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TRANSACTIONS OF
THE NORTHEAST SECTION
THE WILDLIFE SOCIETY

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A HUDSON RIVER TIDEMARSH SNAPPING TURTLE POPULATION¹

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Abstract: Activity of snapping turtles (Chelydra serpentina) was related to season, temperature, and tide. Median in-marsh recapture distance (RD) was 100 m but females moved up to 1 km to nest. In 1974 there were 114 nests on a 2.2-km railroad fill on one side of the marsh. Clutch size was 16-54 ($\bar{x} = 29.6$, $N = 27$). Adults were about 60% male. Large males emerged earlier in spring and had more injuries than females or small males, and smaller RDs and higher recapture rates than small males. Evidence points to male-male aggression and dispersal of smaller individuals. There were about 600 adults: crude density 4/ha, ecological density 16/ha, crude live biomass 23 kg/ha. Harvest was 50-350/year. Few ducks are present during the May-August snapper feeding season. The turtles help keep marsh pools open by disturbing sediments.

The snapping turtle is nearly ubiquitous and often abundant in fresh and slightly brackish waters of the United States east of the Rockies, including estuaries. No population studies of tidemarsh snappers have been published. Data were collected during 1972-75 and reported in a thesis (Kiviat 1976). Additional observations were made during 1976-79.

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STUDY AREA

Tivoli North Bay is a 154-ha fresh-tidal wetland on the east side of the Hudson River in Dutchess County, New York (Kiviat 1978). A fill railroad causeway on the west edge of the bay has 2 openings that connect to a network of tidecreeks and pools in the bay. There are two 1.2-m tide cycles daily.

North Bay is 55% dominated by narrowleaf cattail (Typha angustifolia), 15% purple loosestrife (Lythrum salicaria), 5% trees and shrubs (all in upper intertidal zone); 10% mixed emergent forbs and graminoids, 10% spatterdock (Nuphar advena) and pickerelweed (Pontederia cordata), and 5% bare mud or wild-

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celery (Vallisneria americana) and Eurasian watermilfoil (Myriophyllum spicatum) (in the lower intertidal and subtidal zones). Adjacent to North Bay are 150 ha of subtidal weedbeds, 20 ha of intertidal wetlands, and a deciduous forest on silty-clay bluffs with 15-30%+ slopes up to the 30-m contour.

METHODS

I spent about 150 days in field work, marked 450 snappers and recaptured 85. I set funnel traps baited with fish at tidecreek confluences where there were 20+ cm of water at low tide. Adult snappers entered traps readily at water temperatures of 16-33 C; above 27 C they were in danger of drowning if submersion was prolonged.

I searched shallows and mudflats for 3 hours before and 1 hour after low tide. Turtles were visible only 5-50 cm under the turbid water. In 1975, to obtain an index to seasonal activity, I combined trap and search about 3 times/month during April-August, at sunny midday low tide periods in April-May and twilight low tide periods in June-August.

I trussed snappers for handling (Ernst et al. 1974) and marked them with marginal notches (Cagle 1939) and/or numbered nickel-pin Petersen disk tags in a drill hole in a posterior marginal scute. Of 63 recaptured turtles, 13 lost tags. The smallest turtle to lose a tag had a carapace length (CL) of 162 mm at capture; smaller turtles might have drowned if tags snagged. I released turtles <30 m from capture points, 0.2-24 hours later.

In 1972-73, I sexed adults morphometrically (Mosimann and Bider 1960), but after 1973 I sexed turtles >175 mm CL by feeling for the penis inside the cloaca. Used with care, this method is more accurate on snappers <250 mm CL. I measured midline carapace length with calipers (some workers have measured greatest caliper CL or along-the-curve midline CL). Comparisons of different marking, measuring, and sexing techniques will be published separately.

Scute annuli should equal age in a tidemarsh with predictable water and food, until wear and slowing of growth obscure annuli. I counted annuli on a scrubbed pleural scute on snappers with relatively clear annuli (usually those <16-20 years). Repeated counts varied by ± 2 annuli. I used CL >200 mm as the criterion of maturity in both sexes (Mosimann and Bider 1960, White and Murphy 1973, Christiansen and Burken 1979).

D. C. Buso and I walked the east (bay) side of the railroad causeway 1-2 times most days in June 1974, looking for females and nests. We opened and reburied 1 nest selected at random from each sequential group of 3 found, marking the top of each egg with pencil to avoid turning damage (Ewert 1979). Each nest was numbered and mapped.

ACTIVITY

Extreme dates of observed activity were 15 April to 28 Oct. Catch was highest in May and declined thereafter. Early and late

catches contained a few large turtles and were unpredictable.

Large adults were common in intercreek cattail stands in some areas in late April. About 1 May, these adults moved down into the creek and pool summer habitat and were rare in cattail later.

Trap success and sightings suggested much activity in turbid shallows at low tide. Trails showed that turtles often buried in the intertidal mud as the tide ebbed, sometimes emerging to move down into the water or wander on the mudflat and re-bury.

Spatterdock, submerged plants, and muskrat (Ondatra zibethicus) burrows also provided shelter at low tide on hot days. Perching in the sun (aerial basking) was observed only once in North Bay.

Black-body temperature (BB) is a good index to the sun's heating effect on turtles (Boyer 1965). I measured BB with a lab thermometer painted flat black to the immersion ring, shielded by a clear plastic tube, and held perpendicular to the sunlight near the substrate. Extreme activity temperatures were BB 14-45 C and water (W) 12-33 C. Spring activity at low water temperatures peaked in bright sun with high BB, whereas summer activity with high W peaked at low-light times with low BB.

Adults and immatures tended to sort microclimatically. Adults were most conspicuously active at approximately BB 25-38 and W 16-27; immatures at approximately BB 36-45 and W 26-33. As the season progressed, adults were less, and immatures more, conspicuous. Daytime activity was marked in spring for adults and in summer for immatures. Crepuscular adult activity was pronounced in summer. I did not study possible nighttime activity.

SOCIAL BEHAVIOR

Four times in May I saw males mounting other males. These turtles measured 271-386 mm CL. Hammer (1969, 1971) reported male-male mounting. The function could be sex discrimination or dominance.

I examined 124 turtles for scars. The average number of injured claws per turtle was 0.38 for males (N = 65), 0.11 for females (N = 18), and 0 for immatures (N = 41). Only 2 of the males with injured claws were < 325 mm CL. No immatures had scars on the carapace margin, but adults often had nicks (more in males than females). Marginal nicks could be partly a result of courtship biting, but missing or partly-missing claws are likely an outcome of intermale aggression. Damaging fights between large males have been reported (e.g. Hammer 1969).

MOVEMENTS

Recapture distance (RD), a hypothetical straight line between successive capture points of an individual, was estimated on maps with points plotted to within 30 m of actual capture locations. Errors in RDs were about 2-10%. Observations of mud trails suggested that this amount of error was not biologically important.

Median in-marsh RD for all classes combined was 100 m, small for a species capable of moving several km (see Hammer 1969). Same-year RDs were not significantly different than subsequent-

year RDs for males (t-test, $p > 0.05$). RD was larger and more variable for small adult males than for large males, and RD was larger and more variable for large immatures than for small immatures (Fig. 1). Mean RDs for 50-mm size classes of immatures and adult males were inversely related to percentage of individuals recaptured in each size class (Fig. 1). Low recapture rates of middle-sized turtles suggest higher rates of loss from the population in these size classes (150-300 mm) rather than just larger home ranges within the marsh. These statistics probably reflect dispersal tendencies of subadults and small adult males, and sedentary habits of large males.

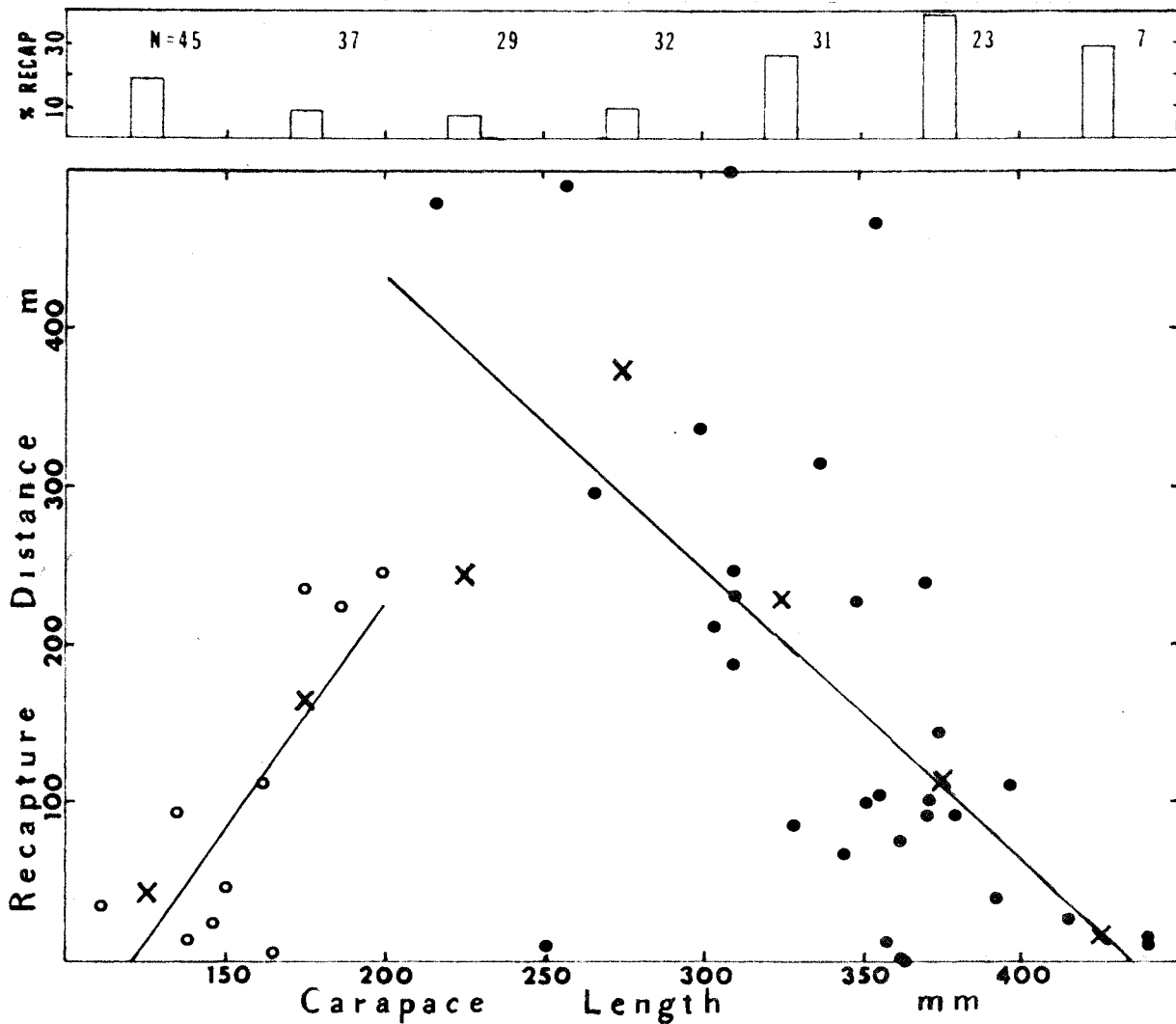


Fig. 1. In-marsh RD vs. CL of immatures and adult males. Mean RDs (Xs) for 50-mm size classes and least-squares regression lines for immatures and adults are shown. Bars (above) are percent recapture rates for 50-mm size classes.

Recapture histories of several large males showed 2-4 captures within small areas. A 440-mm male was found 4 springs in succession in a 0.1-ha pool on a small tidecreek connecting the 2 drainages within the marsh. No other turtle was captured more than once in this pool. However, in other areas it was evident from recaptures and multiple trap captures that at least some adults had overlapping home ranges.

Home ranges estimated as hypothetical circles with radius equal to mean RD (Fitch 1958) were 3-9 ha (Table 1). These are liberal estimates, as the method assumes circular home range; many movements in North Bay followed tidecreeks, and it is reasonable to assume elongated home ranges in this highly heterogeneous habitat.

RDs of nesting (1 of 2 captures on railroad) and non-nesting (both captures in marsh) females were quite different (Table 1). Nesting migrations may involve long forays out of the home range even though nesting sites are directly adjacent to the marsh.

Table 1. RDs and estimated home ranges of North Bay snappers.

Class	Recapture distance (m)			Home range (ha)
	N	Range	$\bar{x} \pm$ SE	
Immatures	10	5-245	103 \pm 31	3.3
Adult males	32	0-499	168 \pm 27	8.9
Non-nesting females	6	31-339	152 \pm 54	7.2
Nesting females	7	336-1061	735 \pm 94	

GROWTH

Larger adults grew slowly (Table 2, Group 1); smaller adults and immatures grew rapidly (Group 2). The Group 2 statistics for adults reflect the high growth rates of the immature and small-adult years. Also, annulus counts are likely to err on the low side because slow recent growth of large adults produces crowded difficult-to-distinguish annuli.

Growth rates of Gibbons (1968), Hammer (1969), and Christiansen and Burken (1979) are somewhat higher. The differences could be ecologic, or artifacts of different measuring and estimating techniques compounded by small sample sizes.

NESTING

In 1974, nests were initiated on the railroad causeway 7-30 June, 90% 13-23 June. (The earliest record was 1 nesting female on 4 June 1970.) All 53 females found on the causeway during the nest study were caught 10-21 June; the delay between peak of females and peak of nests is probably due to individuals being returned to the marsh edge after tagging.

Table 2. Growth in carapace length of North Bay snappers.

Class	CL ^a	N	Growth (mm/yr)	
			\bar{x}	Range
Group 1 ^b				
Immatures	138-165	2	20.0	9-31
Adult males	309-440	8	4.4	0-9
Adult females	269-285	4	1.2	0-2
All above	138-440	14	5.8	0-31
Group 2 ^c				
Immatures	87-197	20	20.1	17-25
Adult males	203-401	20	18.9	7-25
Adult females	216-297	20	18.0	12-24

^aCarapace length at recapture (Group 1) or when annulus count made (Group 2).

^bFrom successive measurements of individuals marked in 1974 and recaptured in 1975.

^cEstimated mean annual growth = (CL - CL at hatchling) / Number of complete annuli. CL at hatching is 28 mm. Almost all turtles in Group 2 were <300 mm CL.

It rained 5-18 mm on each of these days: 12, 16, 17, 18, and 21 June; 39 of the 53 females were found on these days. Hammer (1972) reported nesting stimulated by rain. During the nesting period at North Bay, cattail is releasing pollen and can be used as a phenological indicator of nesting.

Nests on the causeway were in bare or partly-bare sandy-textured (cinder?) soil, oily from the trains. Many nests were clumped where larger marsh creeks or pools approached the causeway; most females emerged at these spots, and subsequent turtle digging exposed and damaged eggs in 3 nests.

Females usually dug body pits before excavating nest chambers on the causeway. Many body pits were abandoned during site selection. Most observed nesting took place in early morning or late afternoon. Four gravid females that had not completed nest preparation were found buried in the soil in extended body pits.

On the east side of the causeway 92 nests were found on the 2.2 km of fill bordering the marsh. Casual checks of the west side of the causeway disclosed 8 nests. Adults can easily cross the tracks but this was rarely seen and I believe most of the females that emerged from North Bay onto the causeway nested on the east side. Around the rest of the bay's perimeter, 21 nests were found, mostly in a single intensive search of the upland border on 2 July.

By 2 July, 11 of the 92 marked nests on the causeway had been opened by mammals. A search on 4 September showed that 46 nests had been opened, many probably during or after hatchling emergence. (Hatchlings were seen emerging from 1 nest on 11 Sep. 1973.)

Of the 46 mammal-opened nests, 9 were unmarked nests missed in the June survey. The ratio marked/unmarked nests gives an estimate of 114 total nests (22 nests missed). Add to this 7 gravid females removed from the railroad before laying by humans, for 121 females that would have nested on the east side of the causeway.

The minimum number of reproducing females in 1974 for the whole bay was 132. If females emerged and nested in random directions, a causeway percentage-of-perimeter estimate gives 356 nests for the whole bay. I deem 250 nests a reasonable estimate.

Clutch size was 16-54 ($\bar{x} = 29.6 \pm 1.8$ SE) in 27 nests sampled 13-28 June 1974 on the east side of the causeway. Nesting North Bay females were 216-330 mm CL ($\bar{x} = 262.4$, N = 54).

POPULATION STRUCTURE

All recent published studies have agreed that males are larger than females both in mean and extreme. Large males emerge before small males and females in spring (Table 3). The difference in numbers of males and females in early spring and spring-summer samples is significant ($X^2 = 12.2$, $P < 0.005$), as is the difference in numbers of large and small males in early spring and spring-summer ($X^2 = 13.1$, $P < 0.005$). However, numbers of females and small males are not significantly different between seasons ($P \sim 0.25$). Trap data were not included in this analysis because of possible sex and size biases.

Table 3. Numbers of large and small adults of both sexes in early spring and spring-summer samples (hand capture only, 1972-78. data pooled).

	201-300 mm		301-450 mm	
	MM	FF	MM	FF
17 Apr-14 May	12	8	45	1
15 May-20 Aug	39	43	36	3

Numbers of males and females in hand samples gradually equalized through the season; however, the later samples contained very few large males. This trend suggests that the 15 May-20 Aug. hand sample (61% males; $X^2 = 6.95$, $P < 0.005$) is representative of the population. Of several male-skewed sex ratios in the literature, only one is significant: Hammer (1972) collected 93 males, 39 females, and 28 unsexed small adults by shooting. If the unsexed individuals are apportioned equally, the sample contains 67% males ($X^2 = 18.2$, $P < 0.005$).

Males live longer (Hammer 1972) and grow more rapidly (Table 2; also Christiansen and Burken 1979) than females. In North Bay, both sexes are present equally up to 300 mm CL, but larger turtles are almost all males (15 May-20 Aug, Table 3). Shorter life expectancy (partly due to vulnerability when nesting) could ex-

plain this pattern.

Immatures seem to emerge still later than females in spring. Immatures 100-175 mm CL frequented shallower and more densely vegetation-covered areas than most adults, and were easily caught by hand. Immatures 175-200 mm showed a transition to adult habitats and behavior. I found only 6 snappers between hatchling size and 100 mm; the smallest were 56 and 74 mm. Pell (1941), Hammer (1969), and Froese and Burghardt (1975) noted immatures inhabiting shallow waters or upstream areas less frequented by adults. Sampling problems make it difficult to assess the numbers of immatures in the population.

DENSITY

The adult population was 600+. Crude density was about 4 adults/ha. Summer habitat is restricted to pools and creeks or <25% of the bay, so ecological density during the main activity season was about 16/ha. Mean weight of 46 adults in 1973 was 6 kg, yielding a crude live-weight biomass estimate of 23 kg/ha. I estimated population size by 2 methods: nest count and harvest.

Number of nests in 1974 was about 250 (min. = 132, max. = 356; see above). Adjustment for some females possibly not producing a clutch annually (Hammer 1972:51) gives a reasonable 275 (132-400) females. Nesting females caught were virtually all >225 mm CL and in-marsh population structure suggested the 201-225 mm size class was about 27% of the "adult" females; this adjustment gives a reasonable 350 (150-550) females. Finally, if the adult population is 39% females, total adults would be about 900 (min. ~300, max. ~1,500).

J. Rodziewicz (pers. commun.) intensively harvested North Bay snappers for market during 1968-71. He estimated the 1968 take at 2.7-5.4 metric tons (~135 kg each low tide period of hunting), and the 1971 take at 1.4-2.7 MT (~115 kg/hunt). I examined 2 of 3 catches he made during my study: 19 April 1973, N = 17, \bar{x} = 7.6 kg; and 22-23 May 1975 (2 hunts), N = 36, \bar{x} = 7.3 kg. The smallest turtles were about 3.5 kg (240-250 mm). Thus on a weight basis, the 1968 harvest comprised about 350-740 turtles over 240 mm. Rodziewicz supposed a harvest rate of 80%. Adjusting for about 25% 201-240-mm adults in my whole-season in-marsh hand sample, the 1968 pre-harvest population was 600-1,200 adults.

Reported snapper densities vary considerably. North Bay estimated ecological density is somewhat less than crude (approximately equals ecological) density reported for shallow 0.4-0.8-ha ponds by Major (1973, 1975) and Froese and Burghardt (1975) if their numbers are adjusted to adults only. Lagler (1943) and Hammer (1972) reported much lower density estimates for lakes and artificial marshes, respectively.

The 1968-71 North Bay harvests are comparable to the 2,298 snappers (presumably adults) removed from a 324-ha Michigan area in 3 years (N.Y. State Conserv. Dep. 1939), although it was not stated if the whole Michigan area was turtle habitat. Both harvest rates approximate 2.4+ adults/ha/yr. The approximate halving of the harvest in the 4th year at North Bay suggests the 1971 pre-harvest population had fallen to half its 1968 biomass. Pre-

sumably, recruitment and growth were unable to compensate for so high a removal rate. After 1971, harvest by several persons was 60+/year.

EFFECTS IN THE ECOSYSTEM

The feeding season of North Bay snappers is about 100 days. Although extreme dates of baited trap captures were 20 April to 11-12 Sep., turtles were seen eating or defecating only 2 May - 1 Aug. (adults) and 3 June - 19 Aug. (immatures). Feeding during the nesting season is suggested by dissection of a female containing shelled eggs and a full gut on 7 June 1974.

Two North Bay snappers (97 and 236 mm) kept in captivity in outdoor tanks for 1-2 months in summer 1973 consumed 1-1.6% of their body weight per day of fish and invertebrates. This indicates a wild food consumption rate of approximately body weight per year, or 23 kg/ha/yr - not very much.

Snappers may be locally important predators on water birds (Coulter 1957, Hammer 1972). Counts of ducks in North Bay showed that peak numbers occurred March-April (Fefer 1973), or outside of the snapper feeding season. I estimated that only a dozen broods each of mallard (Anas platyrhynchos), black duck (A. rubripes), and wood duck (Aix sponsa) used the marsh in 1972. North Bay snappers might affect these small populations, but do not have an opportunity to consume large numbers of ducks.

Frequent burrowing by snappers in soft mud and muskrat holes resuspends sediment, visible as extreme turbidity in areas of concentrated turtle activity at low tide. In concert with rooting by fish, ducks, and muskrats, snappers help maintain open pools and patches of soft mud bare of vascular vegetation. Snappers probably disturb yearly at least 1% of the bay's substrate to a depth of 15+ cm by burrowing, and 20-25% of the substrate to a depth of 2-7 cm by treading. Most of this disturbance occurs in the one-fourth of the marsh that is the summer habitat. Digging of body pits on the railroad causeway also influences soil and vegetation.

DISCUSSION

Snapper sex-size classes in North Bay tend to sort behaviorally and ecologically. Large males (larger than most females) emerged earlier in spring and had more injuries than females or smaller males, and large males had smaller RDs and higher recapture rates than small males and large immatures.

Large males might be territorial, defending their own immediate surroundings, and disproportionately influencing social structure and prey populations. This proposed social system could regulate biomass and provide dispersal to vacant habitats. This hypothesis is supported by the weight-class distributions observed in small ponds by Major (1973), and by observations of a single large male with smaller individuals of both sexes in lake coves or other pockets of habitat (J. Rodziewicz pers. communs., W. Blanco pers. communs.). Furthermore, immatures and small adults are often seen on land or in intermittent waters far from

permanent habitats.

High snapping turtle densities may occur in shallow tidal as well as nontidal habitats. Overall, snapper ecological influence may be more on sedimentation than on energy flow or prey populations. If this role is desirable and snappers are to be harvested, much must be learned about population processes to allow regulation of harvests. Coulter (1957) pointed out that sightings of snappers are a poor clue to abundance. Sample counts of nests and eggs, and in-marsh late spring to early summer hand samples of sex-size structure, may prove useful assessment techniques.

Harvest methods are class-selective. Funnel traps catching small to medium-size males might be used to remove "surplus." If predation on game is a problem, early-spring hand capture of large males could reduce this more powerfully predatory segment. Protection may be warranted locally for nesting females.

Accumulation of high tissue levels of persistent environmental pollutants (Stone et al. 1980) may render snapping turtles in some areas more useful for biological monitoring than for human food. Effects of pollutants on turtle behavior and ecology are not known.

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