Ontogenetic Changes in Habitat Use by Juvenile Turtles, *Chelydra serpentina* and *Chrysemys picta*

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During a 10-year period approximately 1600 turtles were captured and 9500 recaptured in East Marsh on the E. S. George Reserve in southeastern Michigan. Analysis of the marsh depth at point of capture indicates that younger and smaller juvenile Snapping Turtles (*Chelydra serpentina*) and Painted Turtles (*Chrysemys picta*) were more likely than older and larger juveniles to be captured in shallow portions of the marsh. A relationship of increased water depth with turtle size and age continued through to sexual maturity. Hatchlings and one-year-old individuals occupied significantly shallower portions of the marsh than did all other size categories. By resticting their activity to shallow water near shore, younger and smaller turtles may increase their foraging success and reduce the probability of encountering large fish or adult turtle predators.

Key Words: Snapping Turtle, *Chelydra serpentina*, Painted Turtle, *Chrysemys picta*, habitat selection, juveniles, marsh depth.

Organisms produce offspring that are either very different in appearance from the adults, or that appear to be miniature adults. In organisms with complex life cycles, requirements of offspring are obviously different from those of adults (e.g., most frog larvae are aquatic herbivores, whereas adults are terrestrial predators). In contrast, organisms such as lizards and turtles produce young that are essentially miniature adults. Although less profound than the developmental changes observed in organisms with complex life cycles, differences in body size alone may also result in differences in both habitat requirements and diets of juveniles and adults. Differential habitat use associated with age or size of juveniles may result from changes in diet, distributions of food resources of appropriate sizes, size specific risks of predation, or a combination of these factors. Compared to adults, hatchlings of some freshwater turtles are found in shallow or more vegetated portions of marshes (*Emydoidea blanghgii*: Pappas and Brecke 1992), quiet or backwater portions of rivers (*Trachemys scripta*: Moll and Legler 1971; Hart 1983; *Trionyx muticus*: Plummer 1977; *Graptemys nigrinoda*: Lahanas 1982) or protected backwater sections and oxbow lakes (*G. nigrinoda*: Lahanas 1982). In addition, ontogenetic shifts in diet from carnivory as juveniles to primarily herbivory as adults has been reported for the Slider Turtle (*Trachemys scripta*: Clark and Gibbons 1969; Moll and Legler 1971; Hart 1983; Parmenter and Avery 1990), Ouachita Map Turtle (*Graptemys ouachitensis*: Moll 1976), Cooter (*Pseudemys floridana*: Bancroft et al. 1983), and Kefts River Turtle (*Emydura krefftii*: Georges 1982). Age related changes in diets in freshwater turtles suggest, but do not require, that associated changes in habitat use also occur during growth from hatchling to adult stages.

Because of difficulties in capturing hatchlings and small juveniles, most ecological and life history studies of freshwater turtles have concentrated on adults. As a result, the following questions remain: (1) are ontogenetic shifts in habitat use of sufficient magnitude to be considered important, and (2) are ontogenetic shifts in habitat use a widespread phenomenon? Previous studies of life histories of Snapping Turtles (*Chelydra serpentina*) and Painted Turtles (*Chrysemys picta*) (Congdon and Gatten 1989) on the E. S. George Reserve present an opportunity to examine the relationships between ages and sizes of juvenile turtles and marsh depth at the point of capture.

Materials and Methods

This study was conducted on the University of Michigan's E. S. George Reserve, Livingston County, Michigan (approximately 42°28'N, 84°00'W). Detailed descriptions of the habitats on the E. S. George Reserve are in Cantrall (1943), Sexton (1959), Wilbur (1975), Collins and Wilbur (1979), Congdon et al. (1986), and Congdon and Gibbons (1989). About 4.0 ha of water in East Marsh are deep enough to trap; an additional 1.5 ha of seasonally inundated wetland contain grass hummocks interspersed with shallow and narrow water channels. A grid system established in East Marsh in 1977 has marker stakes every 8 m in an X, Y array. In June of 1988, we measured water depth at all 117 grid stakes in East Marsh. Maximum water depth was about 90 cm; however, 70% of the marsh was less than 50 cm in depth (Figure 1).

Except during some nesting seasons when trapping was temporarily suspended, intensive aquatic trapping of East Marsh began in early May and continued through mid-September each year from 1977 through 1986. Turtle traps were either 80, 120 or 140 cm in diameter and consisted of three metal hoops overlain with 3.9 cm webbing which formed a funnel opening at one end. All sizes and types of traps caught all sizes of turtles except the smallest hatchlings. A minimum of 55 traps baited with fish or whole kernel corn were placed throughout East Marsh and trap locations were changed at approximately two week intervals. In addition, each year about 10 unbaited fyke and 15 drift traps were also placed in the marsh. These sets remained in place for the summer. Fyke sets consisted of 10 m long V-shaped wings made of 3.9 cm mesh netting suspended between floats and sinkers and attached directly to unbaited traps. Drift sets consisted of 15 m of netting suspended between floats and sinkers that was stretched between stakes to make an aquatic drift fence with unbaited traps at each end. Thus, about 80 traps were used in East Marsh each year; however, in 1985 and 1986 an extra 30 were set for the entire trapping season (see Congdon et al. 1983, 1987; Congdon and van Loben Sels 1991; for details about other capture methods).

About 1150 Painted Turtles (7200 recaptures) and 450 Snapping Turtles (885 recaptures) have been recorded in East Marsh. Data for the primary analyses for this study were restricted to six years from 1980 through 1986. Data from the years prior to 1978 were excluded because of lower trapping effort and data from 1978, 1979, and 1984 were excluded because of very low water levels during drought (see later discussion). Each captured turtle was individually marked, weighed, straight line plastron length (PL) and carapace length (CL) measured, and released at the grid stake nearest to the point of capture. If possible, the sex of each individual was determined from external examination. Complete measurements and weights of recaptured turtles were usually taken at the first recapture each year and again at the end of the activity season during September and October.

Because most older Snapping Turtles were of unknown age, all Snapping Turtles were first assigned to four categories: (1) adult males, (2) adult females, (3) medium-sized juveniles [CL from 101 — 249 mm], and (4) small juveniles [CL < 101]. Marsh depths at point of capture were initially compared among the four categories.

Ages of many of the turtles were obtained by marking hatchlings at nests or at drift fences as they moved from nests to marshes (Congdon et al. 1987). We selected the minimum known age for nesting females as the upper limit for juvenile categories. Ages of Snapping Turtles not marked as hatchlings, but below 12 years of age (minimum age at nesting), were determined from growth rings. Male Snapping Turtles at the minimum body size of nesting females (200 mm CL) averaged 10 years of age. Painted Turtles that were first captured with fewer than 9 (females) or 6 (males) growth rings were assigned an age based on the number of growth rings. Aging of both species from growth rings was based on the assumption that visible growth rings were laid down annually in juveniles and young adults. Sequential recaptures of juveniles of both species over all age classes during the past 15 years support this assumption. The data sets restricted to only known aged individuals were sufficient to analyze capture location depths for Snapping Turtles less than 13 years of age. Age data were sufficient for all samples of juvenile Painted Turtles prior to the minimum age at sexual maturity of females at age 7. Therefore, all analyses of marsh depths in Painted Turtles were based on age rather than size.

When dealing with recaptures of individuals, problems with independence of observations may occur. Minimum recapture intervals were set for each species based on the assumption that either species can easily traverse the entire marsh within seven days. The much larger data set on *C. picta* allowed a 14 day recapture interval while maintaining adequate sample sizes. Therefore, recaptures less than 8 days apart for Snapping Turtles and 15 days apart for Painted Turtles were excluded from analyses.

All ANOVA results used Type III sums of squares, and differences among means were determined using Duncan's Multiple Range Tests (MRT). Otherwise, the non-parametric Kruskall-Wallis (KW) Test was used (SAS Institute 1988). Unless otherwise stated, levels of significance were accepted at alpha < 0.05. Measures of central tendency and dispersion are presented as the mean ± one standard error unless stated otherwise.

Results

Both size and body mass of Snapping Turtles increase rapidly from hatching through age 12, the age at which females approach sexual maturity (Table 1; Congdon et al. 1987). Analysis of water depth in East Marsh at the site of capture of individuals of all four size categories indicated significant differences among groups (ANOVA; $F_{3,375}$ = 7.77, P = 0.0001). Small juveniles occupied significantly shallower water (37.6 cm) than did the other three categories (50.9 cm; MRT; $P < 0.05$). The differences in body size categories, based on parametric statistics, were confirmed by a non-parametric analysis (KW Test; Df = 3, P = 0.0004). In addition, age effects were analyzed for individuals below the age of 13. Snapping Turtles of different ages were captured at different water depths (ANOVA; $F_{11,103}$ = 2.25, P = 0.017). Older Snapping Turtles were not trapped consistently in greater mean water depths (MRT; $P > 0.05$); however, the youngest turtles were captured in the shallowest water (MRT; $P < 0.05$). Similar results were also found using a non-parametric analysis (KW

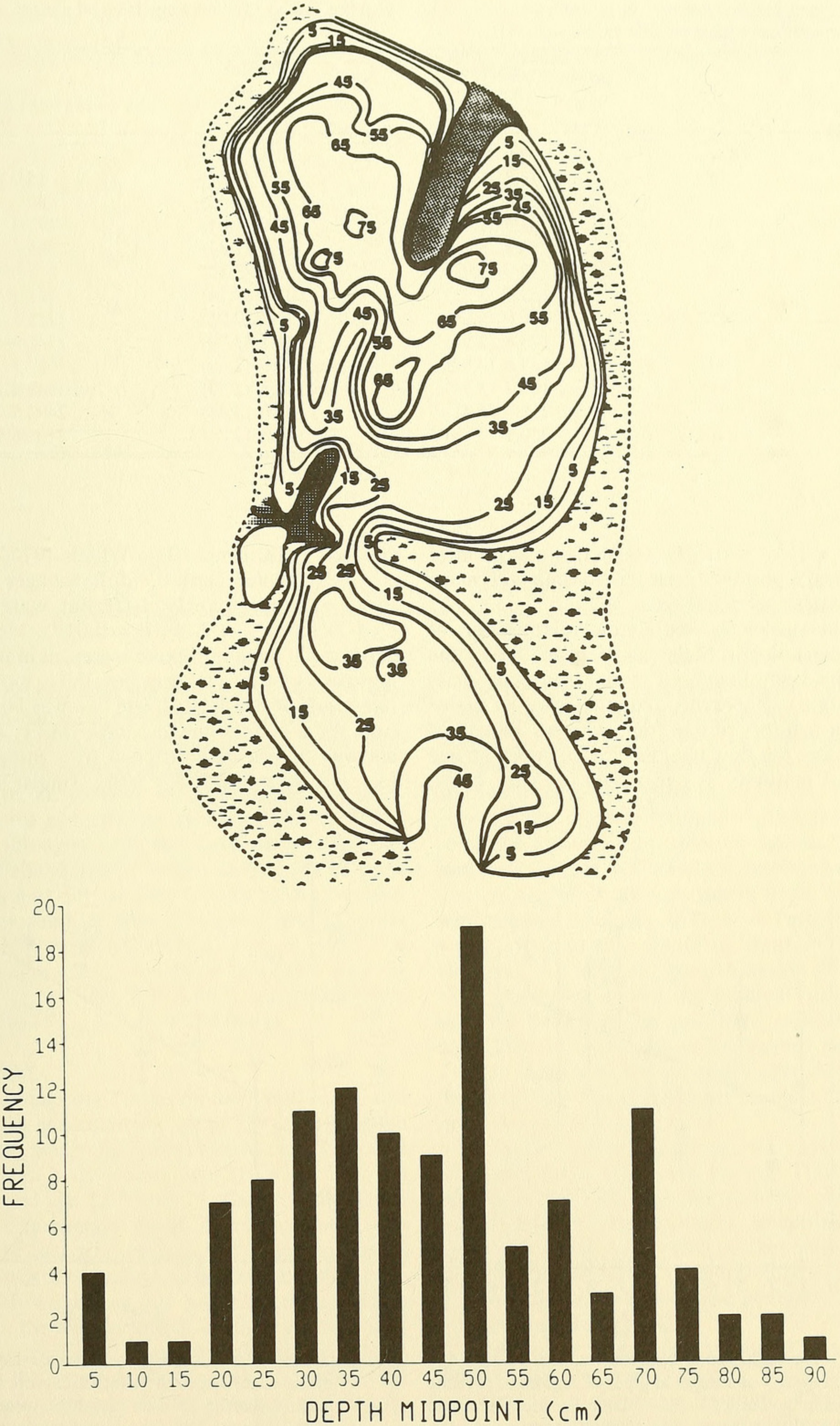

FIGURE 1. Depth contours in cm and frequency histogram of water depths (cm) in East Marsh on the E. S. George Reserve in southeastern Michigan.

TABLE 1. Sizes and body masses of juvenile and young adult Snapping Turtles of known age from all aquatic areas on the E. S. George Reserve [data include means and (1SE)].

Age	N	Carapace length (mm)	Plastron length (mm)	Weight (g)
0	871	29.6 (0.06)	22.1 (0.05)	9.1 (0.05)
1	43	33.8 (1.60)	25.5 (1.31)	15.0 (2.02)
2	38	67.8 (1.88)	52.3 (1.40)	85.7 (7.86)
3	70	86.4 (1.88)	65.6 (1.41)	177.3 (12.20)
4	61	106.3 (3.71)	81.3 (2.83)	364.5 (51.79)
5	56	122.8 (3.93)	93.8 (3.10)	552.0 (68.55)
6	65	139.6 (3.33)	105.5 (2.74)	751.4 (57.46)
7	47	166.0 (4.08)	124.7 (2.91)	1215.5 (90.82)
8	53	173.8 (3.91)	131.1 (3.00)	1341.9 (98.76)
9	33	188.6 (3.60)	142.0 (2.40)	1657.1 (92.24)
10	41	197.2 (3.57)	148.3 (2.59)	1949.4 (103.07)
11	25	218.3 (4.41)	163.6 (3.46)	2492.5 (139.62)
12	26	220.1 (3.18)	167.3 (2.84)	2503.6 (122.49)

Test; $Df = 11$, $P = 0.027$). Marsh depth at point of capture had a positive linear relationship with mean age of turtles captured (Figure 2).

Painted Turtles showed similar relationships of age to marsh depth. Males and females below the age of six years increased in size and body mass (Table 2a,b). However, growth slows as males approach maturity at age four, whereas growth of females does not slow until they reach minimum age at sexual maturity at age seven (Sexton 1959; Gibbons 1968; Ernst 1971; Wilbur 1975; Tinkle et al. 1981). Painted Turtles of different ages were captured at significantly different water depths (ANOVA; $F_{5,54} = 2.99$, $P = 0.019$). Mean water depth at the point of capture increased in the following rank order by age: two, one, three, four, six, and five years. Water depth at age two was not different from those at ages one and three (MRT; $P > 0.05$), but was significantly different from those for ages four and older (MRT; $P < 0.05$). Similar age differ-

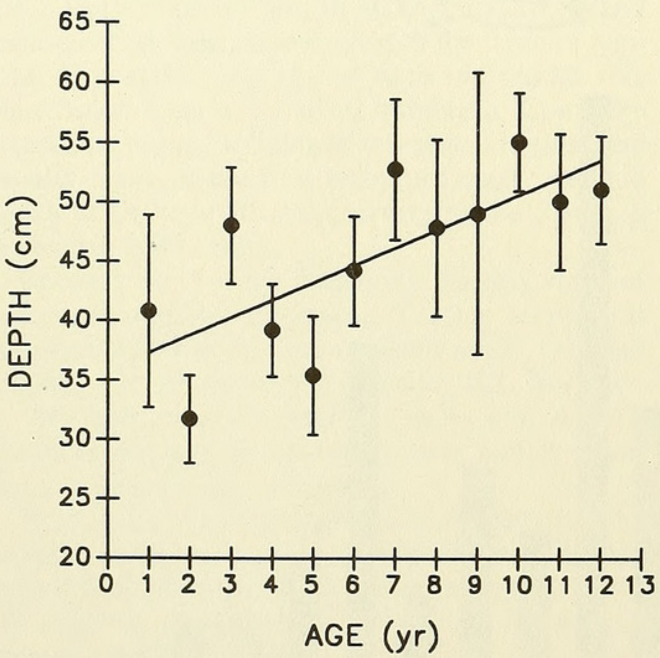

FIGURE 2. The relationship between Snapping Turtle age and mean water depth at point of capture of juvenile Snapping Turtles in East Marsh between 1980 and 1986. Linear regression statistics; depth = 35.8 + 1.47 * age, $SE = 0.36$, $N = 12$, $R^2 = 0.54$, $F_{1,11} = 11.75$, $P = 0.006$.

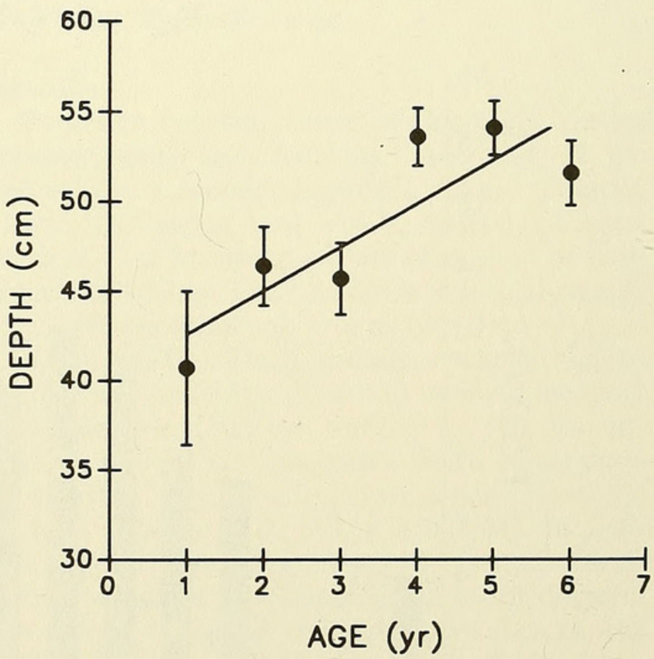

FIGURE 3. The relationship between Painted Turtle age and mean water depth at point of capture of juvenile Painted Turtles in East Marsh between 1980 and 1986. Linear regression statistics; depth = 40.1 + 2.45 * age, $SE = 1.41$, $N = 6$, $R^2 = 0.75$, $F_{1,5} = 11.82$, $P = 0.02$.

TABLE 2. Sizes and body masses of Painted Turtles of known age from East Marsh on the E. S. George Reserve [data include means and (1SE)].

(a) Juvenile and young adult males Age	N	Carapace length (mm)	Plastron length (mm)	Weight (g)
0	394	24.6 (0.09)	22.9 (0.09)	3.7 (0.03)
1	20	56.4 (2.00)	50.8 (1.75)	34.2 (3.22)
2	55	72.3 (0.96)	65.6 (0.96)	63.2 (2.17)
3	37	87.6 (1.43)	80.2 (1.44)	105.3 (5.18)
4	30	95.6 (1.15)	87.8 (1.02)	125.2 (4.01)
5	36	99.8 (1.09)	91.4 (0.92)	138.0 (4.08)
6	16	105.1 (2.25)	95.8 (2.21)	151.1 (9.24)
(b) Juvenile females Age	N	Carapace length (mm)	Plastron length (mm)	Weight (g)
0	394	24.6 (0.09)	22.9 (0.09)	3.7 (0.03)
1	20	62.3 (1.25)	56.6 (1.14)	43.4 (2.83)
2	42	76.3 (0.97)	69.8 (0.93)	74.0 (2.31)
3	37	88.1 (1.88)	81.3 (1.83)	109.1 (7.68)
4	41	97.2 (1.53)	89.9 (1.55)	138.5 (6.08)
5	32	105.5 (1.94)	98.3 (1.88)	172.3 (9.53)
6	28	115.5 (2.69)	107.5 (2.71)	222.0 (14.63)

ences associated with water depths were also found using non-parametric tests (KW Test; $Df = 5$, $P = 0.005$). The linear relationship of water depth with age was also positive (Figure 3).

Because our measure of water depth was static (i.e., it did not change as actual water depth changed throughout the summer), we analyzed the data on Painted Turtles with year and age as class variables and day of year (DOY) as a covariate. The water depth at point of capture was different for different years (ANCOVA; $F_{5,700} = 4.44$, $P = 0.0001$), ages ($F_{5,700} = 3.13$, $P = 0.008$), and for DOY ($F_{1,700} = 7.40$, $P = 0.007$) and DOY * YR interactions ($F_{5,700} = 5.45$, $P = 0.0001$).

Discussion

Female Snapping Turtles on the ESGR reach sexual maturity at a minimum age of 12 years (Congdon et al. 1987). Snapping Turtles increase in CL about 8 times and in body mass about 279 times between hatching and age 12 (Table 1). The only significant difference in average marsh depth associated with captures of four size categories of Snapping Turtles was between the smallest turtles and all other categories. However, as age and size of juveniles increased, the average marsh depth at point of capture also increased; these results indicate that although the major depth changes associated with size or age occur between the youngest and all subsequent age or size classes, more gradual changes in marsh depth at the capture site occur among the older juveniles (Figure 2).

The increase in size among Painted Turtle juveniles is less profound (Table 2a,b) than in Snapping Turtles. By the time male Painted Turtles mature at a minimum age of four years, they have increased CL and body mass by approximately 4 and 34 times, respectively. Female Painted Turtles mature at a minimum age of seven years; by age six they have increased 5 times in CL and 60 times in body mass. The pattern of changes in marsh depth associated with capture locations of Painted Turtle juveniles was similar to that found in Snapping Turtles. However, the slope of the relationship of age with water depth was steeper for Painted Turtles (2.46) than for Snapping Turtles (1.47; non overlap of 2SE). The three youngest age groups of Painted Turtles were trapped at shallowest mean water depths in East Marsh and the three older age groups in the deepest water.

Snapping Turtles through age six were caught in shallower water than were Painted Turtles of the same age. The difference between the species may be related to foraging modes. Snapping Turtles apparently ambush prey while resting on the bottom, whereas Painted Turtles seem to forage more actively in the surface vegetation and possibly throughout the water column.

As expected in any shallow marsh, the relationships among turtle ages (sizes), years, day of the year and water depth are dynamic. Changes may occur seasonally with the social environment, with the development of aquatic vegetation during spring, or as water levels are maintained or increase with rainfall or decrease during dry periods when evaporation exceeds water input to the marsh.

We also examined marsh depth at point of capture during drought years. The slope of the relationship between size or age of turtles and marsh depth during these years was either zero or negative. The differences between drought years and years of normal water level were in part due to our static measure of marsh depth and the rapid drop in water level during the trapping period (i.e., areas that were initially "deep" rapidly became "shallow").

Although we have no data to indicate why juveniles of different ages or sizes of either species were captured in different depths of water, the distribution of appropriate food resources, swimming abilities of juveniles, differences in thermal preferences, social interactions, and predator avoidance may all be involved. Hart (1983) noted that in *Trachemys scripta elegans* in Louisiana, increasing feeding depths paralleled increasing body size and consumption of plants. Painted Turtles have been reported to be primarily carnivorous as juveniles and become increasingly herbivorous with age and size (Sexton 1959). Appropriately sized invertebrate prey may be more abundant or more catchable by juveniles in shallower compared to deeper water, or plants preferred as food by adults may be more common in deeper water.

Active turtles need to surface periodically to breathe. Hatchlings and smaller juveniles of Snapping Turtles are poor swimmers compared to adults (Hammer 1969). Younger turtles may simply stay in shallower water until they develop swimming skills that more easily allow them to reach the surface in deep water.

Because water warms faster in shallow than in deep areas, thermal preferences may be involved in depth choice by turtles. Adult turtles often spend more time in shallow and presumably warmer waters in the early spring and then move to deeper areas as water temperatures rise (Sexton 1959 for Painted Turtles in Michigan; Hart 1983 for Sliders in Louisiana). Hatchling *Trionyx muticus* were more frequent in warmer, quieter water in shallow areas or on the lee of sandbars than in surrounding habitats (Plummer 1977). Growth in Sliders (Gibbons 1970; Christy et al. 1974; Thornhill 1982) and Snapping Turtles (Williamson et al. 1989) is faster at warmer temperatures. Parmenter and Avery (1990) hypothesized that elevated body temperatures and the concomitant increased growth rates result in earlier attainment of sexual maturity in turtles. With faster growth, hatchlings and small juveniles would reach a larger size sooner and thereby be less vulnerable to predation.

As adults, Snapping Turtles may be able to function more effectively at cooler temperatures than Painted Turtles. Snapping Turtles have lower critical thermal maxima (Hutchison et al. 1966) and faster digestive turnover rates (Parmenter 1981) than do Painted Turtles; however, both species showed similar patterns of habitat use in this study. The similarity of pattern suggests that the use of shallow water by juveniles is based on common benefits that juveniles accrue by restricting most of their activity to shallower portions of the marsh.

Little is known about social interactions or age/size dependent behavior in most turtle species including Snapping Turtles and Painted Turtles. Territoriality and other forms of behavioral hierarchies affect dispersion and could produce the kind of habitat segregation reported in this study. Certainly the social environment of juveniles is different from that of adults in both species.

Although age specific mortality schedules of juvenile turtles are few, predator avoidance, including cannibalism, may be an important component in differences in habitat use by individuals of different age and size. Predators capable of taking the smallest sizes of hatchlings and juveniles include mink, otters, raccoons, wading birds, birds of prey, crows, large fish, aquatic snakes, and large bodied turtles. Werner and Hall (1988) presented evidence that juvenile Bluegills (*Lepomis macrochirus*) used shallow, vegetated portions of several Michigan lakes, whereas the adults frequented deeper and more open habitats. Werner and Hall (1988) argued that this pattern resulted from a trade-off between foraging rate (better in open water) and predation risk (higher in open water). As Bluegill approached the size that was too large for easy consumption by bass, individuals moved into deeper water. By restricting their activity to the more shallow portions of East Marsh, small turtles may also avoid predators such as fishes and larger turtles that occupy the deeper areas. However, in doing so, they may increase their vulnerability to predators such as wading birds and raccoons that feed in the shallows. Hart (1983) suggested that juvenile turtles may stay in shallow areas until increasing body size decreases their ability to hide, or vegetation density impairs their ability to escape predators, at which point they move to deeper water.

The findings from this study support the idea that: 1) as juvenile turtles grow older they tend to be found in deeper water, and 2) the phenomenon is widespread among turtles since shifts to deeper water occurred in both Painted Turtles (family Emydidae) and Snapping Turtles (family Chelydridae). Future studies should be designed to determine the reasons for ontogenetic changes in habitat use by juveniles. More detailed studies are necessary to enhance our understanding of the constraints and risks associated with resource acquisition by juveniles. Knowledge of how habitat variability influences juvenile success, population stability and species persistence is critical for conservation and management of turtle populations.

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