

Demographic and Ecological Factors Affecting Conservation and Management of the Diamondback Terrapin (*Malaclemys terrapin*) in South Carolina

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ABSTRACT. – We used mark-recapture data from 1274 original captures and 1131 recaptures during a 16-year population study of diamondback terrapins (*Malaclemys terrapin*) in a South Carolina, USA, salt marsh to examine demography and ecological factors critical for management recommendations and conservation. Adult females were significantly larger but less numerous than adult males. Most of the terrapins captured in the tidal creeks were sexually mature, first- and second-year individuals being absent and third- and fourth-year individuals being scarce, suggesting the use of a different habitat by juveniles. Most individuals exhibited high site fidelity, remaining in the same creek from year to year, although similar creeks were nearby. The observation that individuals rarely moved between adjacent tidal creeks and remained in one small area as adults is of particular significance to management considerations for the species. Terrapin numbers in one creek were high during the 1980s and declined steadily after 1990, with only a single individual being present after 1993. The combination of high site fidelity and limited dispersal by terrapins from other creeks and the onset of recreational crab trapping and other human activities are presumed to have been responsible for the disappearance of the population. Without the implementation of strong measures to assure sustainability of terrapin populations throughout the range, continued population declines are likely.

KEY WORDS. – Reptilia; Testudines; Emydidae; *Malaclemys terrapin*; turtle; conservation; dispersal; management; size; sex ratio; USA; South Carolina

Effective approaches to wildlife management and conservation are ideally based on an understanding of the life history traits and ecology of target species. In addition to local environmental conditions, demographic features of some populations reflect human use and other anthropogenic impacts. Although population ecology is characteristically considered in establishing the special management needs of game species, most non-game species, including freshwater turtles, have been neglected in most instances (Brooks et al., 1988; Lovich, 1994). Turtles are indisputably valuable components of many freshwater habitats, not only by constituting a major proportion of the faunal biomass but also by serving in food web roles as herbivores, carnivores, scavengers, and prey (Iverson, 1982; Congdon et al., 1986; Congdon and Gibbons, 1989). Both freshwater and terrestrial turtles may also provide important links within and among aquatic habitats by serving as vectors of seed dispersal for plants (Braun and Brooks, 1987; Iverson, 1987; Kaczor and Hartnett, 1990; Milton, 1992) and contributing to a variety of other interactions that result in environmental heterogeneity and symbiotic associations (Kaczor and Hartnett, 1990; Lago, 1991; Witz et al., 1991).

Most turtles on which population studies have been conducted possess certain life history traits that are distinct-

ive when compared with many other animals, namely delayed maturity, extended longevity without reproductive senescence, and iteroparity with highly variable nest success (Gibbons, 1987; Wilbur and Morin, 1988). Because of these life history traits related to longevity, many turtle populations are restricted in their abilities to respond rapidly to suites of anthropogenic and natural changes that result in dramatic perturbations in demography (Brooks et al., 1988, 1991; Congdon et al., 1993, 1994; Germano and Joyner, 1988; Galbraith et al., 1997; Heppell, 1998). Consequently, wild populations of turtles are likely inappropriate for “sustainable harvest” (Klemens and Thorbjarnarson, 1995; Burke et al., 2000). Thus, if a management approach or resource use depends on sustainability, data on demography and ecology may be necessary to confirm that harvests can actually be made on a long-term basis if removal quotas are to be realistic. Under such conditions, freshwater turtles are often fitting study organisms.

The diamondback terrapin (*Malaclemys terrapin*) is a small, estuarine emydid turtle with a geographic range from Cape Cod to Texas (Ernst et al., 1994) and is the only turtle endemic strictly to the coastal marshes of the Atlantic and Gulf Coasts of the United States. The terrapin was heavily exploited as a gourmet food item in the late 19th and early



Figure 1. Map showing juxtaposition of tidal creeks populated by diamondback terrapins on Kiawah Island, South Carolina, USA.

20th centuries, whereupon its numbers fell to low levels (McCauley, 1945; Carr, 1952). In effect, the species became commercially extinct so that further harvest was not profitable, as noted three-quarters of a century ago by Hildebrand and Hatsel (1926) who stated that “their numbers soon would be so reduced that fishing for them would not be remunerative.” Because of the economic importance of terrapins in the early 1900s and the dwindling wild stocks, the United States Department of Commerce, Bureau of Fisheries, began experiments with captive propagation that lasted many years (Coker, 1906, 1920; Barney, 1922; Hildebrand and Hatsel, 1926; Hildebrand, 1929, 1932, 1933). The demand for terrapins as a food item eventually decreased, and many natural populations presumably began to recover from years of overharvest.

Today, the terrapin faces new threats, some unquantified but nevertheless real, such as habitat destruction and fragmentation, pollution, incidental drowning in both commercial and recreational crab pots, and mortality on roads (Wood and Herlands, 1997; Roosenburg et al. 1997; Hoyle and Gibbons, 2000). An additional source of mortality for which documentation is available is renewed commercial harvest (Garber, 1988). State laws protect terrapins in several parts of the range, and some populations have been considered as candidates for protection under the U.S. Endangered Species Act (Lovich, 1995; Seigel and Gibbons, 1995).

Our objectives in this paper were to use data from a long-term population study of terrapins to focus on selected aspects of demography and ecology critical to effective management and conservation considerations for the species. Size and age structure, sex ratio, and dispersal within

the marsh ecosystem are all critical population traits. Information on these aspects of the life cycle is needed to formulate management recommendations for this species.

METHODS

Study Site. — Diamondback terrapins were studied non-destructively using mark-recapture techniques for 16 years (1983–98) in the salt marshes and tidal creeks of the Kiawah River separating Kiawah Island and Johns Island, South Carolina, USA (80°E, 32°20'N; Fig. 1). Half of the approximately 3200 ha barrier island is salt marsh habitat. Additional salt marsh borders the mainland side of Kiawah Island, on Johns Island. The climate is subtropical with winter air temperatures falling below 0°C on fewer than 20 days annually. The semidiurnal tidal amplitude in the creeks bordering the Kiawah River is approximately 2 m, with higher tides during periodic tropical storms. Detailed descriptions of the study site and terrestrial portion of Kiawah Island are given by Gibbons and Coker (1978), Gibbons and Harrison (1981), and Gibbons (1990).

Study Techniques. — Several standard turtle-collecting techniques have been used to capture *M. terrapin*, including baited hoop traps, dipnetting, and trawling (Gibbons, 1990). However, the most effective techniques in this study have been seining (10 m, 2.54 cm mesh, with bag) and placing trammel nets (inner net 6 x 6 cm; outer nets 30 x 30 cm) across tidal creeks. Most captures were made during the low tide phases of the tidal cycle. Each turtle captured was given an individual identification code by filing notches or drilling holes in marginal scutes (Gibbons, 1990). We noted the sex (adult males recognizable by enlarged tail) and determined curved, midline plastron length (PL) to the nearest mm for 1189 individuals. Straight-line, midline carapace lengths and body mass (g) were taken for a subset of the total. Age was estimated by counting rings on the plastral and carapacial scutes with careful consideration for the assumptions and validations necessary (Dunham and Gibbons, 1990; Lovich and Gibbons, 1990; Litzgus and Brooks, 1998). The rings were documented to be annual based on multiple-investiga-

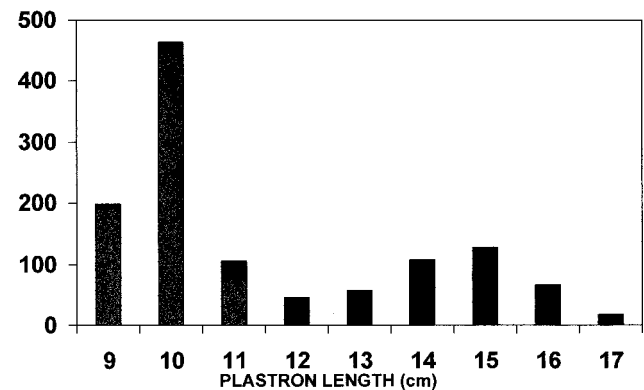


Figure 2. Combined size structure of diamondback terrapin populations from tidal creeks on Kiawah Island, South Carolina, USA, based on initial captures of 1189 individuals for which sex was determined, and showing the extreme sexual size dimorphism characteristic of the species. Males ($n = 714$) are indicated by gray bars; females ($n = 475$) are indicated by black bars.

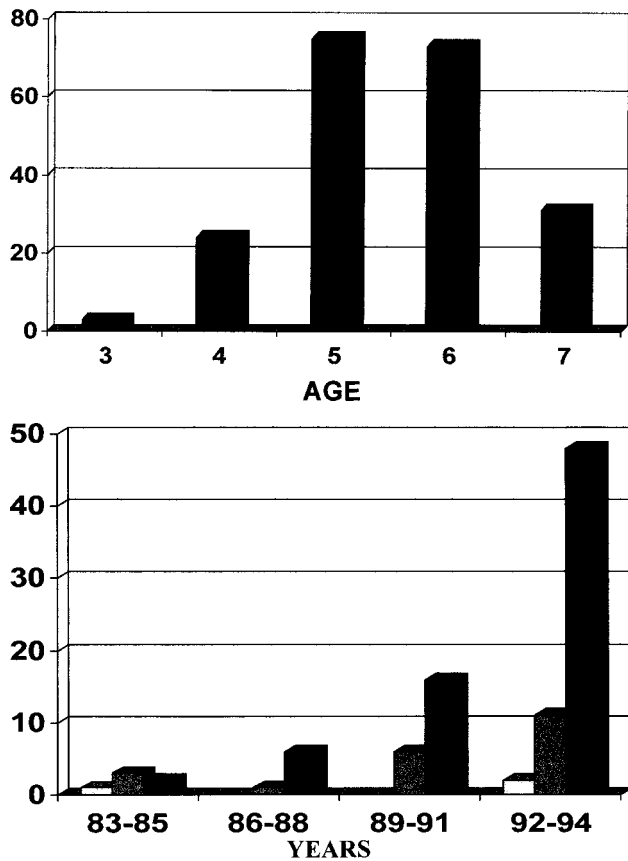


Figure 3. Early age structure of diamondback terrapin populations from tidal creeks on Kiawah Island, South Carolina, USA, based on (top) cumulative initial captures of 209 known-age individuals aged 3–7 yrs, and (bottom) comparative recruitment during different years. Not shown is the single first-year animal that was captured during the study. No two-year-old individuals were captured at any time in any location. Three-year-old terrapins ($n = 3$) are indicated by light gray bars; 4-year-olds ($n = 21$) are indicated by dark gray bars; 5-year-olds ($n = 72$) are indicated by black bars. No 3-, 4-, or 5-year-old recruits were recorded in 1995–97; three 4-year-olds and three 5-year-olds were recorded in 1998.

tor determinations in the same and subsequent years of capture and were verified to be valid for virtually all individuals less than 6 years old and for some as much as 10 years old. Sequential recaptures of terrapins from the four major creeks (Fiddler, Terrapin, Big Sandy, and Oyster; Fig. 1) were used for determination of movements within the study area.

RESULTS

Demographics

Sex Ratio. — A total of 1274 original captures and 1131 recaptures were made during the period of study from 1983 to 1998, of which 1189 were classified by sex (Fig. 2). Males in this population reach maturity at approximately 90 mm PL between their 3rd and 4th year, and females attain maturity at about 138 mm PL between their 6th and 7th year (Lovich and Gibbons, 1990). As previously reported for this population (Lovich and Gibbons, 1990), the sex ratio was male-biased for all captures for which sex could be determined by use of secondary sex characters.

Population Size Structure. — As is characteristic for the species, the maximum size of adult females was greater than that of adult males (Fig. 2). Using only first captures for all measurements, PL of males (mean = 102.6 mm, SD = 5.5, range = 86–125 mm, $n = 751$) was significantly smaller than females (mean = 144.2 mm, SD = 17.3, range = 96–178 mm, $n = 495$). Likewise, carapace length (CL) of males (mean = 120.5 mm, SD = 6.6, range = 95–150 mm, $n = 573$) was significantly smaller than females (mean = 160.2 mm, SD = 18.6, range = 101–202 mm, $n = 406$). The mean weight of males was 242 g (SD = 31.3, range = 159–346 g, $n = 138$) and that of females was 667 g (SD = 186.3, range = 193–986, $n = 63$). Because of the established reliability of scute annuli for age determination in this population, age determinations were made for a large proportion of the smaller individuals captured during the study, allowing a comparison of recruitment rates of different age classes into the creek populations (Fig. 3).

Seasonal Activity, Movements, and Population Persistence

Seasonal Activity. — Terrapin activity was determined by dividing the number of captures each month by the cumulative number of sampling days in that month for all years from 1987 through 1998 (Fig. 4). Female activity peaked in April. Male activity peaked in April with a second peak in October.

Movements and Site Fidelity. — Individual terrapins in most creeks exhibited high home range site fidelity from year to year (Table 1). The 25 recapture records of individuals (9 females, 16 males) that moved to another creek actually involved 30 relocations as four individuals moved from one creek to another and then returned. One of these moved from Fiddler to Oyster twice. One of the long distance migrations was recorded for a Fiddler Creek female that moved from its home range, nested along the dunes of the Kiawah River near its outlet to the ocean, and then returned to Fiddler Creek, a roundtrip distance of ca. 5.5 km from the mouth of Fiddler Creek. Of the 442 individuals that

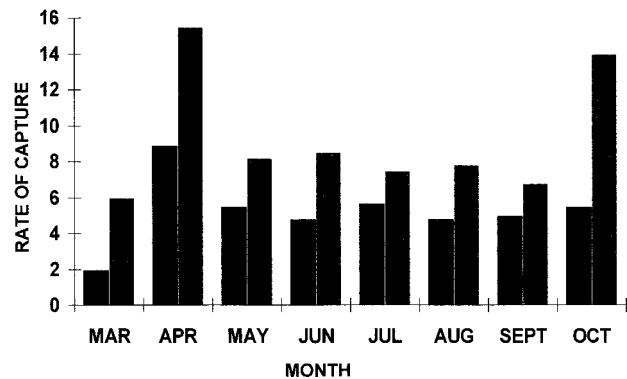


Figure 4. Seasonal captures of diamondback terrapins from tidal creeks on Kiawah Island, South Carolina, USA. Rate of capture was determined by dividing the number of captures and recaptures each month by the cumulative number of sampling days in that month for all years from 1987 through 1998. Males ($n = 1367$) are indicated by gray bars; females ($n = 891$) are indicated by black bars.

Table 1. Comparison of movements of *Malaclemys terrapin* among capture locations in four tidal creeks along the Kiawah River, South Carolina. The numbers in bold indicate the number of individuals that were recaptured in the same creek they had been captured in during a previous year. Individuals with multiple recaptures were recorded only once. No individual turtles were recorded from more than two creeks. The other columns indicate recaptures of individuals that had moved from one location to another. The distances are from the mouth of a creek to the next one (following river), and the minimum intermarsh movement that would be possible for a terrapin to go between creeks. One adult female moved from Terrapin to Captain Sam's Inlet (> 2 km; Fig. 1) during the nesting season, presumably on a nesting excursion.

| Recapture Site | Site of Original Capture | | | |
|--|--------------------------|------------|-----------------------|------------|
| | Big Sandy | Fiddler | Terrapin | Oyster |
| Big Sandy | 51 | 1 | 1 | 1 |
| Fiddler | 0 | 205 | 4 | 4 |
| Terrapin | 0 | 0 | 53 | 0 |
| Oyster | 0 | 6 | 8 | 133 |
| Number of individuals that moved from original capture site | 0 | 7 | 13 | 5 |
| Percent of recaptured individuals that moved to other creeks | 0.0 | 3.41 | 24.5 | 3.76 |
| Distance (km) between tidal creeks | Mouth to mouth | | Minimum through marsh | |
| Big Sandy – Fiddler | 1.13 | | 0.7 | |
| Fiddler – Terrapin | 0.63 | | 0.5 | |
| Terrapin – Oyster | 1.13 | | 0.5 | |

were recaptured a year or more later after initial capture, 5.7% (25 of 442; Table 1) were known to have changed tidal creek locations. However, excluding the Terrapin Creek population from the analysis, only 2.7% of the terrapins in other creeks were known to have relocated to other areas, as 13 of the 25 documented as moving were from Terrapin Creek.

The periods of recaptures of individuals in the same creek (Fiddler) in subsequent years gave an indication of the fidelity of individuals to a particular tidal creek (Table 2). Not only were numerous terrapins recaptured repeatedly in the same small tidal creeks in consecutive years, but many were recaptured in the same section of the creek within 100 m of previous captures.

Because of their site fidelity, it was relatively easy to capture a high proportion of the terrapins in some creeks within a few years. The Fiddler Creek capture:recapture ratios (Fig. 5) were typical of those in the other creeks. In Fiddler Creek, a total of 425 terrapins were captured 915 times from 1987–97, with 205 of the 425 original captures being recaptured at least once a year subsequent to their original capture. During the last 5 years, recaptures ranged from 71–85% (mean = 78%) of the captures in Fiddler Creek. Site fidelity appeared to have been maintained in 1989 and 1990 in both Fiddler and Terrapin creeks after the cataclysmic natural event of Hurricane Hugo in October 1989.

Extirpation in Terrapin Creek and Terrapin Mortality.

— During the course of our study, the terrapin population in Terrapin Creek declined after 1990 to virtually none being present in the creek after 1993 (Fig. 5), despite continued sampling at the same or greater intensity than previously.

Table 2. Number of years between original capture and all subsequent recaptures in different years of 205 non-transient diamondback terrapins in Fiddler Creek. An individual recaptured multiple times in a year was counted only once in each year.

| Number of individuals recaptured | Number of Years since Original Capture | | | | | | | | |
|----------------------------------|--|----|----|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| | 111 | 95 | 89 | 61 | 35 | 41 | 14 | 18 | 13 |

For contrast, in 1983, 17 terrapins were taken with a single seine haul in Terrapin Creek whereas from 1993–98 observations from shore and from trolling boats coupled with the use of trammel nets and seining resulted in the sighting and capture of a single, unmarked adult female in 1996. After 1992, when 11 were captured or recaptured in Terrapin Creek, none of the 186 terrapins originally captured in this creek were recaptured again at any location.

At least 26 terrapins (based on fragmented shell parts in some instances) died in abandoned, recreational crab pots discovered in the Kiawah River and tidal creeks after the construction of a dock across from Terrapin Creek in 1983. We also observed injuries from outboard motor propellers, ($n = 25$; 15 females, 10 males), based on carapace scars recorded from throughout the study area beginning in 1989.

DISCUSSION

Demographics

Adult sex ratios in terrapin populations have been of interest to us since the phenomenon was first examined in detail (Lovich and Gibbons, 1990). At that time some studies reported male bias and others reported female bias. The results of the current study confirm previous observations for the Kiawah Island population in that adult males continue to outnumber adult females. In contrast, other studies have noted strongly female-biased sex ratios (Seigel, 1984; Roosenburg, 1991), possible consequences of sex-specific predation (Seigel, 1980) and mortality in crab pots (Bishop, 1983; Roosenburg, 1991; Roosenburg et al., 1997). In his well-studied population of terrapins in Maryland, Roosenburg (1991) concluded that bias in adult sex ratio was due to differential survivorship between the sexes.

The female bias in Roosenburg's population may be due to high mortality of male terrapins in crab pots, a significant source of mortality for the species (Bishop, 1983; Roosenburg, 1991; Roosenburg et al., 1997). To underscore the potential problem, it should be noted that during 1998 the state of South Carolina Department of Natural Resources gave permits for more than 20,000 commercial crab pots and estimated that more than 35,000 recreational crab pots were in use (Hoyle, 1997). Most crab pots have a diameter that permits entry by small terrapins such as males and immature females, and our observations confirm that most of the female terrapins obtained from crab pots were small, although some were larger.

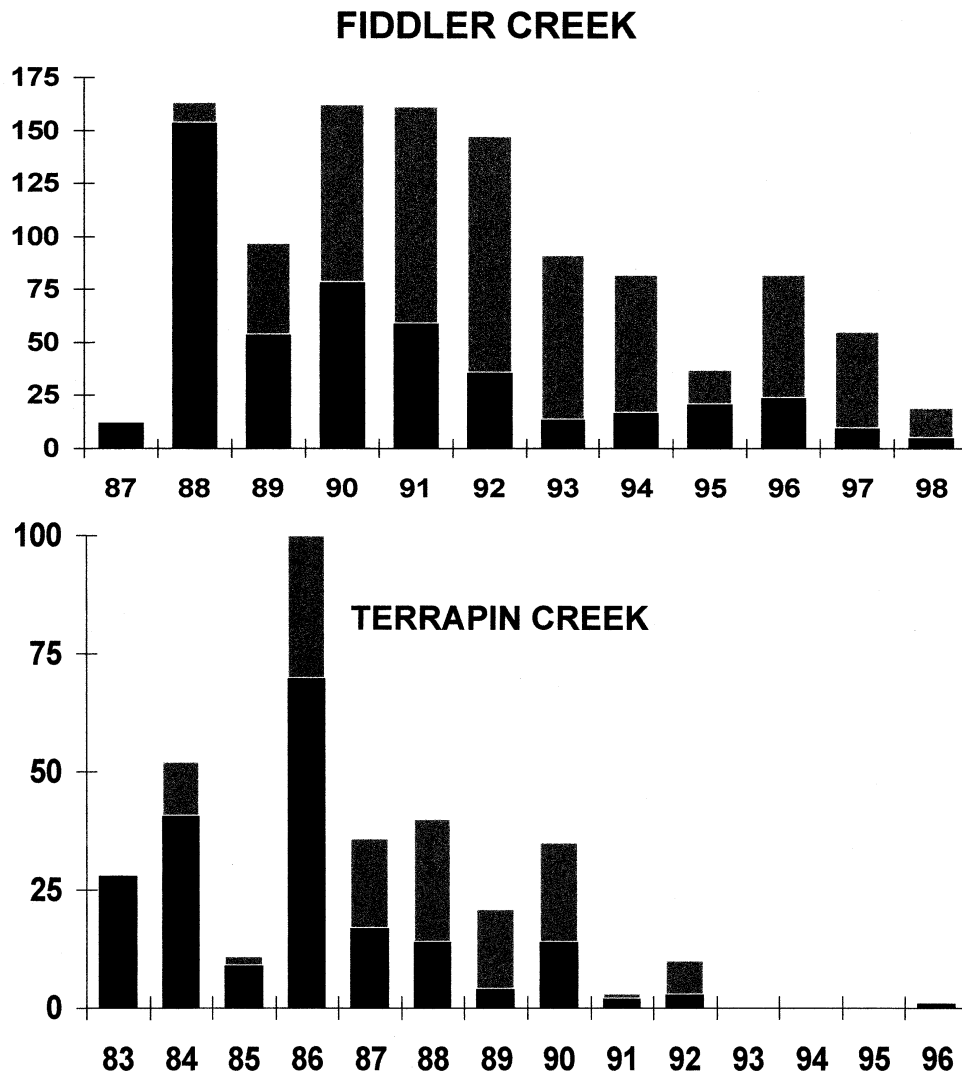


Figure 5. Comparison of annual captures and recaptures of diamondback terrapins from (a) Fiddler Creek and (b) Terrapin Creek on Kiawah Island, South Carolina, USA, showing disappearance of Terrapin Creek population. The number of different individuals captured during each year is indicated on the y-axis. Original captures of individuals are indicated by lower, black portion of bar; recaptured individuals are indicated by gray portion of bar.

The question remains as to why we continue to see a male-biased population at Kiawah Island, in spite of crab trapping, which targets smaller terrapins like males. One possibility is that intensive crab trapping is a relatively recent phenomenon in the Kiawah study area that has yet to have sufficient impact to alter sex ratios appreciably. Our data showing the virtual disappearance of marked animals from Terrapin Creek during the course of the study provide circumstantial evidence for an increase in crab trapping. Indeed, the proximity of the mouth of Terrapin Creek to the Kiawah River dock (Inlet Cove), which did not become operational until 1983, provides easy access to recreational crabbers, and crab pots have been in almost daily use there during seasons when terrapins are active.

It is also possible that there is geographic variation in the susceptibility of terrapins to crab pots based on potential food items. The diet of terrapins is relatively varied (Ernst et al., 1994), and they may be differentially attracted to crab pots baited with fish or chicken. Terrapins also eat crabs,

especially small ones (Tucker et al., 1995, 1997), so terrapins entering crab pots in search of food may vary regionally in their selectivity for particular food items.

One of the most significant findings relative to population structure is the total absence of two-year-old individuals in our samples (Fig. 3). The smallest females we found were approximately the same size as the smallest males collected. Thus, it would appear that prior to attainment of age three and a CL of about 90 mm both sexes probably occupy habitats that are not typically sampled by terrapin researchers. Juveniles apparently remain in high marsh areas in a secretive mode for several years after hatching (Lovich et al., 1991) and thus their numbers are underestimated. An alternative explanation, that the Kiawah populations had experienced reproductive failure for several seasons, is inadequate because new (unmarked) recruits of older age classes (five- and six-year-olds) appeared in successive years although younger individuals were seldom found. Also, the absence of younger age

classes has been noted by other investigators throughout the range of the species (Hurd et al., 1979; Seigel, 1984). Efforts to accurately model the demography of terrapin populations will be compromised until more data are available on this missing age group.

Seasonal Activity, Movements and Population Persistence

An observation of particular significance to management considerations for the species is that individuals rarely move between adjacent tidal creeks, but instead remain in one small area for extended periods as adults. Seigel (1984) noted similar observations during a study lasting 18 months in Florida. The limited long-distance travel and interchange among tidal creeks by *Malaclemys* (5.0% of recaptured individuals, Table 1) in the tidal creeks at Kiawah is comparable to that of a freshwater species of turtle (*Trachemys scripta*) in which 244 of 4768 (5.1%) were documented to have moved primarily overland to other habitats that ranged from 0.2 to 9 km away (Gibbons et al., 1990). In contrast, the distances moved by *Malaclemys* between tidal creeks were much less, and overland travel was never required. Furthermore, it should be noted that the overall proportion of relocation by the Kiawah terrapins is biased by the high frequency of movement of individuals from the Terrapin Creek population, which included more than half of the individuals that were documented as moving between creeks, and would be approximately half of that reported for *T. scripta* if this single tidal creek population were excluded.

Five reasons have been identified as to why adult freshwater turtles make extrapopulational movements (Gibbons et al., 1990) that would be comparable to these movements by terrapins among Kiawah Island tidal creeks. Two are related to reproduction, namely nesting by adult females and mate seeking by males. The other three involve seeking food resources, departure from an unsuitable habitat, and migration for purposes of hibernation or estivation. Although diet would not appear to be a problem in the salt marsh habitat where crustaceans and mollusks are locally abundant (Tucker et al., 1995), local densities of prey organisms undoubtedly fluctuate seasonally and annually and could prompt individuals to seek more productive areas.

A habitat could become unsuitable for turtles for a variety of reasons. Loss of wetland habitat through drying out often impacts pond turtles but is an unlikely hazard for a tidal species. An explanation proposed for decline in some turtle species has been increased human recreational activities (Garber and Burger, 1995), which for diamondback terrapins would include recreational crabbing and boating. In Terrapin Creek, frequent boating might have degraded the habitat, and crab trapping could have resulted in unsustainable levels of mortality, eventually resulting in most individuals either dying or leaving permanently.

Migratory movements by *Malaclemys* seeking hibernacula have not been observed in the Kiawah Island popu-

lation and would not be expected, as freezing conditions would never be encountered in a South Carolina tidal creek below the low tide level. Dormancy has been observed during the summer, with individuals burying in the mud in areas above normal high tides (Tucker et al., 1995). However, moving to another creek would not be a solution for avoiding unfavorable summer conditions.

One crucial observation is that, although the highest proportion of movement was observed among individuals in the Terrapin Creek population, none of these individuals was captured anywhere for the six years following the last captures in Terrapin Creek in 1992. We believe these turtles were removed from the population rather than having moved in response to dietary changes or to disturbance by people. Localized recreational crab trapping is the most likely explanation for the disappearance of the Terrapin Creek population. Small-scale but continual destruction can eliminate a significant portion of a creek's terrapin population, which will not be readily replaced by immigrants from other creeks because of the low rate of extrapopulational movement. Our data for Terrapin Creek (Fig. 5) underscore the sensitivity of local terrapin populations to overharvest; management plans for the species should consider human impacts in this regard.

Mortality

Mortality from crab pots is happening to terrapins individually and as populations throughout their range. In nearby Charleston, South Carolina, Bishop (1983) estimated that the mean daily terrapin catch per baited crab pot was 0.16 in April and May with a capture mortality of 10%. With 743 commercial trappers known to have been active at the time and an estimated 2853 crab pots set daily, approximately 285 terrapins died per day. Bishop concluded that the impact of crab trapping posed no threat to the survival of terrapin populations in the area, a conclusion that is at odds with more recent opinions (Seigel and Gibbons, 1995; Hoyle, 1997). Even Bishop's (1983) statement that "the population is not in danger of a decline" seems contradictory to his earlier statement in the same paper that "terrapin populations could not sustain long-term harvest."

In another study, Roosenburg (1991) found a single unattended crab pot in Maryland that contained the entire shells of 49 turtles and the remains of others, or approximately 1.6–2.8% of the entire population in his study area. Hoyle (1997) calculated that recreational crab trapping typical of the region could remove individuals from a tidal creek similar to Fiddler Creek at a rate that would not be sustainable.

Our records of 25 carapace injuries from outboard motor propellers also suggest that an increased use of outboards in the Kiawah River could potentially result in an increase in mortality rate. Of note is that the sex ratio of injured turtles was 1.5 females to 1 male, one explanation being that adult females are more likely to encounter boat

traffic by entering the open river during nesting excursions. Roosenburg (1991) found that 19.7% ($n = 227$) of female and 2.2% ($n = 16$) of male terrapins bore scars from propeller cuts. The number killed by such encounters is unknown. In New Jersey, Garber and Burger (1995) observed a strong negative correlation between the number of nesting females and the number of boats in an adjacent bay over a period of 17 years. Disruption by beachgoers may also serve to discourage nesting by terrapins.

Kiawah Island has undergone extensive residential and recreational development since the early 1970s and the consequences have not always been favorable for wildlife. In fact, previous investigators predicted that terrapins could suffer from impacts of urban development unless efforts were made to protect the ecological integrity of the island (Gibbons and Harrison, 1981). Subsequent research on Kiawah Island has confirmed decreases in reptile and amphibian density and diversity associated with increased road and trail density (Gaddy and Kohlsaas, 1987). The decline of the Terrapin Creek population was probably facilitated by increased access of recreational crab trappers to the area.

Summary: Challenges and Recommendations

Diamondback terrapins show extraordinarily high home range site fidelity, most individuals remaining from year to year in the same tidal creek, with little or no interchange among the adult populations of adjoining creeks. Even female terrapins capable of making long excursions for nesting forays characteristically return to the same region of the marsh every time. Juvenile terrapins in their first and second years of growth are virtually absent from the tidal creeks inhabited by the adults, and third and fourth year individuals are present in significantly lower proportions than are the age classes in the adult population. Consequently, extirpation of terrapins in a particular section of marsh habitat could conceivably create a void that could take a generation or more of recruitment to fill. And, unless the source of extirpation is removed, terrapins might never return.

Without the current threats imposed by crab pots and other recreational and commercial activities, the terrapin might be considered a "recovering species." After decades of overharvest ending early in this century, terrapin populations began the slow road to recovery. The vastness of their habitat and the fact that salt marshes were generally undeveloped 100 years ago provided them with safe haven in which to rebuild their populations. Today the terrapin faces renewed significant threats to its survival including mortality from crab pots and boat propellers, habitat degradation, and death or stress due to human recreational impacts. As a result, terrapin populations are declining in some areas (Seigel and Gibbons, 1995). Significant local declines have been documented in Florida (Seigel, 1993) and in portions of our South Carolina study area (e.g., Terrapin Creek; Fig. 5b).

As if this were not enough, a market for consumption of terrapins is recrudescing, particularly in the Chinese restaurants of New York City. Some vendors may sell as many as 2000–3000 terrapins in a single year. Most are collected in Virginia, the Carolinas, Maryland, or New Jersey, with some coming from nearby areas, including Long Island and Jamaica Bay. Based on this information, Garber (1988) conservatively estimated that over 10,000 terrapins were sold in New York each summer, with females retailing at up to \$20 apiece. Continued exploitation, coupled with all the other problems terrapins face in the modern world, bodes poorly for the future of the species unless prudent management recommendations are implemented immediately.

Some recommendations are easily implemented and inexpensive. The installation of terrapin excluder devices on crab pots is cheap, effective, and has virtually no effect on the number or size of crabs captured (Wood, 1997). Converting the entry into a crab pot from a horizontal to a vertical opening has also been suggested as a means of keeping most terrapins out while not affecting the entry of blue crabs (Hoyle and Gibbons, 2000), and the effectiveness is easily testable. Either of these simple structural modifications would probably save thousands of terrapins annually. Representatives of conservation agencies could meet with commercial trappers to explain the problem and encourage them to perform the simple modification to their existing pots. Extensive trapping in the same area should be discouraged due to the possibility of local terrapin extirpation.

A similarly inexpensive recommendation would be the seasonal closure of terrapin nesting areas. The dunes between the Atlantic Ocean and the Kiawah River are favored by humans and female terrapins alike, with possible impact upon the terrapins, their nests, and their hatchlings. Placing the dunes off-limits from April through July would go a long way toward resolving the user conflict for the terrapins. Alternatively, the dunes could be closed from one hour before to one hour after high diurnal tides (peak terrapin nesting) during the same time frame, although the constantly changing time schedule would be more difficult to enforce.

More difficult, but just as important, is the curtailing of the trade in terrapins. Contrary to popular belief, commercial exploitation of turtles is unlikely to be "sustainable." Several recent and comprehensive studies have demonstrated the susceptibility of long-lived species like turtles to population decline when subjected to levels of mortality associated with commercial harvest (Congdon et al., 1993, 1994; Galbraith et al., 1997).

Unless prudent measures are implemented throughout the range of the terrapin, continued population declines are likely. The comeback of the species in the first half of the 20th century has given us a second chance to preserve an important macroconsumer of the salt marsh ecosystem and a culturally significant reptile (Tucker et al., 1995). We may not get a third chance.

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LITERATURE CITED

- BARNEY, R.L. 1922. Further notes on the natural history and artificial propagation of the diamond-back terrapin. *Bull. Bur. Fish.* 38:91-111.
- BISHOP, J.M. 1983. Incidental capture of diamondback terrapin by crab pots. *Estuaries* 6:426-430.
- BRAUN, J. AND BROOKS, G.R., JR. 1987. Box turtles (*Terrapene carolina*) as potential agents for seed dispersal. *Am. Midl. Nat.* 117:312-318.
- BROOKS, R.J., GALBRAITH, D.A., NANCEKIVELL, E.G., AND BISHOP, C.A. 1988. Developing management guidelines for snapping turtles. In: Szaro, R.C., Severson, K.E., and Patton, D.R. (Eds.). *Management of amphibians, reptiles, and small mammals in North America*. U.S. For. Serv. Gen. Tech. Rep. RM-166:174-179.
- BROOKS, R.J., BROWN, G.P., AND GALBRAITH, D.A. 1991. Effects of sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). *Can. J. Zool.* 69:1314-1320.
- BURKE, V.J., LOVICH, J.E., AND GIBBONS, J.W. 2000. Conservation of freshwater turtles. In: Klemens, M.W. (Ed.). *Turtle Conservation*. Washington, DC: Smithsonian Institution Press, pp. 156-179.
- CARR, A.F. 1952. *Handbook of Turtles. The Turtles of the United States, Canada, and Baja California*. Ithaca, NY: Cornell Univ. Press, 542 pp.
- COKER, R.E. 1906. The natural history and cultivation of the diamond-back terrapin with notes on other forms of turtles. *North Carolina Geol. Surv. Bull.* 14:1-69.
- COKER, R.E. 1920. The diamond-back terrapin: past, present and future. *Science Monthly* 11:171-186.
- CONGDON, J.D. AND GIBBONS, J.W. 1989. Biomass productivity of turtles in freshwater wetlands: a geographic comparison. In: Sharitz, R.R. and Gibbons, J.W. (Eds.). *Freshwater Wetlands and Wildlife*. U.S. Dept. of Energy Symp. Ser. No. 61, pp. 583-591.
- CONGDON, J.D., GREENE, J.L., AND GIBBONS, J.W. 1986. Biomass of freshwater turtles: a geographic comparison. *Amer. Midl. Nat.* 115:165-173.
- CONGDON, J.D., DUNHAM, A.E., AND VAN LOBEN SELS, R.C. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biol.* 7(4):826-833.
- CONGDON, J.D., DUNHAM, A.E., AND VAN LOBEN SELS, R.C. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *Amer. Zool.* 34(3):397-408.
- DUNHAM, A.E. AND GIBBONS, J.W. 1990. Growth of the slider turtle. In: Gibbons, J.W. (Ed.). *Life History and Ecology of the Slider Turtle*. Washington: Smithsonian Inst. Press, pp.135-145.
- ERNST, C.H., LOVICH, J.E., AND BARBOUR, R.W. 1994. *Turtles of the United States and Canada*. Washington: Smithsonian Institution Press, 578 pp.
- GADDY, L.L. AND KOHLSAAT, T.L. 1987. Recreational impact on the natural vegetation, avifauna, and herpetofauna of four South Carolina barrier islands. *Natural Areas Journal* 7:55-64.
- GALBRAITH, D.A., BROOKS, R.J., AND BROWN, G.P. 1997. Can management intervention achieve sustainable exploitation of turtles? In: Van Abbema, J. (Ed.). *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference*. N.Y. Turtle and Tortoise Society, pp. 186-194.
- GARBER, S.D. 1988. Diamondback terrapin exploitation. *Plastron Papers (New York Turtle and Tortoise Society)* 17:18-22.
- GARBER, S.D. AND BURGER, J. 1995. A 20-year study documenting the relationship between turtle decline and human recreation. *Ecological Applications* 5:651-689.
- GERMANO, D.J. AND JOYNER, M.A. 1988. Changes in a desert tortoise (*Gopherus agassizi*) population after a period of high mortality. In: Szaro, R.C., Severson, K.E., and Patton, D.R. (Eds.). *Management of amphibians, reptiles, and small mammals in North America*. USDA Forest Service, General Technical Report RM-166, pp. 190-198.
- GIBBONS, J.W. 1987. Why do turtles live so long? *Bioscience* 37:262-269.
- GIBBONS, J.W. 1990. Turtle studies at SREL: a research perspective. In: Gibbons, J.W. (Ed.). *Life History and Ecology of the Slider Turtle*. Washington: Smithsonian Inst. Press, pp. 19-44.
- GIBBONS, J.W. AND COKER, J.W. 1978. Herpetofaunal colonization patterns of Atlantic Coast barrier islands. *Am. Midl. Nat.* 99:219-233.
- GIBBONS, J.W. AND HARRISON, J.R. III. 1981. Reptiles and amphibians of Kiawah and Capers Island, South Carolina. *Brimleyana* 5:145-162.
- HEPPELL, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998:367-375.
- HILDEBRAND, S.F. 1929. Review of experiments on artificial culture of diamond-back terrapin. *Bull. U. S. Bur. Fish.* 45:25-70.
- HILDEBRAND, S.F. 1932. Growth of diamond-back terrapins: size attained, sex ratio and longevity. *Zoologica (New York)* 9:551-563.
- HILDEBRAND, S.F. 1933. Hybridizing diamond-back terrapins. *J. Heredity* 24:231-238.
- HILDEBRAND, S.F. AND HATSEL, C. 1926. Diamond-back terrapin culture at Beaufort, N.C. *U. S. Bur. Fish., Econ. Circ.* 60:1-20.
- HOYLE, M.E. 1997. The impact of recreational crab traps on diamond-back terrapins, *Malaclemys terrapin*. Master's Thesis, University of Georgia.
- HOYLE, M.E. AND GIBBONS, J.W. 2000. Use of a marked population of diamondback terrapins (*Malaclemys terrapin*) to determine impacts of recreational crab pots. *Chelonian Conservation and Biology* 3:735-737.
- HURD, L.E., SMEDES, G.W., AND DEAN, T.A. 1979. An ecological study

- of a natural population of diamondback terrapins (*Malaclemys t. terrapin*) in a Delaware salt marsh. *Estuaries* 2:28-33.
- IVERSON, J.B. 1982. Biomass in turtle populations: a neglected subject. *Oecologia* 55:69-76.
- IVERSON, J.B. 1987. Tortoises not dodos, and the tambalacoue tree. *J. Herpetol.* 21:229-230.
- KACZOR, S.A. AND HARTNETT, D.C. 1990. Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida Sandhill community. *Am. Midl. Nat.* 123:100-111.
- KLEMENS, M.W. AND THORBJARNARSON, J.B. 1995. Reptiles as a food resource. *Biodiversity and Conservation* 4:281-298.
- LAGO, P.K. 1991. A survey of arthropods associated with gopher tortoise burrows in Mississippi. *Entomol. News* 102:1-13.
- LITZGUS, J.D. AND BROOKS, R.J. 1998. Testing the validity of counts of plastral scute rings in spotted turtles, *Clemmys guttata*. *Copeia* 1998:222-225.
- LOVICH, J.E. 1994. Biodiversity and zoogeography of non-marine turtles in Southeast Asia. In: Majumdar, S.K., Brenner, F.J., Lovich, J.E., Schalles, J.F., and Miller, E.W. (Ed.). *Biological Diversity: Problems and Challenges*. Pennsylvania Academy of Science, pp. 380-391.
- LOVICH, J.E. 1995. Turtles. In: LaRoe, E.T., Farris, G.S., Puckett, C.E., Doran, P.D., and Mac, M.J. (Eds.). *Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems*. Washington, DC: U.S. Department of the Interior, National Biological Service, pp. 118-121.
- LOVICH, J.E. AND GIBBONS, J.W. 1990. Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. *Oikos* 59:126-134.
- LOVICH, J.E., TUCKER, A.D., KLING, D.E., GIBBONS, J.W., AND ZIMMERMAN, T.D. 1991. Behavior of hatchling diamond-back terrapins (*Malaclemys terrapin*) released in a South Carolina salt marsh. *Herpetol. Rev.* 22:81-83.
- MCCAULEY, R.H. 1945. *The reptiles of Maryland and the District of Columbia*. Privately printed, Hagerstown, Maryland, 194 pp.
- MILTON, S.J. 1992. Plants eaten and dispersed by adult leopard tortoises *Geochelone pardalis* (Reptilia: Chelonii) in the southern Karoo. *S. Afr. J. Zool.* 27:45-49.
- ROOSENBERG, W.M. 1991. The diamond back terrapin: habitat requirements, population dynamics and opportunities for conservation. In: Chaney, A. and Mihursky, J.A. (Eds.). *New perspectives in the Chesapeake system: a research and management partnership*. Proceedings of a conference. Maryland: Chesapeake Research Consortium Publication No. 137, pp. 227-234.
- ROOSENBERG, W.M., CRESKO, W., MODESITTE, M., AND ROBBINS, M.B. 1997. Diamondback terrapin (*Malaclemys terrapin*) mortality in crab pots. *Conservation Biology* 2:1166-1172.
- SEIGEL, R.A. 1980. Predation by raccoons on diamondback terrapins, *Malaclemys terrapin tequesta*. *J. Herpetol.* 14:87-89.
- SEIGEL, R.A. 1984. Parameters of two populations of diamond back terrapins (*Malaclemys terrapin*) on the Atlantic coast of Florida. In: Seigel, R.A., Hunt, L.E., Knight, J.L., Malaret, L., and Zuschlag, N.L. (Eds.). *Vertebrate Ecology and Systematics. A Tribute to Henry S. Fitch*. Univ. Kansas Mus. Nat. Hist. Spec. Publ. 10:77-87.
- SEIGEL, R.A. 1993. Apparent long term declines in diamondback terrapin populations at the Kennedy Space Center, Florida. *Herpetological Review* 24:102-103.
- SEIGEL, R.A. AND GIBBONS, J.W. 1995. Workshop on the ecology, status, and management of the diamondback terrapin (*Malaclemys terrapin*), Savannah River Ecology Laboratory, 2 August 1994: final results and recommendations. *Chelonian Conservation and Biology* 1:240-243.
- TUCKER, A.D., FITZSIMMONS, N.N., AND GIBBONS, J.W. 1995. Resource partitioning by the estuarine turtle *Malaclemys terrapin*: trophic, spatial, and temporal foraging constraints. *Herpetologica* 51:167-181.
- TUCKER, T., YEOMANS, R., AND GIBBONS, J.W. 1997. Shell strength of mud snails (*Ilyanassa obsoleta*) may deter foraging by diamond-back terrapins (*Malaclemys terrapin*). *American Midland Naturalist* 138:224-229.
- WILBUR, H.M. AND MORIN, P.J. 1988. Life history evolution in turtles. In: Gans, C. and Huey, R.B. (Eds.). *Biology of the Reptilia*. Vol. 16. New York: Alan R. Liss, Inc., pp. 387-439.
- WITZ, B.W., WILSON, D.S., AND PALMER, M.D. 1991. Distribution of *Gopherus polyphemus* and its vertebrate symbionts in three burrow categories. *Am. Midl. Nat.* 126:152-158.
- WOOD, R.C. 1997. The impact of commercial crab traps on northern diamondback terrapins, *Malaclemys terrapin terrapin*. In: Van Abbema, J. (Ed.). *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference*. N.Y. Turtle and Tortoise Society, pp. 21-27.
- WOOD, R.C. AND HERLANDS, R. 1997. Turtles and tires: the impact of roadkills on northern diamondback terrapin, *Malaclemys terrapin terrapin*, populations on the Cape May Peninsula, southern New Jersey, USA. In: Van Abbema, J. (Ed.). *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference*. N.Y. Turtle and Tortoise Society, pp. 46-53.

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