AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS
Aquatic Conserv: Mar. Freshw. Ecosyst. (2008)
Published online in Wiley InterScience
(www.interscience.wiley.com). DOI: 10.1002/aqc.999

Ecological effects of major injuries in diamondback terrapins: implications for conservation and management

K. K. CECALA[a,*], J. W. GIBBONS[b] and M. E. DORCAS[a]
[a]*Department of Biology, Davidson College, Davidson, North Carolina 28035-7118 USA*
[b]*Savannah River Ecology Laboratory, University of Georgia, Drawer E, Aiken, South Carolina 29802 USA*

ABSTRACT

1. Many turtle species frequently suffer major injuries due to attempted predation or anthropogenic factors. Diamondback terrapins (*Malaclemys terrapin*) are one species known to be affected by anthropogenic activity, but little is known about the causes of injuries. In declining diamondback terrapin populations, learning more about causes and results of injuries can be helpful in developing sound management plans.
2. Patterns of limb loss and major shell injuries were examined in a population of terrapins studied for 24 years at Kiawah Island, South Carolina to infer the causes and effects of injuries and possible predators on terrapins.
3. The rate of shell injuries increased temporally, possibly as a result of increased watercraft activity. Because no differences in rates of limb loss were found between males and females, limb loss probably results from aquatic encounters (i.e. limb loss does not appear to be the result of terrestrial predation during nesting). Furthermore, males experienced reduced body condition when injured, and terrapins with a major injury had lower survivorship than uninjured terrapins.
4. Therefore, in addition to reducing sources of mortality and protecting nesting habitat, measures to protect terrapins from watercraft activity may increase the survivorship of adult terrapins.

Received 25 November 2007; Revised 9 June 2008; Accepted 29 June 2008

KEY WORDS: *Malaclemys terrapin*; limb loss; shell injury; turtle; salt marsh; survivorship

INTRODUCTION

Major injuries occur relatively frequently in many turtle species as a result of anthropogenic and natural factors (Fergusson *et al.*, 2000; Dodd, 2001; Saumure *et al.*, 2007). Anthropogenic causes of injury include agricultural mowing (Saumure and Bider, 1998), motorized activity (automobiles or watercraft; Gibbons *et al.*, 2001; Szerlag and McRobert, 2006) and predation by human-subsidized animals (animals that benefit from human presence, e.g. raccoons; Dodd, 2001; Draud *et al.*, 2004). Injuries may reduce foraging success, reduce the ability to escape predators, and may interfere with reproduction, thus affecting population viability (Werner and Anholt, 1993).

The diamondback terrapin (*Malaclemys terrapin*) is the only exclusively estuarine turtle in the USA, and populations appear to be declining throughout its range (Seigel and Gibbons, 1995; Gibbons *et al.*, 2001; Dorcas *et al.*, 2007). In the early 1900s, diamondback terrapin populations were reduced dramatically by commercial harvest throughout the East Coast of the USA (Carr, 1952), and harvesting of this species continued in Maryland at least until 2006 (Brennessel, 2006). Increased human activity in coastal areas has further reduced terrapin populations. Associated anthropogenic causes of decline include watercraft use (Gibbons *et al.*, 2001), crab trapping (Wood, 1997; Dorcas *et al.*, 2007), increased automobile traffic (Szerlag and McRobert, 2006), and urbanization of marsh and nesting habitats critical to terrapin populations (Seigel and Gibbons, 1995). Learning more about the ecology of a species and causes of population declines is essential for understanding and managing anthropogenic threats, and has long been recognized as the first step towards recovery (Hickey, 1969; Peakall, 1976).

*Correspondence to: Kristen Cecala, Warnell School of Forestry and Natural Resources, The University of Georgia, Athens, GA 30602–2152. E-mail: cecalak@warnell.uga.edu
[a]Current address: Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602-2152.

Like other turtle species, diamondback terrapins often exhibit major injuries including missing limbs and major shell damage (Saumure and Bider, 1998; Dodd, 2001; Heithaus *et al*., 2005). Examining patterns of limb loss and other major injuries can allow inference about the causes of injuries and/or the types of predators affecting terrapins (Schoener, 1979). If human-subsidized, terrestrial predators, such as raccoons or crows (Feinberg and Burke, 2003), prey on diamondback terrapins, female terrapins should exhibit higher frequencies of limb loss as a result of attempted predation during nesting. Alternatively, if major injuries result primarily from aquatic encounters, male and female terrapins should exhibit relatively equal rates of limb loss. If increased motorized activity (e.g. automobile or motorized watercraft) results in major shell injuries, then the frequency of shell injuries should increase over time as terrapin habitats become more heavily populated by humans, and watercraft activity increases.

Data from a 24-year study of diamondback terrapins in the salt marshes adjacent to Kiawah Island, South Carolina, USA, were used to examine patterns of major injuries. Since the 1980s, Kiawah Island has experienced rapid human population growth (62% growth since 1993; Charleston County Public Record), during which boating activity has increased as well (J. W. Gibbons, pers. observ.). The hypothesis that increased human activity over time would be associated with increased rates of injuries to diamondback terrapins was tested. Specifically, the following was examined: (1) how has the frequency of injury types (limb loss or major shell damage) changed over time; (2) are females injured more frequently than males; (3) does the frequency of limb loss vary spatially; and (4) do injuries affect body condition or survivorship of diamondback terrapins?

METHODS

Terrapins were collected from five tidal creeks associated with the Kiawah River in Charleston County, South Carolina (Fiddler Creek, Oyster Creek, Stingray Slough, Sandy Creek, and Terrapin Creek; see Dorcas *et al*., (2007) for a map and description of the study area). These creeks were located at the south-western end of Kiawah Island and characterized by salt marsh vegetated primarily with *Spartina alterniflora*. Sampling for terrapins began in 1983 with Terrapin Creek, before including Fiddler Creek in 1988, Oyster Creek and Stingray Slough in 1990, and Sandy Creek in 1992. Although increases in boating activity in this region were not studied directly, the use of boats has increased concomitantly with the significant increase in human population size and motorized activity on Kiawah Island since the inception of this study (J. W. Gibbons, pers. observ.). While automobile activity has increased on Kiawah Island, the effect of automobile traffic appears to have minimal impacts on this terrapin population, but the impacts of watercraft activity are unclear (Dorcas *et al*., 2007).

Although sampling efforts varied, in general, each creek was sampled at least once each year except between the years 2000 and 2002. Over 1450 individuals were captured representing more than 2800 captures. Capture methods consisted primarily of seining and the use of trammel nets. Each terrapin captured was sexed, aged when possible, individually marked, and measured for length (for details see Dorcas *et al*., 2007). In some years, mass (to the nearest gram) was measured. All major injuries were recorded including limb loss and major shell damage before releasing terrapins at their point of capture. Limb loss was defined as one or more missing feet or legs. Major shell damage (hereafter referred to as shell damage) was defined as an injury to two or more adjacent vertebral/costal or plastral scutes or three or more adjacent marginal scutes.

A contingency table was used to examine injury frequencies to determine if any limb is lost more frequently than others. To test the questions addressed in this study, data were transformed using an arcsine transformation (Sokal and Rohlf, 1981), and regression analysis was used to determine if the frequency of major injuries had increased temporally. Forward stepwise logistic regression analyses were used to determine if plastron length at an individual's first capture with an injury, sex (females, $N = 543$; males, $N = 851$), or creek where an individual was captured best predicted limb injuries or all major injuries (SAS v. 9.1, SAS Institute, Cary, USA). An ANCOVA (plastron length as the covariate) was used to assess body condition of injured terrapins (terrapins with limb loss or shell damage) relative to non-injured terrapins and a Tukey HSD pairwise-comparison to examine differences in body condition between those with a major shell injury and those that experienced limb loss (Minitab v.12.1; Minitab Inc., State College, PA, USA). The significance of all tests was evaluated at $\alpha = 0.05$.

To determine if survivorship differed between injured and non-injured terrapins, an open population model, the Cormack–Jolly–Seber model (CJS), was used to estimate survivorship between groups and among years. Assumptions of this model included no change in recapture probability or survivorship between marked and unmarked individuals, no mark loss or confusion, immediate release after capture, and constant emigration rates. For these analyses, only data collected from Fiddler Creek were used because data were collected most consistently since 1988 (Dorcas *et al*., 2007). This dataset fits these assumptions well with clear individual codes having no known negative consequences, relatively short periods of time spent in captivity after capture (i.e. 1–2 days), and no known changes in emigration rates (Gibbons *et al*., 2001; Tucker *et al*., 2001). Because sexual dimorphism in size occurs in terrapins and the cause of injury may vary between sexes, males and females were analysed independently. To test for model fit and overdispersion, a bootstrap goodness-of-fit test was used on a global model. If support for this model was above 0.10, the $\hat{c}$ (χ^2/df) was adjusted and model testing proceeded. Models were constructed assuming either constant survivorship or variable survivorship (φ) over time or between injured and uninjured terrapins while maintaining the assumption that recapture probabilities (p) varied temporally. Akaike's Information Criterion (AIC) was used to assess individual model fit. All analyses were conducted using Program MARK (White and Burnham, 1999).

RESULTS

Overall, 10.8% of captured terrapins had a major injury; either a lost limb (8.0% of population; Table 1) or major shell damage (2.8% of population; Table 1). Only four terrapins had experienced shell damage and were missing a limb, all of them female. Limb loss occurred at relatively similar

DOI: 10.1002/aqc

frequencies among all four limbs (Table 1, $\chi^2 = 3.046$, df = 3, $P = 0.385$). Both males and females appeared to be injured at equal frequencies ($\chi^2 = 2.448$, df = 1, $P = 0.118$; 7.4% of males and 9.9% of females have a major injury). The frequency of limb injuries did not change over time (Figure 1; linear regression; $R^2 = 0.178$, $P = 0.064$), but the frequency of major shell injuries increased temporally (Figure 1; linear regression; $R^2 = 0.395$, $P = 0.003$).

Table 1. Percentage of terrapins experiencing major injuries in a population from Kiawah Island, South Carolina

	Percentage of population	Percentage of injured terrapins
All injures	10.8	
Limb loss	8.0	
Multiple limb loss	0.9	
Right front		29.3
Left front		24.8
Right rear		18.8
Left rear		24.0
Shell damage	2.7	
Carapace		70.7
Plastron		29.2

Larger turtles (i.e. longer plastron length and by association older turtles) had higher rates of major injuries, including limb loss and shell damage (Figure 2; forward stepwise logistic regression, $P = 0.0054$). Alternatively, when limb loss was examined alone, creek location was the only variable affecting the likelihood of limb loss (Figure 3; forward stepwise logistic regression, $P < 0.001$). Terrapins captured in the Kiawah River had the highest frequency of injury (0.18) and terrapins captured in Sandy Creek had the lowest (0.047; Figure 3).

Female terrapins did not experience reduced body condition after sustaining a major injury (Figure 4, F = 0.50, df = 110, $P = 0.610$). Furthermore, no differences in the body condition of terrapins were found between those that experienced limb loss and those that experienced major shell damage ($t = -0.607$, $P = 0.817$). In contrast, males that had sustained a major injury did have lower body condition (Figure 4, F = 6.15, df = 287, $P = 0.002$), although those with

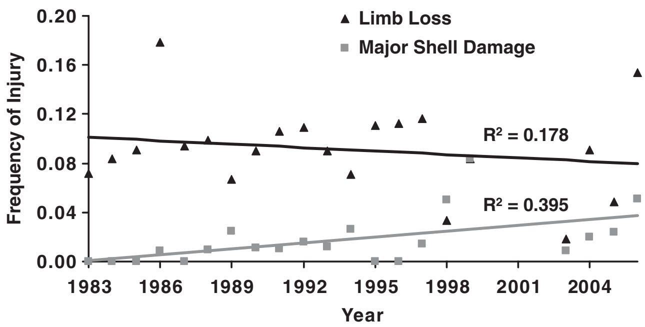

Figure 1. Frequency of shell damage increased temporally ($Y = 0.0016\ X - 3.188$, $R^2 = 0.395$, $P = 0.003$), but frequency of limb loss did not appear to have changed since 1983 ($Y = -0.0009\ X + 1.9395$, $R^2 = 0.178$, $P = 0.064$). Sampling did not occur between 2000 and 2002.

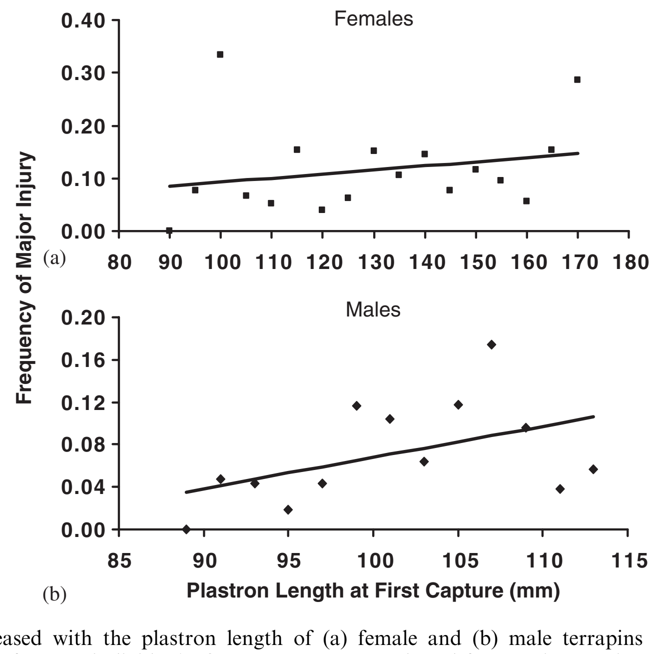

Figure 2. Frequency of injury increased with the plastron length of (a) female and (b) male terrapins (forward stepwise logistic regression, $P = 0.0054$). Plastron lengths from an individual's first capture were used, and frequencies are the mean value of 5 mm intervals.

DOI: 10.1002/aqc

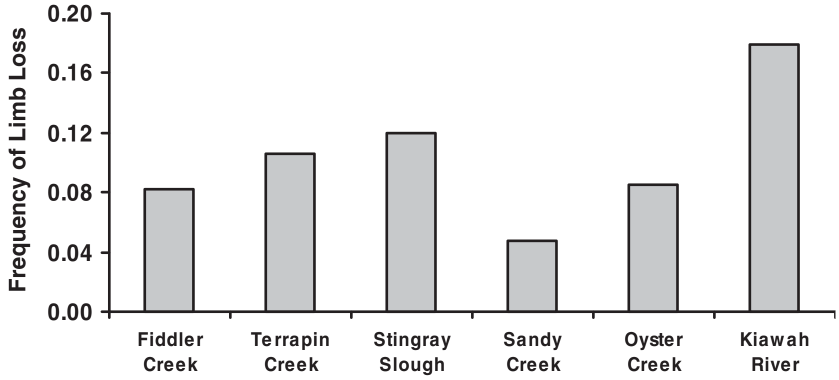

Figure 3. Frequency of limb loss varied among tidal creeks, but terrapins captured in the larger Kiawah River had the highest frequency of limb loss (forward stepwise logistic regression, $P = 0.0018$).

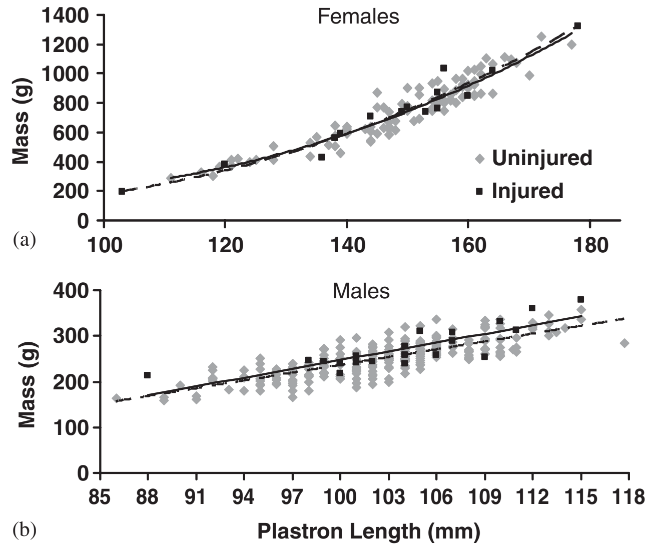

Figure 4. Injured male terrapins experienced reduced mass as a result of major injuries (ANCOVA; (a) females; F = 0.50, df = 110, $P = 0.610$, (b) males; F = 6.15, df = 287, $P = 0.002$). Solid lines represent uninjured terrapins and dashed lines represent injured terrapins. Data for females were fitted with a binomial trend line and data for males were fitted with a linear trend line.

Table 2. Results of CJS model testing in Program MARK using QAICc w to evaluate each model

Model[a]	Number of parameters	QAIC	QAICc w
Males ($\hat{c} = 1.06632$)[b]			
$\varphi^{gt}p_t$	17	1541.83	0.99457
φp_t	16	1552.25	0.00542
$\varphi^{t}p_t$	29	1570.55	0.00000
Females ($\hat{c} = 1.16159$)			
$\varphi^{gt}p_t$	18	741.91	0.57543
φp_t	17	742.52	0.42456
$\varphi^{t}p_t$	31	765.90	0.00000

[a] φ represents yearly survival and p represents yearly recapture probabilities. g represents whether differences between injured and non-injured terrapins were compared and t represents whether the model accounted for temporal variation in survival and recapture probability.
[b] Owing to sexual dimorphism and because possible differences in the causes of injury may differ between sexes; males and females were analysed separately.

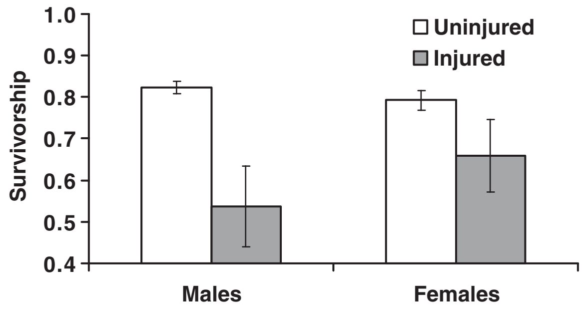

Figure 5. Injured terrapins had lower survivorship than non-injured terrapins. Model averaged estimates were obtained from a CJS model using Program MARK. These estimates were taken from the best fit model, $\varphi^{g}p_{t,}$ for both males and females. Error bars represent ± 1 SE.

shell damage did not have reduced body condition ($t = 0.646$, $p = 0.7947$), whilst those missing one or more limbs did ($t = 3.466$, $P = 0.002$) when compared to non-injured animals.

The goodness of fit testing of the global models did not reject the original assumptions (males, $P = 0.24$; females, 0.12). The model with the highest support assumed annual survivorship differed between injured and non-injured terrapins and did not vary temporally for males ($\varphi^{g}p_{t}$; Table 2, Figure 5). Similar to males, the best fit model for females assumed constant annual survivorship over time with differences between injured and non-injured terrapins ($\varphi^{g}p_{t}$; Table 2, Figure 5).

DISCUSSION

Diamondback terrapins on Kiawah Island appeared to experience injuries at biologically-significant rates, with larger (i.e. older) terrapins having a higher probability of having been injured. Males and females experienced little difference in injury frequencies, suggesting that nesting activity does not expose females to potential terrestrial predators more often than males. Terrapins did not experience higher rates of injury to any one limb, but limb loss was more frequent than major damage to the shell. Although limb loss is more frequent, the frequency of captures with limb loss may have decreased from 1983 to 2006, but the incidence of major shell damage increased (Figure 1), suggesting increased watercraft activity as a likely cause due to concomitant increases in motorized activity with increased population size on Kiawah Island. Injuries experienced by terrapins at Kiawah Island resulted in decreased survivorship. For a declining population such as the one at Kiawah Island (Dorcas *et al*., 2007), such information about the causes of injury can assist in developing sound management plans.

Examining injury frequencies between sexes and among creeks allowed us to develop inferences about the causes of injuries to diamondback terrapins (Schoener, 1979). Because nesting exposes females to terrestrial predators (e.g. raccoons), females should be injured more often than males (Feinberg and Burke, 2003), but because the frequency of major injuries did not vary between the sexes, terrestrial predators were unlikely to be a major cause of such injuries and limb loss was probably a result of aquatic encounters similar to those found in sea turtles (Heithus *et al*., 2002). Furthermore, if limb loss occurred in aquatic habitats, larger predators would be more likely to be present in the Kiawah River where terrapins experienced a higher limb loss rate than in smaller tidal creeks. Although undocumented, some potential explanations for differences in limb injury probabilities among creeks may be a factor of their proximity and ease of access to watercraft activity, recreational crabbing activity, or proximity to larger and deeper bodies of water, potentially permitting the access of more predators.

Predation on diamondback terrapins has been reported on adults during nesting and on juveniles during hatching and emergence from hibernation (Lazell and Auger, 1981; Feinberg and Burke, 2003; Draud *et al*., 2004), but researchers know little about aquatic predators on terrapins. Sea turtles are known to experience injuries as a result of attempted predation by several species of sharks (Fergusson *et al*., 2000; Heithaus *et al*. 2002, 2005), but sharks captured in many tidal creeks of Kiawah Island (adult bonnethead sharks — *Sphyrna tiburo*, and juveniles of other species) would be unlikely to prey on diamondback terrapins (F. Schwarz, pers. commun.). Alternative explanations of injury may be severe bites by fish such as toadfish (*Opsanus beta*; F. Schwarz, pers. commun.) or claw pinches from common crabs in the area, such as large blue crabs (*Callinectes sapidus*) and stone crabs (*Menippe mercenaria*). These bites or pinches may occur during terrapin foraging but are unlikely to completely sever a limb. But, such altercations may cause enough damage to result in the loss of a limb (F. Schwarz, pers. commun.). Although the importance of studying terrestrial predators is well known (Feinberg and Burke, 2003; Draud *et al*., 2004), this study demonstrates the importance of examining predation by aquatic predators as well.

Terrapins with either healed shell damage or limb loss had lower survivorship than uninjured terrapins. Although the direct mechanism reducing their survivorship is unknown, many aspects of their ecology may be affected by limb loss or major shell damage. Initially, terrapins must expend additional energy to heal damage to the shell or limbs as well as overcome any opportunistic infections, but the effects of limb loss are long term. The estimates of survivorship in this study are almost certainly conservative because injured terrapins must have survived until capture after an injury, and no measure of the direct mortality rate associated with cryptic, injurious aquatic-encounters (e.g. attempted predation) or boat traffic was conducted.

Male terrapins with shell damage did not experience reduced body condition compared with uninjured terrapins, but male terrapins missing a limb did. Insufficient sample sizes of injured ($N=22$) and uninjured female terrapins ($N=88$) probably prevented detection of differences in female body conditions. Limb loss will obviously reduce body mass, but the results of this study suggest that limb loss may also affect the overall body condition of injured terrapins by reducing their foraging and/or basking success.

Adult terrapins missing a limb probably experience a reduction in their ability to avoid predators as a result of the loss of agility and speed. Although terrapins at Kiawah Island feed primarily on periwinkle snails (Tucker *et al*., 1995), they may be unable to forage successfully for other prey items such as crabs. Furthermore, some injuries may affect their ability to bask as a result of difficulties emerging from or retreating to the water. Reduced foraging success and reduced basking ability could lead to lower body condition and potentially reduced reproductive capabilities (Lack, 1966). In May 2007, a female was captured with three missing limbs that was extremely thin (and without eggs, when most other females at the same time had detectable eggs). Reproduction may also be hampered in males by the loss of a rear limb that may render these individuals incapable of copulating, as reported for *Glyptemys insculpta* (Burger and Garber, 1995). Likewise, female terrapins missing a rear limb may be unable to dig a successful nest.

Although anthropogenic factors appear to have little effect on limb loss, watercraft activity as a consequence of anthropogenic growth on Kiawah Island has apparently increased the likelihood that a terrapin will experience a major shell injury. In a declining population such as the terrapin population on Kiawah Island that faces many other threats such as crab trapping (Seigel and Gibbons, 1995; Roosenburg *et al*., 1997; Dorcas *et al*., 2007), an additional threat to survival may serve to critically endanger populations. Reducing the rate of injuries is particularly important because these injured terrapins with reduced survivorship and reproductive output will have potentially lower fitness. One method of reducing the threat of injury or mortality to these

DOI: 10.1002/aqc

terrapins would be to limit watercraft activity in small tidal creeks. Because terrapins are less active within small creeks during high tide (Harden *et al.*, 2007), restricting motorized watercraft access to the creeks during mid and low tides would potentially reduce the threat of shell injuries. Further research on the cause of limb loss and shell damage in terrapins will aid in determining effective methods to prevent major injuries to terrapins.

ACKNOWLEDGEMENTS

Marilyn Blizard, Sophia McCallister, Bill Daniel, Nancy Peters, and Resort Quest Kiawah Island Vacation Rentals provided lodging or arranged for housing. Marilyn Blizard and Meg Hoyle were especially helpful in facilitating interactions with regulatory agencies and the Town of Kiawah Island. Tony Tucker provided thorough records for several years of terrapin data from the Kiawah population, and Judy Greene helped manage the database and greatly assisted with numerous other tasks. Numerous UGA-SREL and Davidson College personnel assisted with sampling and processing terrapins. Steve Price assisted with statistical analysis. Andrew Grosse assisted with manuscript preparation. This research was approved by the Davidson College Institutional Animal Care and Use Committee (Protocol♯ 3-04-11). Funding was provided by Duke Power, the Department of Biology and the Office of the Vice President for Academic Affairs at Davidson College, National Science Foundation Grants (REU DBI-0139153 and DEB-0347326) to MED, and the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, U.S. Department of Energy through Financial Assistance Award number DE-FC09-96SR18546 to the University of Georgia Research Foundation.

REFERENCES

Brennessel B. 2006. *Diamonds in the Marsh: A Natural History of the Diamondback Terrapin*. University Press of New England, Hanover and London.

Burger J, Garber SD. 1995. Risk assessment, life history strategies and turtles, could declines be prevented or predicted. *Journal of Toxicology and Environmental Health* **46**: 483–500.

Carr AF. 1952. *Handbook of Turtles The Turtles of the United States, Canada, and Baja California*. Cornell University Press, Ithaca, NY.

Dodd CK. 2001. *North American Box Turtles: A Natural History*. University of Oklahoma Press, Norman, Oklahoma.

Dorcas ME, Willson JD, Gibbons JW. 2007. Crab trapping causes population decline and demographic changes in diamondback terrapins over two decades. *Biological Conservation* **137**: 334–340.

Draud M, Bossert M, Zimnavoda S. 2004. Predation on hatchling and juvenile diamondback terrapins (*Malaclemys terrapin*) by the Norway rat (*Rattus norvegicus*). *Journal of Herpetology* **38**:467–470.

Feinberg JA, Burke RL. 2003. Nesting ecology and predation of diamondback terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York. *Journal of Herpetology* **37**: 517–526.

Fergusson IK, Compagno LJV, Marks MA. 2000. Predation by white sharks, *Carcharodon carcharias* (Chondrichthyes: Lamnidae), upon Chelonians, with new records from the Mediterranean Sea and a first record of the ocean sunfish, *Mola mola* (Osteichthyes: Molidae), as stomach contents. *Environmental Biology of Fishes* **58**: 447–453.

Gibbons JW, Lovich JE, Tucker AD, Fitzsimmons NN, Greene JL. 2001. Demographic and ecological factors affecting conservation and management of diamondback terrapins (*Malaclemys terrapin*) in South Carolina. *Chelonian Conservation Biology* **4**: 66–74.

Harden LA, DiLuzio NA, Gibbons JW, Dorcas ME. 2007. Spatial and thermal ecology of diamondback terrapins (*Malaclemys terrapin*) in a South Carolina salt marsh. *Journal of the North Carolina Academy Science* **123**: 154–162.

Heithaus MR, Frid A, Dill LM. 2002. Shark-inflicted injury frequencies, escape ability, and habitat use of green and loggerhead turtles. *Marine Biology* **140**: 229-236.

Heithaus MR, Frid A, Wirsing AJ, Bejder L, and Dill LM. 2005. Biology of sea turtles under risk from tiger sharks at a foraging ground. *Marine Ecology Progress Series* **288**: 285–294.

Hickey JJ (ed.). 1969. *Peregrine Falcon Populations, Their Biology and Decline*. The University of Wisconsin Press: Madison.

Lack D. 1966. *Population Studies of Birds*. Oxford University Press: London.

Lazell Jr JD, Auger PJ. 1981. Predation on Diamondback Terrapin (*Malaclemys terrapin*) eggs by dunegrass (*Ammophila breviligulata*). *Copeia* **1981**: 723–724.

Peakall DB. 1976. The peregrine falcon and pesticides. *Canadian Field-Naturalist* **90**: 301–307.

Roosenburg WM, Cresko W, Modesitte M, Robbins MB. 1997. Diamondback terrapin (*Malaclemys terrapin*) mortality in crab pots. *Conservation Biology* **11**: 1166–1172.

Saumure RA, Bider JR. 1998. Impact of agricultural development on a population of wood turtles (*Clemmys insculpta*) in southern Québec, Canada. *Chelonian Conservation Biology* **3**: 37–45.

Saumure RA, Herman TB, Titman RD. 2007. Effects of haying and agricultural practices on a declining species: The North American wood turtle, *Glyptemys insculpta*. *Biological Conservation* **135**: 581–591.

Schoener TW. 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology* **60**: 1110–1115.

Seigel RA, Gibbons JW. 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 Biology* **1**: 241–243.

Sokal RR, Rohlf FJ. 1981. *Biometry*. W.H. Freeman and Company: San Francisco, CA.

Szerlag S, McRobert SP. 2006. Road occurrence and mortality of the northern diamondback terrapin. *Applied Herpetology* **3**:27–37.

Tucker AD, FitzSimmons NN, Gibbons JW. 1995. Resource partitioning by the estuarine turtle *Malaclemys terrapin*: trophic, spatial, and temporal foraging constraints. *Herpetologica* **51**: 167–181.

Tucker AD, Gibbons JW, Greene JL. 2001. Estimates of adult survival and migration for diamondback terrapins: conservation insight from local extirpation within a metapopulation. *Canadian Journal of Zoology* **79**: 2199–2209.

Werner EE, Anholt BR. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* **142**: 242–272.

White GC, Burnham KP. 1999 . Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46**(Supplement): 120–138.

Wood RC. 1997. The impact of commercial crab traps on northern diamondback terrapins, Malaclemys terrapin terrapin. In *Proceedings of Conservation, Restoration, and Management of Tortoises and Turtles--An International Conference*, Van Abbema J (ed.). New York Turtle and Tortoise Society: New York; 21–27.