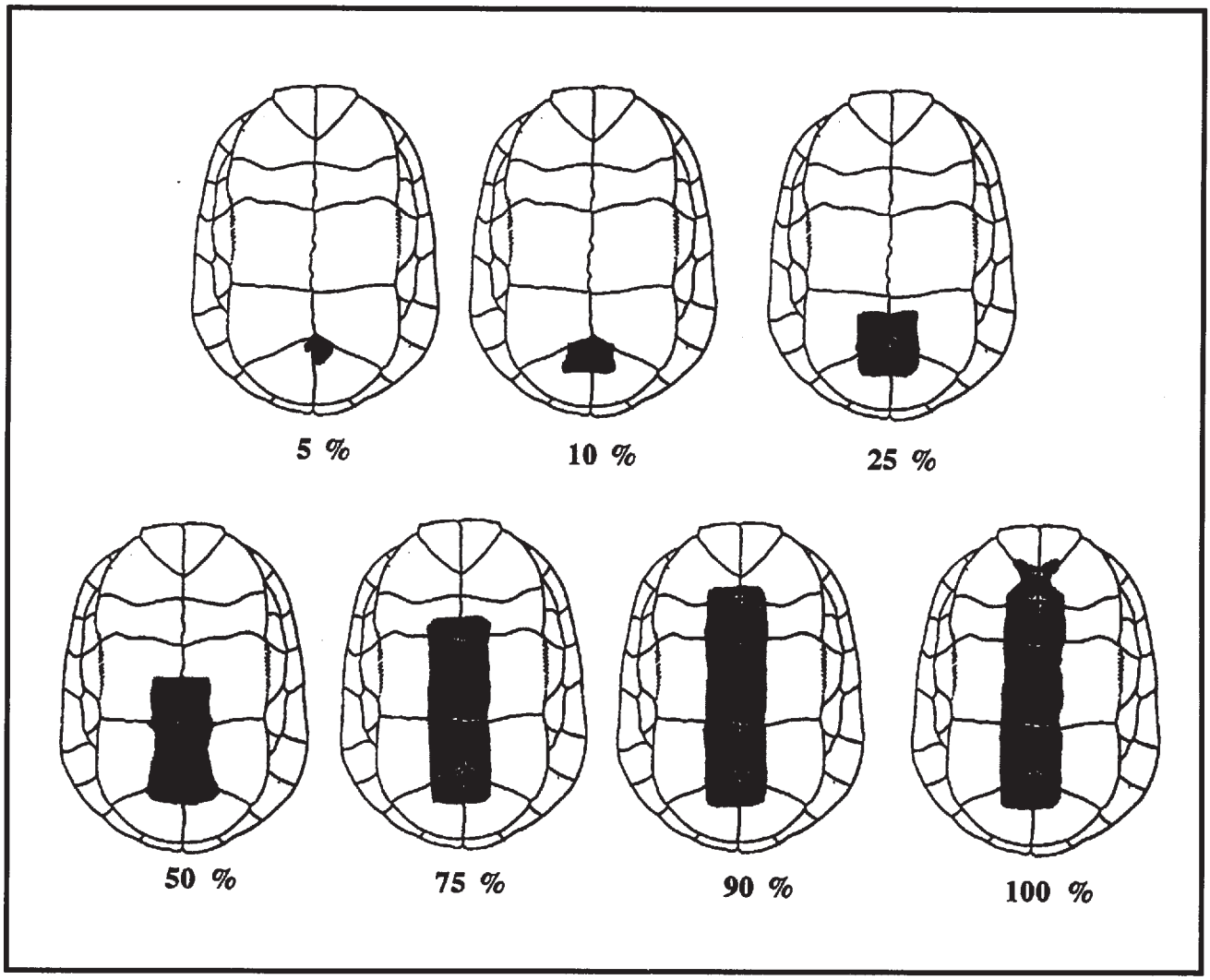

Figure 3. Measurement technique for determining plastral figure percent coverage. Pure *Chrysemys picta picta* typically has 0% coverage, pure *C. p. marginata* typically 100% coverage. Intermediate percentages to the nearest 10% interpolated between figures presented. Adjustments for discontinuous or faded figures are also incorporated. Separate areas of pigment are totaled, and very faded or narrow areas of pigment are adjusted (e.g., an animal with 50% overall pattern extent but with a very faded or narrow pattern is roughly adjusted to 25%). Deep subsurface areas of irregular melanistic smudges occurring in some animals are not counted as plastral pattern.

Table 3. Taxonomic, morphometric, and reproductive analysis of four separate populations of *Chrysemys picta* in central Massachusetts and southern New Hampshire. Population sizes: Massachusetts: 1. Fort Devens (n = 546), 2. Sudbury (n = 235), 3. Westminster area (n = 56); New Hampshire: 4. Epping area (n = 61). Results expressed as mean ± S.D., range, n for the individual data set, and ANOVA Fisher PSLD significant (S) or not significant (ns) differences at 95% confidence levels between the various populations (1:2, 1:3, 1:4, 2:3, 2:4, and 3:4). Lengths in mm, mass in g.

Feature	1 Fort Devens	2 Sudbury	3 Westminster	4 Epping
costal disalignment %	30.4 ± 15.6 5.8 – 79.9 n = 517 1:2 S 1:3 ns	26.6 ± 15.2 0.8 – 81.8 n = 233 1:4 ns 2:3 S	33.7 ± 17.1 9.3 – 85.6 n = 32 2:4 ns 3:4 ns	28.1 ± 14.7 6.9 – 66.7 n = 61
costal bar width	2.7 ± 0.7 0.9 – 6.2 n = 517 1:2 ns 1:3 S	2.7 ± 0.7 1.0 – 7.0 n = 233 1:4 S 2:3 S	3.1 ± 0.8 1.9 – 5.4 n = 32 2:4 ns 3:4 ns	2.8 ± 0.8 1.5 – 5.5 n = 61
plastral figure %	6.3 ±13.0 0 – 80 n = 545 1:2 S 1:3 S	5.5 ± 11.4 0 – 75 n = 235 1:4 S 2:3 S	5.0 ± 11.0 0 – 60 n = 48 2:4 S 3:4 S	7.8 ± 13.6 0 – 50 n = 61
plastral figure ≥ 15 % (% of pop.) plastral figure % in this group	15.9 31.6 ± 17.4 15 – 80 n = 82 1:2 S 1:3 S	15.3 27.2 ± 15.3 15 – 75 n = 36 1:4 S 2:3 S	10.4 32.0 ± 16.8 15 – 60 n = 5 2:4 S 3:4 ns	23.0 30.0 ± 12.1 15 – 50 n = 14
male carapace length	120.6 ± 10.7 95 – 147 n = 313 1:2 S 1:3 ns	120.8 ± 9.6 96.2 – 145.3 n = 177 1:4 S 2:3 ns	—[1] 2:4 ns 3:4 ns	126.2 ± 12.9 95 – 141.5 n = 33
female carapace length	133.7 ± 14.7 98.2 – 164 n = 187 1:2 ns 1:3 ns	137.7 ± 13.1 102.5 – 169.6 n = 52 1:4 S 2:3 ns	—[1] 2:4 ns 3:4 ns	144.9 ± 20.3 101.4–172.5 n = 25
male body mass	199 ± 49 105 – 340 n = 311 1:2 S 1:3 ns	195 ± 39 115 – 300 n = 177 1:4 ns 2:3 ns	—[1] 2:4 S 3:4 ns	240 ± 56 120 – 325 n = 33
female body mass	312 ± 98 125 – 555 n = 182 1:2 ns 1:3 ns	322 ± 81 130 – 550 n = 52 1:4 S 2:3 ns	—[1] 2:4 S 3:4 ns	426 ± 152 145 – 645 n = 25
nesting female carapace length	142.0 ± 8.7 118.5 – 158 n = 43 1:2 ns 1:3 ns	144.3 ± 7.6 132.5 – 156.5 n = 10 1:4 ns 2:3 ns	139.0 ± 6.3 129 – 155.5 n = 31 2:4 ns 3:4 S	152.1 ± 9.7 134 – 166.3 n = 11
nesting female gravid body mass	384 ± 67 220 – 510 n = 42 1:2 S 1:3 ns	373 ± 38 310 – 420 n = 10 1:4 S 2:3 ns	366 ± 47 265 – 485 n = 30 2:4 S 3:4 S	471 ± 88 340 – 625 n = 11
clutch size	6.8 ± 1.2 4 – 10 n = 43 1:2 S 1:3 ns	6.3 ± 1.2 5 – 8 n = 10 1:4 S 2:3 S	6.6 ± 1.3 4 – 9 n = 32 2:4 S 3:4 S	7.8 ± 2.1 5 – 12 n = 11

[1] Data for this population not included because of bias in collection method (primarily hand-collected nesting adult females), whereas the other three populations include primarily net-trapped animals of both sexes of all sizes.

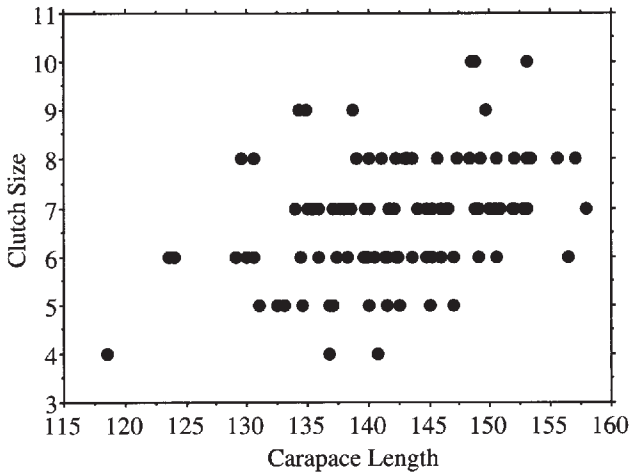

Figure 4. *Chrysemys picta* carapace length vs. clutch size relationship in central Massachusetts for $n = 104$ gravid females. Carapace length (total) $x = 142.2 \pm 7.7$ mm (range 118.5 – 158.0 mm); clutch size $x = 6.77 \pm 1.27$ (range 4 – 10); correlation $r = .382$, r-squared = .146.

populations significantly smaller. In addition, it is highly doubtful that Long Island represents a significantly isolated island population, and because of its relatively southern location would in fact be expected to harbor a primarily *picta* type population with only minimal *marginata* influence, probably no different from any typical mainland population.

To further analyze the zone of hybridization between the two subspecies, we have undertaken a comparative study of various populations of painted turtles in New England. We hope to avoid the problems of the Pough and Pough study by analyzing only large populations of animals to look for the kinds of minor differences that only become statistically significant in larger study samples. Work in Massachusetts and New Hampshire presented in this paper has yielded data on 995 painted turtles, including 546 from a population at Fort Devens in east-central Massachusetts, 235 from Sudbury in eastern Massachusetts, 56 from the Westminster region of west-central Massachusetts, and 61 from the Epping area of southeastern New Hampshire. Additional data is being concurrently gathered from populations in southern and eastern Maine, including island populations (Rhodin 1993; Rhodin and Mittelhauser 1994; Rhodin *in prep.*), as well as comparative material from other New England sites.

To document the degree of *marginata* vs. *picta* influence in any single study population, we measured the mean costal disalignment percent (Hartman 1958), the costal bar width (Hartman 1958), and the plastral figure percent coverage in all animals. This last feature has not previously been quantitatively analyzed, and we here introduce a method whereby it can be estimated. Specimens of pure *marginata* typically have a large plastral figure; pure *picta* have no figure. However, individuals often have reduced or partial figures indicating partial penetrance of the *marginata* phenotype. By estimating the percentage of figure presence in each individual specimen, a mean populational plastral figure percent may be determined (Fig. 3). Though subject to high variation and difficulty in estimating each individual accurately, when estimating percentages for large numbers of animals in different populations the means become statistically significant, and we have found this method extremely useful in delineating the degree of *marginata* influence in hybrid populations.

It is not our intent in this paper to give a full analysis of painted turtle variation in New England, but rather to provide baseline data for the Massachusetts and New Hampshire populations studied. This will facilitate further analysis as our data become more comprehensive and a more critical synthesis can be presented. In this paper we present data on subspecific taxonomic features and morphometrics of the populations studied, and include preliminary reproductive parameters as well.

Being a widespread species, *Chrysemys picta* demonstrates extensive geographic reproductive variation in such features as size and weight of nesting females, clutch size, egg length, egg width, and egg mass. Much of this geographic variation has recently been analyzed and summarized by Iverson and Smith (1993), but no data from populations anywhere in the New England area were available for their analysis. The data we present here provide an initial reference point for our local region in the ongoing study of the overall continentwide geographic variation in the reproductive ecology of painted turtles.

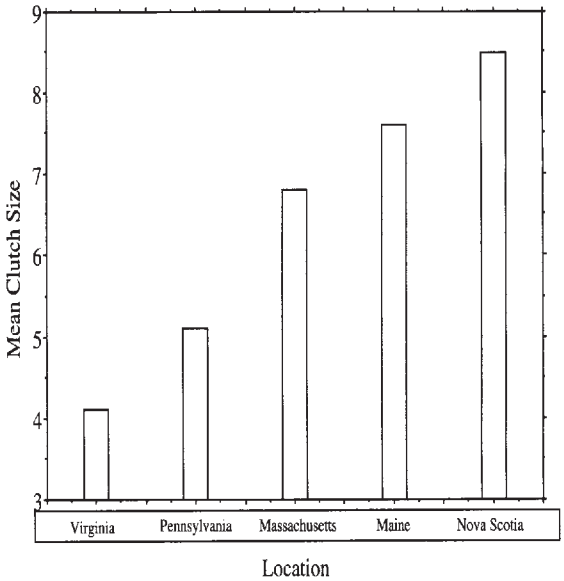

Figure 5. Geographic variation in clutch size for five populations of *Chrysemys picta* from eastern North America, arranged from south (Virginia) to north (Nova Scotia). Data for Massachusetts from present study, Maine data from Rhodin and Mittelhauser (1994), other locations summarized by Iverson and Smith (1993).

Our results are presented in Tables 1-3 and Figs. 4-5. Morphometrics of Massachusetts turtles are summarized in Table 1, reproductive parameters of Massachusetts turtles are in Table 2, and populational differences in taxonomic, morphometric, and reproductive characteristics of three discrete Massachusetts populations and one New Hampshire population are in Table 3. Egg clutch size vs. carapace length for Massachusetts females is shown in Fig. 4, with geographic variation of clutch size in eastern North America presented in Fig. 5.

In general, our populations in mainland Massachusetts and New Hampshire all exhibit a low degree of *marginata* influence in what appears to be populations of primarily *C. p. picta*. Preliminary analysis of populations on Mount Desert Island in midcoastal Maine show that those turtles exhibit a significantly higher degree of *marginata* influence than these southern mainland populations (Rhodin 1993; Rhodin *in prep.*). Based on these data, our preliminary hypothesis as to the distribution and extent of hybridization between the two subspecies of painted turtles in New England is summarized in Fig. 2D. Further work is clearly needed, and, with increasing numbers of painted turtle populations measured and characterized as to degree of *marginata* influence, we should be able to refine our view of the distribution, systematics, and dispersal history for these beautiful members of our New England fauna.

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