of Mizoram into the plains of Cachar, Assam, and the Jiri river and its tributaries in the Assam-Manipur border. These areas need to be declared as chelonian sanctuaries, and widespread awareness campaigns need to be undertaken to wean potential consumers away from eating turtle meat and eggs and to remove the superstitious beliefs from their minds.

Although poaching is a problem, turtles have historically received community-sanctioned religious protection in many temple tanks in this region. Examples include softshell turtles protected in the Kamakhya temple at Guwahati, Assam and *Aspidaretes gangeticus* in the Tripureshwari temple at Udaipur, Tripura. More recently, the Shiva temple at Tinsukia, Assam has started offering turtles sanctuary. Thus ex-situ conservation of chelonians in community and temple tanks and in public gardens could also constitute a useful mechanism for conservation.

References

Das, I. 1996. Biogeography of the Reptiles of South Asia. Florida: Krieger Publishing Company, 87 pp.

F.S.I. 2000. State of Forest Report 1999. Dehra Dun: Forest Survey of India (Ministry of Environment and Forests), 113 pp.

Gupta, A. and Guha, K. 2002. Tradition and conservation in Northeastern India: an ethical analysis. Eubios Journal of Asian and International Bioethics 12: 15-18.

Myers, N., Mittermeier, R.A., Mittermeier, C.A., Da Fonseca, G.A.B., and Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature, London 403: 853-858.

Pawar, S.S. and Choudhury, B.C. 2000. An inventory of Chelonians from Mizoram, North-East India: new records and some observations on threats. Hamadryad 25(2): 144-158.

A Nine Year Study of Eastern Box Turtle Courtship with Implications for Reproductive Success and Conservation in a Translocated Population

BILL BELZER

Biology Department, Clarion University/Venango Campus, 1801 West First St, Oil City, PA 16301

The eastern box turtle, *Terrapene carolina carolina*, has low reproductive success (Madden, 1975; Doroff & Keith, 1990; Klemens, 1989; Zeiller, 1994; Klemens, 2000; Dodd, 2001). Integration of the evidence presented here, and from my previous field studies in northwestern Pennsylvania (Belzer, 1999a, 1999b, 1999c), with that found in discussions of declining *Terrapene* populations (e.g. Murphy, 1976; Stickel, 1978; Halgren-Scaffidi, 1986; Williams and Parker, 1987; Doroff and Keith, 1990; Dodd and Franz, 1993; Lieberman, 1994a and 1994b; Tyning, 1997; Hall *et al.* 1999; Miller, 2000; Niederriter, 2000; Dodd, 2001), suggests that perpetuation of this species' populations requires high reproductive activity; and that a high adult population density is critical for that required level of sexual interaction.

Courtship Encounters

Over the last nine years, we have regularly monitored 43 eastern box turtles with radio telemetry (Belzer, 1999a). These turtles were released into the McKeever and Buttermilk Hill Nature Sanctuaries, in Pennsylvania's Mercer and Venango counties (respectively). This has provided exceptional opportunities to observe reproductive behavior. Neither courtship nor mating was observed during the initial years of the repatriation studies (Belzer, 1999b). At that time, the first 10 turtles were kept within a 12 ha core of the 80 ha McKeever habitat (Belzer, 1999c).

My initial hypothesis (that pheromonal or other distant cues would bring distant box turtles together for mating) failed to reconcile the lack of observed mating activity with the fact that box turtle copulation lasts for hours. It would be difficult to miss all mating activity, even in a small population, when all the animals are located many times a week. Moreover, my naive notion that box turtles would probably detect distant potential mates, and move to them, failed to accommodate Stickel's (1989) report that she saw mating only among adults whose home ranges overlapped, not among ones with separated home ranges.

In the earliest years of my studies, I sometimes found individuals near one another (e.g. 5-20 m), but never together. Later, as more turtles were added to the site, we found more interacting turtles. A male's recognition of a female often starts with a series of brief, energetic, erratic head and body jerks or lunges toward the female, after which he approaches her. Males would walk within one meter of a female obscured by vegetation, and pass by her location as if oblivious to her presence. I discovered that if I removed the object obstructing the male's view, the male generally turned sharply toward her as soon as he noticed her. He would then close in on her, court and often copulate.

I also observed males walk past females who were not hidden, but who were motionless and withdrawn into their closed shells. The males appeared oblivious to the proximity of such potential mates even though the females were in plain view. If the female moved or was moved by me with a branch, the male would suddenly turn around, close in and begin courtship.

In short, our male eastern box turtles seemed to approach females only when they actually saw and recognized them.

Experiment 1: Effect of visibility on mate finding

My revised hypothesis became that visual cues are critical for finding potential mates in an eastern box turtle population. In 1997, I initiated several field tests to assess male responses to hidden and visible females.

In each trial, a test male was placed 10-40 cm from a hidden female. Females were obscured from the male by either hiding the female under a thin layer of dead grass or leaves (n=21), by creating a straight wall of either bark, cardboard or twigs and leaves (n=32), or by employing a collapsible, I-shaped barrier (n=22) (Figure 1).

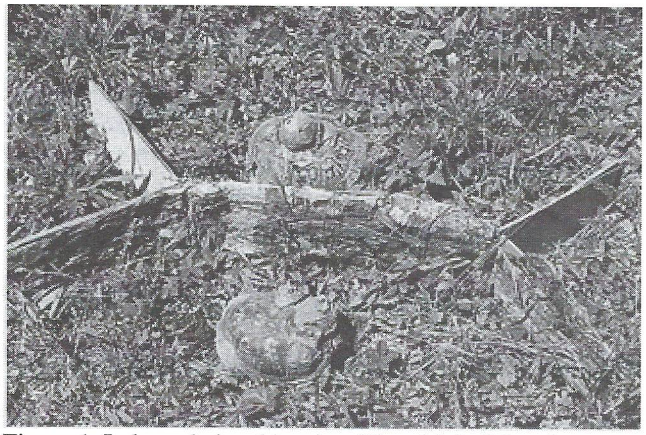

Figure 1. I-shaped visual barrier; 12cm high; 36cm long.

Between 1997 and 2001, 75 trials were run using 23 males and 20 females. The tests were conducted between 6am and 7pm and between May and October to minimize daily or seasonal effects on male's behavior.

Observations and videotaping were done by either remote control or by a single individual (1) standing, unhidden about 3 m from turtles, (2) hiding on the ground behind shrubbery with binoculars; or (3) in a tree blind 7 m from the turtles recording behavior through a peep hole with a video camera.

In only one trial did a male ever walk to the visual barrier and climb over it to find the concealed female. In this case the female had been rummaging in the dried leaves comprising the barrier. This rustling sound, just 10 cm from the male's face, appeared to attract the male's attention. His approach to the barrier was not the typical erratic, energized movement pattern seen when a male recognizes the presence of a female; only after climbing over the leaves and seeing the female did he display the characteristic movements. In the other 74 trials, the males sat in place, generally four to ten min (maximum 25 min.) before walking away.

As soon as the male started to walk away, the barrier was removed and the male's reaction to the visible female recorded (Table 1). When the females remained motionless (n=35), the males approached and courted 62.9 % of the time. When the females were already moving when the barriers were removed (n=16), the males approached and courted the females in 75 % of the cases. In two of the cases where the male did not court the female, the male looked at the female and took a step or two toward her, but then veered off and departed; in the other two cases, the male simply ignored the females and left. In 24 of the trials, the female initially remained motionless, but then started to move around. In 87.5 % of those cases, the males approached and courted the female after she started to move. In the 3 cases where the males did not approach, the males had already walked over a meter away from the female before she started to move. At such a distance, the line-of-sight for the departing males was partially obscured by grass or other ground cover.

Most courting males seemed uninhibited by our presence, but some of the more timid would cease courtship and depart the area if we approached. The tests introduced unknown variables that might disturb some animals more than others. For example: Does handling a male to set up the trial cause stress which overrides the male's normal detection of, and response to, females? Does handling a female cause stress that might inhibit release of pheromonal or other attractants?

Non-handled males, observed incidentally in their habitat, showed the same generalized behavioral pattern as experimental males (namely, males walking past motionless or hidden females, but then moving to the females after a visual barrier is eliminated). Experimental handling, therefore, did not seem to greatly distort behavior.

To assess the possibility that moving a female to the test site might have inhibited the release of some signal needed to attract males, or that moving a male to the test site might override his ability to detect a sex attractant or other signal from a hidden female, I varied which subject was moved the short distance to the trial site. Courtship occurred (after the visual barrier was removed) in 73% of 22 trials where only the female was relocated; in 71% of 31 trials where only the male was relocated; and in 77% of the 22 trials where both subjects were relocated. Therefore, relocation had no effect on the outcome.

To assess whether, by chance, I might be setting males on a side of the barrier away from which they happened to have an innate (or acquired) inclination to turn, I ran retrials of 12 males wherein, once the male turned away from the barrier but then returned and approached (and courted) the female after she became visible, the barrier was reestablished on the opposite side of the female, the male replaced on the opposite side of the barrier, and then retested. As usual, regardless of the side of the barrier, the males did not approach females when they were out of view, but generally did approach them when the visual barrier was lifted.

Table 1. Most males approached and courted the females after removal of the visual barrier.

Female's Behavior after Removal of Barrier	Male's Behavior toward Female after Barrier is Removed		Total
	Approach & Court	Did Not Approach	
Motionless	22	13	35
Moving	12	4	16
Initially Still, then Moving	21	3	24
Total	55	20	75

Movement v. Sex in Attracting Males

During our early years of fieldwork I observed a male chase down and court a moving male that had just been carried to the area. The courting male failed to notice or approach a nearby motionless female even after he gave up courting the closed male. It appeared that movement was an important factor in attracting the suitor. Male-male courtship has been reported among box turtles (e.g., Ewing, 1935; Boice, 1970; Ernst and Barbour, 1989). We often find that when a male courts another male, the male being courted closes up, and the suitor eventually leaves when he gets no response. However, if the male being courted fails to close up, and turns to confront the suitor, the courtship often turns into a fight (e.g. see Belzer 1999d). I conducted various experiments to begin to evaluate the importance of movement versus sexual cues in attracting a male and eliciting courtship behavior.

Experiment 2: Choice between a Hidden Male and Female

I conducted 18 trials to see whom a test male would approach when he had a choice between a hidden male and a hidden female. For these trials, a male and female were each carried to the test male's location, and placed anterior to, and equidistant from, the untouched test male. Small piles of leaves and dried grass were placed atop the introduced males and females to obscure them from the test male's view. The arrangement formed an equilateral triangle (sides of approximately 40 cm) of three turtles, all facing the same compass bearing, with the test male at the posterior vertex facing forward along a midline between the two anterior, hidden animals. Movement and visibility proved to be important in attracting a test male.

When the concealed male moved and became visible, the test male approached and began to court him (n=6). When the female moved, she was courted (n=4). When neither concealed turtle moved, the test male departed the area (n=8) walking either between the two hidden animals (n=3) or angling off and walking by the hidden female (n=2) or the hidden male (n=3) with no apparent notice of the hidden animals. When a turtle did move and emerge from cover, one always emerged before the other, thus the test male had a clear choice of one moving animal.

Possible Close-Range Signals In Courtship

Courtship of a male was often abandoned much sooner than courtship of a female. This fact, plus the observation that "sniffing" along the marginals (particularly posterior marginals) is often a prelude to courtship (Ernst, 1981; Belzer, unpublished), may suggest that at close range, some olfactory (or tactile) cues might promote continued courtship. But such hypothesized cues do not appear necessary to initiate courtship, because we have often seen males (particularly the more aggressive ones) immediately climb atop a female's (or male's) carapace and begin advanced phases of courtship (snapping at the anterior marginal scutes while balancing atop the carapace) without ever probing the tail or marginals.

Experiment 3: Courting a Moving Bone Fragment

Relevant to the suggestion of possible olfactory cues extending courtship once it has begun, I tested males' reactions to "decoy" females. I conducted 18 trials where I tested different males responses to a nearly complete skeletal carapace (n=6), a wooden decoy (n=6) and a plastic decoy (n=6) (Figure 2).

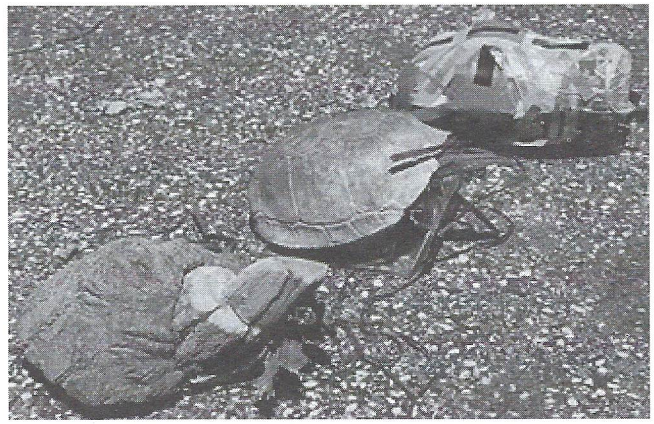

Figure 2. Wood, skeletal, and plastic decoys used to attract males.

In two cases I lured more aggressive males to chase after and court the empty carapace being maneuvered from above by a line and pole. The bony fragment was mounted on a piece of Plexiglas with leaves attached to its perimeter to substitute for the missing plastron. In each case, the male would pursue and climb upon the shell as long as I continued to keep it moving. When I stopped moving the shell, the male would pause, shift down to the side of the carapace, probe the marginals with his nose, and then begin to walk away. If I immediately started to move the shell again, the departing male would turn, chase after and climb back atop it, but then abandon the carapace once again as soon as I stopped moving it.

The carapace used in my tests was a nearly complete (pieces of marginal bones chewed off, and holes chewed through two pleural) skeletal assemblage that I had collected in 1958 at a 400 ha, southeastern Pennsylvanian summer camp that (then, but not now) had a dense box turtle population. I found its anterior end slightly protruding from the soil. Most of the carapacial bones were deeply weathered and soil-stained. This still-articulated assemblage had long been completely devoid of scutes, ligaments or tissue before I found it, and no other parts of the skeleton remained nearby. During the four decades after being removed from the soil, this specimen sat on bureaus in my various residences. It is highly unlikely that it contains any olfactory sex attractants (and plastic or wood models would not likely emit any sex attractants), yet movement of such decoys did initiate the first steps of courtship by some males.

I was able to stimulate five of the 18 males to pursue (for 15 minutes) the plastic and wood decoys being moved in circles around a rock or log by fish line. However, none of the males ever climbed atop these decoys. In general the males would pursue the decoys with their neck fully extended and close to the ground, as if to sniff at its rear. In one of the decoy trials, another male happened to walk past the test male; the test male immediately turned his attention to the real turtle, pursued him, and began to probe at his marginals and sniff, and then climb atop his carapace and began to court. Thus, although decoys might elicit some prelude to courtship, test males could obviously distinguish a decoy from a real turtle.

In contrast to their behavior with the empty carapace, males do not immediately abandon courtship of a living female when she closes up in her shell. They may continue the courtship for over an hour, even if the female remains closed and motionless, but eventually the males abandon a closed up female. If the male sees the female open up again and move, he will often return to pursue and court again (Belzer unpublished). This same behavior pattern was observed among males in a native Delaware population (H. Niederriter, pers. comm.)

Thus, while vision and movement seem very important for getting mates together, other very close range, (olfactory?) cues seem to play some final role in promoting courtship in this species once individuals have found one another.

Olfaction

While there is evidence for close-range chemosensory behavioral cues in some chelonians (e.g. Rose, 1969; Owens *et al.*, 1982; Halpern, 1992; Halpern and Holtzman, 1993), there is little evidence to suggest much role in longer range behaviors (Lutz & Musick, 1997; Halpern, 1992). Describing eastern box turtle behavior, Allard (1948) remarked: "The writer has never been able to demonstrate with satisfactory conclusiveness that the box turtle possesses a sense of smell which will advise it of distant objects, although there is some evidence that particular individuals may appreciate odors when in near contact with a substance."

Even at close range, Auffenberg (1965) reported that in some species of *Geochelone* (where olfaction demonstrably initiates copulatory attempts) the first phase of sex discrimination is entirely visual (with sexually active males challenging any tortoise-sized moving object).

My evidence argues that visual cues are critical in getting *Terrapene* mates together. This view is similar to that for *Chrysemys picta* by Vogt (1979) and Halpern (1992) where "...in the absence of visual and tactile cues, traps with males are equally likely to attract males as are traps with females. These results have been interpreted to suggest that female pheromone, if present, is not capable of attracting males at a distance but requires direct contact".

Experiment 4: Pairs (and even Large Aggregations) of Concealed Females Fail to Attract Males

To further assess the possibility that olfaction might play some role in getting mates together, we conducted five trials in which two females (to intensify any olfactory cues) were placed inside a cylindrical, 60 cm diameter corral made of thick, opaque, blue cotton cloth fastened to a circular wire frame 60 cm tall. A thin nylon cord was fastened to the frame and threaded through a pulley on an overhanging tree limb, so that an observer hidden in a blind in a different tree could pull the line to tilt the corral up and expose the interior. In each test, a male was placed outside the corral, his behavior observed, and then the corral lifted before he abandoned the area. This was done first with the corral empty and then repeated with two females placed in the corral.

In all five cases, the males eventually walked away from the corral when it was empty. When it was lifted to reveal the empty interior, one male looked back when attracted by the motion, but then continued to walk away from the area; a second male took no note of the movement and proceeded to walk away; a third male was frightened by the movement and closed his shell before eventually resuming his exodus; and the other two males interrupted their exodus and returned to explore the apparatus when it was lifted, before proceeding to abandon the site.

When two females were inside the opaque corral, the males behaved in the same way. They displayed no attraction to it; none approached or probed its edges, nor remained near it for an extended time. In one case, as the male was departing, one of the enclosed females climbed up and over the rim before the corral was raised. The thump she made when falling to the ground outside the corral attracted the departing male's attention. He turned back, returned, chased her down and began to court. In the other four cases, at least one female walked out of the corral when it was raised. This attracted the departing male's attention and he returned to court. In one of those cases, when the male was courting the first female to emerge, he abandoned her tightly closed shell to chase after the second one when she emerged.

Thus, even when two females are close at hand, males seem unaware of them unless the females are visible. These observations help explain why if I took a female from a courting male, and hid her in a box 2.5 m away, the male would continue rummaging for up to 20 minutes where he had last seen her, in a seemingly confused pattern (intermittently pausing, looking around, walking in tight circles, probing the soil, walking away a few steps and then doubling back, etc). In only one case did the male home in on the box and that was when the female was vigorously scratching to get out. In that case, he walked completely around the box once and then returned to where he had last seen the female and resumed his rummaging in the leaves and soil.

Even stronger evidence for the importance of close range visual, and the lack of distant, cues in enabling males to find females comes from seven consecutive years (1995 - 2001) when most or all females in the habitat were confined (6-8 weeks) to a pen located in the core of the 80 ha McKeever Environmental Center preserve. The pen is a 900 m^2 area enclosed by a one-meter tall opaque black silt-fence fabric constructed on a south-facing slope. A stream passes by 25 m to the south (lower end) of the fence, and a wetland encompasses the southern end of the pen and adjacent habitat. The pen was used for studies of nesting behavior and nest-site selection for six to eight weeks each June and July. A defacto test of male behavior occurred each year because all males remained at-large in the surrounding habitat, so their movements before, during, and after females were concentrated in the pen could be compared. Even when ALL females from the habitat are in the pen, the males do not converge on the area nor change their movement patterns. These data are now being prepared for future publication. We also had the opportunity to telemeter the one native male turtle found in the region (in contiguous woods about 1400 m from our research population) and follow his movements for one year. During that year, he too failed to gravitate toward the females inside the McKeever preserve.

Certainly, if free-ranging males could detect females at distances, they would have been attracted to the females' pen. That these males, who appeared oblivious of such large concentrations of females, had a strong mating proclivity was demonstrated by periodically carrying one to the pen and placing him inside, at which point he promptly moved to, courted, and often copulated with, the first female he saw (Belzer 1999d).

Discussion on Finding Mates

Courtship behavior can vary among male eastern box turtles. For example, males often prod and "sniff" another turtle before mounting to begin courtship, but some do not. A few of our males pursue a female in a lock-step pattern (taking steps only when she steps, and halting when she halts). One male climbed atop and began to court a male who had already mounted a female and was courting her (Sue Seibert - pers. comm.). Some males refuse to court when a human observer is nearby, but have been discovered copulating and so obviously do court females when not under observation. Some males will court an unresponsive female for over an hour whereas others will abandon the effort after 15 minutes. Despite behavioral idiosyncrasies in the hundreds of courtships we observed, and despite variations in our method of observing and testing the turtles' responses to each other, a common behavioral denominator emerged: males don't move to concealed females, even when close to them. It was only when females became visible that males moved to them and began to court. In many cases, not only visibility, but also movement by the female, was required to elicit approach by the male.

The generality of this finding among our males is remarkable in that the displaced males were donated from many different parts of Pennsylvania (Belzer, 1999b). The behavior can therefore not be dismissed as the genetic peculiarity of a particular deem. And it can't be dismissed as a behavioral artifact caused by lack of a home range because some of these males had reestablished stable home ranges in their new habitat years previously (see Belzer 1999b). Moreover, the same behavioral requirement (for a male to see a female before approaching to court) was seen when I repeated several tests with the one native male who resides near our research site. Tests similar to ours are being planned for native box turtle populations in Delaware (Jacob Bowman, pers. comm.).

Our findings show that male eastern box turtles cannot find females who are not close enough to be seen or heard. In self-sustaining populations, the close contacts needed to initiate a male's recognition of a female's presence (and consequent courtship) are probably matters of chance encounters, the likelihood of which is improved by knowledge of where females had been found in the past within his home range. This view of box turtle behavior is consistent with Stickel's (1989) failure to observe mating between box turtles that did not share overlapping home ranges within their habitat.

Such a basis for reproductive behavior has an important conservation implication: if pet collecting, vehicular traffic, etc. thin native populations, then reproductive activity diminishes. Dense adult populations must be conserved wherever they still remain since chelonian population losses are not compensated by increased reproduction or faster maturation (Brooks, 1997).

Population Density and Recruitment

Although female box turtles may retain viable sperm for years (Gist and Jones, 1987), the proportion of infertile eggs increases as access to males declines (Halgren-Scaffidi, 1986; Dodd, 2001). That observation on egg fertility is consistent with the evidence that while turtle sperm may deteriorate little over periods of weeks or months during their storage in male or female ducts (Gist, *et al.*, 2001), their fertilizing ability may deteriorate over longer periods during retention in the female reproductive tract (Hildebrand, 1929; Gist and Congdon, 1998; Gist *et al.*, 2000; Gist, 2002 pers. comm.). Some box turtle clutches are completely infertile (Ernst *et al.*, 1994). Even when females have frequent encounters with males, 20% or more of their eggs may be infertile (Allard, 1935; Ernst *et al.*, 1994). That incidence of infertile eggs among females with continuous access to males matches our observations at the Buttermilk Hill Nature Sanctuary during 1999 and 2000. A group of six females had been confined with nine males in a 1.2 ha area. They produced 18 eggs with four showing no signs of development.

Besides improving fertility, high adult population density fosters multiple copulation and multiple paternity, important for sustaining a deem's adaptability (Halgren-Scafidi, 1986; Mrosovsky *et al.*, 1995; Lovich, 1996; Rovero *et al.*, 1999).

Embryonic Development and Recruitment

Juvenile recruitment is precarious because of the small clutch size (mean=4 eggs) (e.g. Harless and Morlock, 1979; Ernst *et al.*, 1994; Dodd, 2001). Compounding the contribution of small clutches to poor recruitment is the frequent failure of eggs to survive or develop in the field (Zeiller, 1994). Predation destroys many (e.g., Madden, 1975; Ernst *et al.*, 1994; Dodd, 2001) and sometimes all nests (Karen Kovalchick, pers. comm.; Belzer *et al.*, unpublished). When clutches escape predation, embryonic development is often terminated by climatic stresses (Halgren-Scaffidi, 1986; Zeiller, 1994; Tucker *et al.*, 1997; Tucker and Packard, 1998).

In our experience with 42 clutches (mean clutch=4 eggs; range = 1-7 eggs), at the McKeever Environmental Learning Preserve between 1995 and 2001, only six of 30 eggs left in-situ and successfully protected against predation by screen barriers, initiated embryonic development. The actual development among those nests would doubtless have been less because during the extended droughts of some seasons, we watered selected nests to assess the developmental toll from soil desiccation. Only 8% of eggs among the in-situ nests that were not watered during droughts showed embryonic development. This lower figure agrees with Don Zeiller's (1994) assessment of the dismal prospects for in-situ box turtle nests.

In contrast, 91 eggs developed among 123 eggs that were moved to incubators at either 75°F or 85°F, and 96-98%rh, in a medium of 1.7:1 (wt:wt) water:vermiculite.

This picture of the poor prospects for in-situ eggs was reflected in another small study (Belzer, Seibert, Atkinson, unpublished), in which eggs from each of six clutches were divided between artificial and in-situ incubation to serve as matched pairs. Development among eggs left in the soil was 17% (but zero if we exclude the eggs from nests artificially watered during droughts). Development occurred in 70% of the artificially incubated eggs.

Hatchling Survival and Recruitment

When eggs escape predation, and are fortunate enough to encounter environmental conditions that enable their development, the resulting juveniles have a poor prospect of surviving the eight to 10 years needed to develop shells durable enough to withstand predator attacks (Madden, 1975; Ernst *et al.*, 1994; Dodd, 2001; Belzer *et al.*, 2002). Our findings on the poor prospects for box turtle eggs and juveniles are in agreement with the low recruitment found in studies of native populations (e.g., Doroff & Keith, 1990; Klemens, 1989 & 2000). Survivorship does not reach that of adults till juveniles reach about 250-300g (Yahner, 1974; Murphy, 1976)

Concluding Remarks

A species with the low recruitment capacity of the eastern box turtle cannot easily rebound from population losses. Study of a relatively dense Maryland box turtle population (25/ha during the 1940's) in the vast Patuxent Wildlife Refuge (Hall *et al.*, 1999), has seen a continuous decline in density (down to 6/ha by the 1990's) and, so far, an inability to recover from its mid-century population losses to floods. In contrast to this well buffered population in Patuxent's 4,800 ha preserve, consider the condition of most contemporary box turtle populations whose densities are much lower and are annually decimated by the consequences of habitat fragmentation and human intrusion. If a population's density is already diminished, rebounds from even small losses can become impossible (Williams & Parker, 1987). In a 10-year study of recruitment in the Dunlap Hollow box turtle population of Wisconsin, after its historically high density had fallen to 3/ha, the population was found to be unable to sustain loss of even one adult per year for the deem to avoid extinction (Doroff & Keith, 1990; Klemens, 2000). With annual population losses (to winter kill and other natural events) of 7% to 20% (Yahner, 1974; Williams & Parker, 1987; Grobman, 1990), let alone added losses to legal or illegal pet collection, many destabilized contemporary populations of box turtles have undoubtedly already passed their threshold to gradual extinction (cf. Holly Niederriter, 2000). Similarly, studies of alligator snapping turtle population dynamics indicate that 98% adult survivorship is needed to avoid eventual (if gradual) extirpation (Reed *et al.*, 2002). This high survivorship requirement for the alligator snapping turtle is virtually identical to that for the Dunlop Hollow, WI box turtle population. Very small losses (just one or two extra adults each year) can result in a gradual (but inexorable) decline toward extirpation (Doroff & Keith, 1990; Reed *et al.*, 2002), which is imperceptible in the short term.

The literature on declining box turtle populations suggests to me that a self-sustaining population may need adult densities of more than 25/ha in order to achieve sufficient reproductive activity to rebound from events that thin the population (e.g., Carpenter, 1957; Williams, 1961; Adler, 1970; Murphy, 1976; Stickel, 1978; Davis, 1981; Schwartz *et al.*, 1984; Halgren-Scaffidi, 1986; Williams & Parker, 1987; Doroff & Keith, 1990; McCollough, 1997; Tyning, 1997; Hall *et al.*, 1999; Niederriter, 2000; Julie Miller, 2000). Many existing box turtle populations lack such densities, and their critical instability, and gradual declines, generally go unnoticed (e.g., Williams, 1961; Murphy, 1976; Stickel, 1978 & 1989; Davis, 1981; Schwartz *et al.*, 1984; Halgren-Scaffidi, 1986; Williams & Parker, 1987; Doroff & Keith, 1990; McCollough, 1997; Tyning, 1997; Hall *et al.*, 1999; Quinlan *et al.*, 1999; Niederriter, 2000; Julie Miller, 2000).

The centenarian longevity of adult box turtles (Graham & Hutchison, 1969; Murphy, 1976; Stickel 1978; Miller, 2001) enables geriatric remnants of a doomed population to persist for many decades and thereby mask a critical insufficiency of juvenile recruitment (Klemens 1989, 1997, and 2000). Reviewing 25 years of study of a native box turtle population at the University of Delaware, Holly Niederriter (pers. comm., 1999) remarked: "The perception during the 1970's and even during the early 1980's was that this population was a healthy one. Surely, finding 30 turtles on a 14.8 ha site would not cause most biologists to be alarmed, but now it is clear that this population was declining even when many turtles were still being found." At the American Fisheries Society 1999 Symposium on the conservation of long-lived species, D. Crouse (1999) noted critical management lapses for species like this: "Long lived species are particularly vulnerable because the very longevity of older individuals introduces a delay in management response... this matter of perception (makes) this a serious problem... persistent older stages mask declines in (juvenile) recruitment until the problem is well advanced making recovery even more difficult."

Remarkably, when box turtle populations have been studied long enough, previously unnoticed declines have become apparent. What we often regarded as "good numbers" in box turtle density, and indicative of population stability, were revealed as deficient only after generations of study. Inferences from the densities of most contemporary box turtle populations may make the notion of normal densities of over 25/ha seem incredible, but such densities were commonplace a century ago, and in some places regarded a "nuisance", but they have largely disappeared today (e.g. Murphy, 1976; cf. Breisch, 1997 and McCullough, 1997). In insular regions, dense populations can still be found (e.g., Dodd *et al.*, 1994). I have personally known only two populations with densities over 25/ha (one in a 400 ha summer camp in SE PA, which was surrounded by thousands of hectares of woodland and farms during the 1960's, and one on a 15 ha knoll in SW MO bounded by hundreds of hectares of woodland, golf course and farmland during the 1970's). Although those populations still persist some three and four decades later, the present densities are nothing like they once were and their former undeveloped habitat buffers are much smaller or gone.

The published studies on native populations noted in this paper reveal that densities which many would regard as normal and adequate for long term population stability, have turned out (in hind sight) to be too low to enable rebound from losses, and the time for intervention (to try to slow the population's inevitable demise) was passed decades before. This emerging insight from studies of living populations is confirmed by archaeological findings. The Iroquois in western New York used box turtles for a variety of purposes. Box turtle numbers were eventually depleted, so the Iroquois had to switch to snapping turtles instead (Adler, 1970). Now, with more than 200 yrs to recover in the persistent (and remote, extensive) habitat of those western NY locales, box turtle populations have not returned.

With box turtle populations becoming even more fragmented, and recruitment declining, measures are needed to save extant deems. We have completed the first nine years of tests on the feasibility of using donated, homeless adult eastern box turtles to establish a self-sustaining, resident population inside preserves where ancestral populations had been completely extirpated (e.g. Belzer 1999b, 1999c, and unpublished data). These turtles included wild caught pets and otherwise displaced individuals whose natal Pennsylvania homes were unknown (Belzer, 1996 and 1999b). We now know that despite many consecutive years of intensive day-to-day monitoring, and retrieval when animals move out of the preserve, well over 60% of the displaced turtles failed to establish new home ranges within the confines of the 80 ha McKeever preserve. A complete picture from our initiation of similar studies at the much larger Buttermilk Hill Nature Sanctuary will not be known for many years but in our first year of work we already found that translocated box turtles will abandon even this 200 ha preserve. This reflects Bob Cook's (1996) finding of high emigration from a 400 ha preserve at New York's Gateway National Recreation area. It is clear that the costs for this approach to repatriation is prohibitive and fails to create a population density that would enable long-term survival of any established population. My pessimistic conclusion concerning the futility of using adult animals to rebuild declining or lost box turtle populations was echoed by a repatriation study in the Albany Pine Bush Preserve of NY (Kallaji, 1998; 1999 pers. comm.). Repatriation often fails and is widely regarded as a dubious conservation tool for many species (Reinert, 1991; Dodd and Siegel, 1991; Reinert and Rupert, 1999). Existing knowledge on density decline and ineffective remedial options already warns that the immediate lesson we need to learn is that populations need strong protection while their densities are high; this species is poor at recovering from losses.

Even as we continue to study the behavior of our relatively few adults who seem to have developed home ranges following relocation, we are initiating an assessment of the possible utility of headstarted juveniles as a repatriation tool that might at least slow population declines (Belzer, et al 2002). Although a strategy with poor prospects (Taubes, 1992; Heppell *et al.*, 1996; Morafka *et al.*, 1997), headstarting sometimes is productive (Shaver, 1996) and needs to be evaluated for box turtles since no alternative may remain for trying to reverse this species' declining numbers.

The growing understanding of the peculiar and precarious population dynamics of long lived species with low reproductive potential, like *Terrapene*, should serve as notice to management agencies for the need to launch immediate, aggressive, proactive conservation policies to protect adults. Trying to increase numbers of eggs and hatchlings (to compensate for losses of adults) will not work since the younger stages are almost all lost.

"Many species replace their population losses by producing numerous offspring who mature early to offset low survivorship; others produce a few offspring invested with high survival prospects. Box (and many other) turtles are different: maturity isn't reached till age 10 or so; a female lays few if any eggs each year; eggs & hatchlings rarely survive. How can adults sustain a population?... By staying in the habitat a long time (e.g.70-80 yrs) ... Removing adults strikes at the heart of this population mechanism... (Belzer, 2000)." A female box turtle can produce eggs as long as she lives (Miller, 2001); and probably needs those eight or more decades of egg production to leave an adult replacement in her population.

The traditional management approach of waiting till adult population declines are obvious before exercising aggressive conservation measures for a species is a dead end strategy for eastern box turtles and species like it; by the time adult population declines are significant, it is too late. Barry Yoeman (2002) recently highlighted the common disconnect in chelonian management: "There's a reason wildlife managers haven't thought in those terms: Most of the animals we try to protect such as deer, rabbits, and quail, are relatively short-lived (and produce numerous viable young)". His remarks echo insights published by Congdon *et al.* (1993), and the alert issued to wildlife managers (quoted above in these concluding comments) by Deborah Crouse (1999). In long-lived species like *Terrapene*, the key to population stability is retaining aged adults in the habitat for their full, long lives (e.g., Congdon *et al.*, 1993; Crouse, 1999; Musick, 1999; Miller, 2001; Yeoman, 2002). As summarized by Ron Nussbaum (in Yeoman, 2002): "... what would a conservationist do with this information? Well, you would make sure the adults survive..."

My findings on *Terrapene* behavior illustrate that failing to protect adult densities undermines even the very first steps (mating encounters) needed for any hope of progressing to that rare event of a new adult's recruitment into an aging population.

Acknowledgements

The magnitude of these studies would have been impossible without the help and advice of many people. I am deeply grateful to them all. Some major benefactors were: Susan Seibert, Ben Atkinson, Maggie Byrne, Ann Davis, Peter Jenkins, Kathie Goodblood, and Monica Held for grueling nighttime vigils to determine which females are nesting and to mark or protect nest sites; Mimi Halpern for leads into the literature on chelonian chemoreception; Julie Miller for leads into the literature on the population dynamics of long-lived species; Robert Cook and Howard Reinert for advice on the ecological issues associated with repatriation studies; Kelly Seibert & Shawn Wigle for remote videotaping; The McKeever Environmental Learning Center and Jerry Stanley & Kathie Goodblood of the Buttermilk Hill Nature Sanctuary for permission to conduct our field studies within their preserves; Mike Kallaji for sharing unpublished data; Ed Belzer for advice on experimental controls; and Heather Kalb for editorial improvements in the submitted manuscript. Some of the funding for this work came from a Clarion University Foundation Projects Grant and from two summer sabbatical awards granted by Clarion University of Pennsylvania.

Literature Cited

Ackerman, L. 1997. The Biology, Husbandry and Health Care of Reptiles Volume I: The Biology of Reptiles. T.F.H. Publications, Neptune City, NJ. 382 pp.

Adler, K. 1970. The influence of prehistoric man on the distribution of the box turtle. Ann Carnegie Mus 41(9):263-280.

Allard, H.A. 1935. The natural history of the box turtle. The Scientific Monthly 41:325-338.

Allard, H.A. 1948. The eastern box turtle and its behavior. J. Tenn Acad Sci. 23:307-321.

Auffenberg, W. 1965. Sex and species discrimination in two sympatric South American tortoises. Copeia 1965(3): 335-342.

Belzer, B. 1996. Box turtle repatriation in Northwestern Pennsylvania. Box Turtle Research & Conservation Newsletter 4:12-13.

Belzer, B. 1999a. Survival among translocated eastern box turtles. Box Turtle Research & Conservation Newsletter 8:7-8.

Belzer, B. 1999b. Home range establishment by translocated eastern box turtles. Box Turtle Research & Conservation Newsletter 8:3-7.

Belzer, B. 1999c. Repatriation criteria. Box Turtle Research & Conservation Newsletter 8:2-3.

Belzer, B. 1999d. Eastern box turtle aggression. Box Turtle Research & Conservation Newsletter 8:13-14.

Belzer, B, and M.B. Steisslinger. 1999. The box turtle: Room with a view on species decline. The Amer Biol Teacher 61(7):510-513.

Belzer, W. 2000. Comments by Dr. W. Belzer commending a ban on box turtle collecting submitted to PA Fish and Boat Commission Herpetology Advisory Committee Meeting, May 15, 2000.

Belzer, W.R., S.Seibert, and B. Atkinson. 2002. Putative chipmunk predation of juvenile eastern box turtles. Turtle and Tortoise Newsletter. 5:8-9.

Boice, R. 1970. Competitive feeding behaviors in captive *Terrapene c. carolina*. Animal Behav 18:703-710.

Boiko, V. 1984. The participation of chemoreception in the organization of reproductive behavior in *Emys orbicularis* (Testudines, Emydidae). Zool Zh 63:584-589.

Breich,A. 1997. The status and management of turtles in New York. (editor) T.F. Tyning , Status and Conservation of Turtles in the Northeastern United States. Mass Audubon Society. Serpent's Tale publishing Lanesboro, MN. p.11-14.

Brooks,R.J. 1997. Dynamics of a northern population of snapping turtles: How can long-lived species be conserved?" (editor) T.F.Tyning, Status and Conservation of Turtles in the Northeastern United States. Mass Audubon Society. Serpent's Tale publishing Lanesboro, MN. p.31-33

Carpenter, C.C. 1957. Hibernation, hibernacula and associated behavior of the three-toed box turtle (*Terrapene carolina triunguis*). Copeia 1957:278-282.

Cook, R.P. 1996. Movement and ecology of Eastern box turtles repatriated to human habitat" Box Turtle Research & Conservation Newsletter 5:8.

Congdon, J.P., A.E. Dunham, and R.C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conservation Biology 7(4):826-833.

Crouse. D.T. 1999. The consequences of delayed maturity in a human-dominated world. (ed) A. Musick, Life in the Slow Lane: Ecology and Conservation of Long-lived Marine Animals. Amer. Fish. Soc. Symposium #23, American Fisheries Society, Bethesda, MD. p.195-202.

Davis, M. 1981. Aspects of social and spatial experience of eastern box turtles, *Terrapene carolina carolina*." Ph.D. diss. University of Tennessee, Knoxville.

Dodd, C.K., Jr. 2001. North American Box Turtles: A Natural History. Univ of Oklahoma Press, Norman, OK. 1231 pp.

Dodd, C.K., Jr and R. Siegel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47:336-350.

Dodd, C.K., Jr., and R. Franz. 1993. The need for status information on common herpetofaunal species. Herp Rev 24:47-50.

Dodd, C.K., Jr, R. Franz, and L.L. Smith. 1994. Activity patterns and habitat use of box turtles (*Terrapene carolina bauri*) on a Florida island, with recommendations for management. Chel Conservn Biol 1(2):97-106.

Doroff, A.M. & L.B. Keith. 1990. Demography and ecology of an ornate box turtle (*T. ornata*) population in south-central Wisconsin." Copeia 1990: 387-399.

Ernst, C.H. 1981. Courtship behavior of male *Terrapene carolina major* (Reptilia, Testudines, Emydidae) Herp Rev 12(1):7-8.

Ernst, C.H. and R.W. Barbour. 1989. Turtles of the World. Smithsonian Inst Press, Wash, D.C. 313 pp.

Ernst. C.H., J.E. Lovich, and R.W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Inst Press, Wash DC.

Ewing, H.E. 1935. Further notes on the reproduction of the eastern box turtle, *Terrapene carolina* (Linne). Copeia 1935:102.

Gist, D.H. and J.M. Jones. 1987. Storage of sperm in the reptilian oviduct. Scanning Microscopy 1:1839-1849.

Gist, D.H. and J.D. Congdon. 1998. Oviductal sperm storage as a reproductive tactic of turtles. J Exp Zool 282:526-534.

Gist, D.H., T.W. Turner, and J.D. Congdon. 2000. Chemical and thermal effects on the viability and motility of spermatozoa from the turtle epididymis. J. Reproduction and Fertility 119:271-277.

Gist, D.H., S.M. Dawes, T.W. Turner, S. Sheldon, and J.D. Congdon. 2000. Sperm storage in turtles: a male perspective. J. Exp Zool 292:180-186.

Graham, T.E. and V.H. Hutchison. 1969. Centenarian box turtles. International Turtle and Tortoise Society Journal 3:25-29.

Grobman, A.B. 1990. The effect of soil temperature on emergence from hibernation of Terrapene carolina carolina. Amer Midland Naturalist 124:366-371.

Halgren-Scaffidi, L. 1986. Habitat, home range and population study of the eastern box turtle (*Terrapene carolina*). MS thesis, Univ Maryland, College Park, MD.

Hall, R.J., P.F.P. Henry, and C.M. Bunck. 1999. Fifty-year trends in a box turtle population in Maryland. Biol Conserv 88:165-172.

Halpern, M. 1992. Nasal chemical senses in reptiles: Structure and function. (editors) C. Gans and D. Crews, Biology of Reptilia. Univ of Chicago Press, Chicago, IL. p.423-523.

Halpern, M. and D. Holtzman. 1993. Chemosensing and Chemosignaling in Reptiles: Proceedings of a satellite conference on 'Reptilian Chemical Senses and Signals'. Brain, Behavior and Evolution Vol 41(no's 3-5). Karger, Basel, Switzerland.

Harless, M. and H. Morlock. 1989. Turtles: Perspectives and Research. Robert E. Krieger Publishing Co. Malbar, Florida. 695 pp.

Heppell, S.S., L.B. Crowder, and D.T. Crouse. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. Ecol. Appl. 6(2):556-565.

Hildebrand, S.F. 1929. Review of experiments on artificial culture of diamond back terrapins. Bull U.S.Bureau of Fisheries 45:25-70.

Kallaji, M. 1998. Albany pine bush eastern box turtle experimental release project - Interim Report. New York State Department of Environmental Conservation, Endangered Species Unit. Delmar, New York. 11 pp.

Klemens, M.W. 1989. The methodology of conservation. (editors) R. Swingland and M.W. Klemens, The Conservation Biology of Tortoises. IUCN Species Survival Commission, no.5. Gland, Switzerland. p.1-4.

Klemens, M.W. 1997. Conserving *Clemmys*. (editor) T.F. Tyning, Status and Conservation of Turtles in the Northeastern United States. Mass Audubon Society. Serpent's Tale publishing Lanesboro, MN. p.23-24.

Klemens, M.W. 2000. Turtle Conservation. 334 pp. Smithsonian Inst Press, Wash, DC. p.20-21.

Lieberman, S. 1994a. Biological Data submitted in support of USFW proposal to add *Terrapene* spp. to Appendix II of the Convention on the International Trade in Endangered Species. S. Lieberman. Chief of the Branch of Operations, Office of CITES Management Authority, U.S. Fish & Wildlife Service 4401 N. Fairfax Drive Room 432 Arlington, VA 22203.

Lieberman, S. 1994b. Can CITES save the box turtle? Endangered Species Tech Bull 19(5):16-17.

Lovich, J.E. 1996. Possible demographic and ecologic consequences of sex ratio manipulation in turtles. Chelonian Conservn & Biol 2:114-117.

Lutz, P.L., and J.A. Musick (eds). 1997. The Biology of Sea Turtles. CRC Marine Sci Series. CRC Press Boca Raton, Florida. 448 pp.

Madden, R.C. 1975. Home range, movements, and orientation in the eastern box turtle *Terrapene carolina carolina*. Ph.D. diss. City Univ of NY.

McCollough, M. 1997. Status and conservation of turtles in Maine. (editor) T.F. Tyning, Status and Conservation of Turtles in the Northeastern United States.. Mass Audubon Society. Serpent's Tale publishing Lanesboro, MN. p.7-11.

Miller, J.K. 2000. Suburban sprawl and the three-toed crawl: A demographic population study of the three-toed box turtle across 35 years of land-use change. M.S. thesis, U of Idaho. Moscow Idaho. 95 pp.

Miller, J.K. 2001. Escaping senescence: Demographic data from the three-toed box turtle (*Terrapene carolina triunguis*). Exp Gerentol 36(4-6):829-32.

Morafka, D.J., K.H. Berry and K. Spangenberg. 1997. Predator-proof field enclosures for enhancing hatching success and survivorship of juvenile tortoises: a critical evaluation. (editor) J.V. Abbema, Proceedings, Conservation, Restoration, and Management of Tortoises and Turtles, An International Conference. A Joint Publication of the New York Turtle and Tortoise Society and the WCS Turtle Recovery Program, NY, p.147-165.

Murphy, J. (1976) The natural history of the box turtle. Bulletin Chicago Herp Soc 11:2-47

Musick, A. 1999. Ecology and conservation of long-lived marina animals. (ed) A. Musick, Life in the Slow Lane: Ecology and Conservation of long-lived Marine Animals. American Fisheries Society Symposium #23, American Fisheries Society, Bethesda, MD. p.1-10.

Niederriter, H. 2000. Ecology of eastern box turtles (*Terrapene carolina carolina*) in an isolated forest fragment in Northern Delaware. M.S. thesis. Univ of Delaware.

Owens, D., M. Grassman, and J. Hendrickson. 1982. The imprinting hypothesis and sea turtle reproduction. Herpetologica 38:124-135.

Quinian, M., C. Swarth, and M. Marchand. 1999. Characteristics of a high-density eastern box turtle population on Maryland's costal plain. Symposium on Conservation and Ecology of Turtles of the Mid-Atlantic Region, held Oct 30 & 31, 1999 at the National Wildlife Visitor Center of the Patuxent Research Refuge, Laurel Maryland.

Reed, R.N., J. Congdon and J.W. Gibbons. 2002. The Alligator Snapping Turtle [*Macrochleys (Macroclemys) temminckii*]: A review of ecology, life history, and conservation, with demographic analyses of the sustainability to take from wild populations. A report to the Division of Scientific Authority, United States Fish and Wildlife Service. Univ of Georgia, Savannah River Ecology Lab. 17pp.

Reinert, H.K. 1991. Translocation as a conservation strategy for amphibians and reptiles: Some comments, concerns, and observations. Herpetologica 47(3):357-363.

Reinert, H.K., and R.R. Rupert, Jr. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. J of Herpetology 33(1):45-61.

Rose, F.L. 1969. Tortoise chin glands fatty acid composition: behavioral significance. Comp. Biochem. Physiol. 32:577-580.

Rovero, F., M. Lebboroni, and G. Chelazzi. 1999. Aggressive interactions and mating in wild populations of the European pond turtle *Emys orbicularis*. J of Herpetology 33(2):258-263.

Schwartz, E.R., C.W. Schwartz, and A.R. Kiester. 1984. The three-toed box turtle in Central Missouri, Part II: A nineteen-year study of home range, movements and population. Missouri Dept of Conservation Terrestrial Series #12, Jefferson City, MO. 30pp.

Shaver, D,J. 1996. Head-started Kemp's ridley turtles nest in Texas. Marine Turtle Newsletter 74:5-7.

Stickel, L.F. 1978. Changes in a box turtle population during three decades. Copeia 1978:221-225.

Stickel, L. F. 1989. Home range behavior among box turtles (*Terrapene c. carolina*) of a bottomland forest in Maryland. J. Herpetol. 23:40-44.

Taubes, G. 1992. A dubious battle to save the Kemp's ridley sea turtle. Science:256:614-616.

Tucker, J.K., F.J. Janzen, and G.L. Paukstis. 1997. Response of embryos of the red-eared turtle (*Trachemys scripta elegans*) to experimental exposure to water-saturated substrates. Chelonian Conservation and Biology 2(3):345-351.

Tucker, J.K., and G.C. Packard. 1998. Overwinter survival by hatchling sliders (*Trachemys scripta*) in west-central Illinois. J of Herpetology 32(3):431-434.

Tyning, T. 1997. The quick decline of slow turtles." (ed) T.F.Tyning (ed), Status and Conservation of Turtles in the Northeastern United States. Mass Audubon Society. Serpent's Tale publishing Lanesboro, MN. p. X.

Vogt, R. 1979. Spring aggregating behavior of painted turtles, *Chrysemys picta* (Reptilia, Testudines, Testudinidae). J. Herpetology 13: 363-365.

Williams, E.C., Jr. 1961. A study of the box turtle, *Terrapene carolina carolina* (L), population in Allee Memorial Woods, Indiana. Indiana Acad Sci 71:399-406.

Williams, E.C., Jr and W.S. Parker. 1987. A long-term study of a box turtle (*Terrapene carolina carolina*) population at Allee Memorial Woods, Indiana, with emphasis on survivorship." Herpetologica 43:328-335.

Yahner, R.H. 1974. Weight change, survival rate and home range change in the box turtle, *Terrapene carolina*. Copeia 1974:546-548.

Yoeman. B. 2002. Can turtles live forever? Discover, June 2002:61-66.

Zeiller, D. 1994. So You Like Turtles, 88 Norman Place, Tenafly NJ 05670.