Amphibians and Reptiles
Status and Conservation in Florida

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KRIEGER PUBLISHING COMPANY
Malabar, Florida
2005
The Diamondback Terrapin in Florida Bay and the Florida Keys: Insights into Turtle Conservation and Ecology

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Introduction

An estuary is a unique environment that simultaneously provides some of the highest animal productivity in the world and yet is one of the harshest habitats for most animals to survive (Correll, 1978; Day et al., 1989). Among the uniquely adapted estuarine animals is the diamondback terrapin (Malaclemys terrapin). Diamondback terrapins require an estuarine environment and survive only in brackish coastal waters and salt marshes. This turtle also has a remarkable and demonstrative history with humans. Diamondback terrapins were once commonly found in large numbers; however, near the turn of the 20th century terrapin populations were severely reduced by commercial harvest for turtle meat. The remnant populations continue to suffer from anthropogenic factors such as water development, pollution, boat traffic, crab trapping, and human consumption. The research required to conserve and manage these remnant populations provides the framework to examine broader issues of turtle conservation. The long documented history for this species increases the value of studies that examine the consequences of the earlier population collapses in the modern context.

There is considerable concern among herpetologists regarding the status of turtle populations globally (Klemens, 2000). These long-lived animals have generally lengthy generation times and low overall fecundity. Yet their physiological features allow turtles to be robust with regard to many environmental stresses. Populations can rebound from depredations, but it takes more time than with shorter-lived animals. Unfortunately, there are very few sources of information regarding the recovery of turtle populations from depletion or extirpation. Examination of diamondback terrapin populations may provide key insights, as these populations attempt to recover from the heavy depletions of the early 1900s documented by several authors (Carr, 1952; Dittus, 1966). The current populations represent a recovery from a severe bottleneck and can provide a reference model for other turtle populations and species currently entering their own bottlenecks.

The generally resilient nature of diamondback terrapins, their life history characteristics, and wide distribution in coastal habitats allow information about this species to act as a reference both in turtle conservation and in the examination of delicate coastal ecosystems.

Today, terrapin populations are again threatened throughout their range (Garber, 1990), and this time the estuarine habitats that were largely intact in the 1930s that allowed their populations to rebound are now increasingly altered (Ernst et al., 1994). There are hundreds of estuaries along the Atlantic shores of the United States, with the majority of the human population and its industry found within the 10% of land along the coasts. With this concentrated settlement and industry, we find pollution, agricultural and urban runoff, over crowding, destruction, and other impacts to these estuarine environments, especially in salt marshes, sea grass beds, and mangroves (Hatcher et al., 1988; Thorne-Miller and Catesa, 1991; Fourqurean and Robblee, 1999). Populations of diamondback terrapins throughout their range have been affected by these types of environmental stressors and, being turtles, are uniquely suited to provide data on the consequences (Stone et al., 1980; Olafson et al., 1983). Florida Bay, in the southernmost range of diamondback terrapins, is a prime example of the negative consequences of anthropogenic influences on an estuarine environment and is typified by eutrophication, algae blooms, increased turbidity, hypoxia, and correlated abundance of pathogens leading to mass mortality in sponges, sea grass beds, and nursery habitats. These detrimental effects have inevitably led to declines in wildlife populations throughout the system (Fourqurean and Robblee, 1999).

In this chapter, we integrate our current observations with existing data on terrapin life history charac-
teristics and sources of decline. We also provide results from ongoing research for populations in south Florida, specifically Florida Bay and the Florida Keys, and examine the implications of that research both for diamondback terrapins and for turtle populations worldwide.

Diamondback Terrapin Biology

The diamondback terrapin is the only estuarine emydid turtle found in North America. These turtles occupy a range of estuarine habitats from Massachusetts to Texas (Carr, 1952). Female terrapins will stray from this habitat only to transcend the high tide mark to lay their eggs (Palmer and Cordes, 1989). As a consequence, diamondback terrapins have evolved physiological and behavioral specializations to cope with the widely fluctuating physicochemical parameters in the estuarine environment (Ernst and Bury, 1982). Since salinity may be the most significant factor limiting the number of reptiles in brackish habitats, diamondback terrapins have evolved unique physiological adaptations. Among these are the presence of a lachrymal salt gland activated only during dehydration, storing extracellular fluid intracellularly, and drinking of rain water whenever available (Dunson and Mazzotti, 1989).

The abiotic severity of the estuarine habitat does have some selective advantages for the terrapin. These estuarine areas are rich in nutrients and food sources and low in competition. Here, the diamondback terrapin is a top carnivore feeding primarily on crustaceans and mollusks that are found in these waters (Tucker et al., 1990).

Taxonomists recognize seven subspecies of diamondback terrapin across the species range. These subspecific divisions are based solely on geographic and morphological characteristics (Figure 20.1). The seven subspecies, from Massachusetts to Texas, are the northern diamondback terrapin (Malaclemys terrapin), the Carolina diamondback terrapin (Malaclemys terrapin centrata), the Florida east coast diamondback terrapin (Malaclemys terrapin tequesta), the mangrove diamondback terrapin (Malaclemys terrapin rhizophorarum), the ornate diamondback terrapin (Malaclemys terrapin ornata), the Mississippi diamondback terrapin (Malaclemys terrapin pileata), and the Texas diamondback terrapin (Malaclemys terrapin littoralis). The subspecies of diamondback terrapin have similar characteristics, including a large plastron anchored to the carapace by a wide bridge, and a short and broad skull. The carapace is usually gray, brown, or black, the plastron is yellow, and the skin of the head, neck, and limbs is typically gray (Ernst and Bury, 1982). Despite the gross physical similarities, interpopulational variability has led to taxonomic subdivision. It is notable that we have seen that large samples from a single locality often show color pattern variations, which can resemble or obscure the described characters of other subspecies. Alongside the morphological variations, the subspecific populations are found in very different climatic conditions in North America. The very different seasonal cycles of the northern subspecies have led to differing life history specifics from their southern counterparts.

For example, diamondback terrapins are known to display biased sex ratios throughout their range. Although most populations studied are female-biased, our study populations from the Lower Keys are more strongly biased than any other populations reported. Populations on the east coast of central Florida exhibit a 5:1 female-biased ratio (Seigel, 1984), whereas those farther north in the Maryland Patuxent River have a 3:1 female bias (Boosnenc, 1990). In South Carolina, Lovich and Gibbons (1980) report a slight male bias at 1.78:1. The populations we examined in south Florida show a female bias of 9:1 in Everglades Nisional Park, 5:1 across the Middle Keys, and 21:1 in the Lower Keys. There are several explanations for these sex-biased ratios including skewed sampling rates between the sexes, environmental sex determination (ESD), differential maturity and mortality, or differences among subspecies. Our current mark and recapture data indicate equal recapture rates between males and females; hence skewed sampling remains possible but unlikely. Our working hypothesis for the extreme bias we have found
in the Lower Keys (21:1) includes ESD (higher tem-
peratures during incubation lead to a preponderance of female) as affected by the latitude, and differential
mortality based on our observation of bald eagle (Haliaeetus leucocephalus) predation. Most eagle nests
contain terrapin shells, and the predation appears to
be locally restricted to male terrapins and juvenile fe-
nales. We believe this is to be a result of size con-
straints on eagles handling terrapins during predation.
Diamondback terrapins exhibit dramatic female-
dominated sexual size dimorphism. One consequence of
this is the potential for skewed sampling prefer-
ferring female captures over males as a result of the
smaller males being harder to locate than the larger
females. The average plastron length in males at ma-
turity is 80 to 90 mm, whereas it is 160 to 175 mm in
females (Cagle, 1952). Likewise, Cagle reported the
average weight of males at maturity to be 250 g and
710 g in females. In Florida Bay populations, we have
found a mean plastron length of 181 mm and average
weight of 985 g in females (n = 445) and 125 mm and
290 g in males (n = 45). Females have proportionally
wider heads than males, and males have longer, thicker
tails with the cloacal opening situated posterior to the
shell margin allowing ease of field identification (Lovich and Gibbons, 1990). The greater body size of the
female increases the reproductive potential, as clutch
size is positively correlated to body size in diamond-
back terrapins (Montevetchi and Burger, 1975). There
is an apparent difference in diamondback terrapins from
large clutch sizes/male egg size in the north, to small
clutch sizes/large egg size in the south (Montevetchi and
Burger, 1975; Siegel, 1980a). In south Florida, we have
not located any successful nests, but we have x-
rayed females (n = 17) and found a mean clutch size of
5.62. Sexual maturity in diamondback terrapins is based
on size. Males are known to reach a mature size as
young as two years of age, whereas female do not reach
a mature size until seven or eight (Ridley-Onsley, 1922).
Growth of the sexes is rapid and constant for the first 2
years of life, slowing for males at maturity. Females
continue to grow at the faster juvenile rate until they
reach maturity at the age of seven (Seigel, 1984).

Historical Terrapin Bottleneck and Current Risks

Low reproductive rates overall, high nest mortal-
ity, and adult-biased population structure make terrap-
ins highly sensitive to perturbations, which alter sur-
vivorship, particularly of adults. This is then the crux of
any attempt toward conservation in turtles, gener-
ally, as current direct-harvest methods are concentrated
on adults. Furthermore, although the general cause of
the declines is often known, it is sometimes not clear
what specific direct and indirect factors are leading to
the decline of a given population.

Diamondback terrapins earned the dubious distinc-
tion as "the most celebrated of American turtles," a
reflection of the popularity of this turtle as a gourmet
food item in the early 20th century (Cassatt, 1975).
Intensive harvest for human consumption of the diamond-
back terrapin originally led to a significant decline throughout its range. By 1929, populations of terrapin
were so reduced that only 374 kilograms were brought
to the market (Garber, 1990). In 1944, after a 14-year
population rebound, the commercial market for ter-
rapin peaked at 204,300 kilograms of terrapin meat col-
lected for human consumption (Balcock, 1988). The
demand for turtle soup has since diminished, yet di-
amondback terrapin populations have never fully recov-
ered. With their slow rate of maturation, terrapins can
not withstand heavy harvest and still maintain healthy
population levels (Ernst and Barbour, 1972). Minimum
size restrictions have been imposed on commercial
hunters making it illegal to harvest smaller terrapins.
Unfortunately, this size restriction diverts attention to
collectors of larger reproductively mature females.
Many states are considering a minimum and maximum
size restriction to limit the number of mature females
captured. Conservation efforts must not myopically focus only
on adult terrapins, but also their nesting beaches and
hatchlings. Specifically, efforts should focus on reduc-
ing or minimizing the many anthropogenic obstacles
that female terrapins must overcome in order to pro-
duce a successful nest. The goal of conservation efforts
should succinctly amount to allowing adults to persist
and enable them to produce sufficient viable hatchlings
to replace themselves as individuals. An ancillary goal
might be to allow re-growth of the current populations
with a goal of reclamation of areas now extirpated of
terrapins. However, this may be more difficult than we
currently understand. As terrapins are philopatric to
nesting areas, the use of bulleheads and water front
construction may eliminate entire breeding colonies
or crowd nesting into the reduced habitats that remain
(Rosenburg, 1990). The development of waterfront
property thus constrains the available areas for diamond-
back terrapin nesting sites and the construction of bulk-
heads and seawalls pose an insurmountable barrier for
female terrapins. Thus, they are often forced to lay
their eggs in the only sandy areas accessible (Seigel,
1980a). These suboptimal locations may expose the
nests to thermal stress in high erosion areas, or they
may be inundated by high tide thereby drowning the
embryos. The overall degradation of nesting areas may
reduce reproductive success and increase nest mortal-
ity (Roosenburg, 1994), as well as after ESR ratios of young from nests set in these suboptimal areas. Another threat to diamondback terrapin hatchlings, nests, and adults is artificially increased predation. Near the nesting beaches, natural predators of the eggs, hatchlings, and adult females include foxes (Vulpes vulpes), raccoons (Procyon lotor), crows (Corvus brachyrhynchos), and gulls (Larus atricilla (Butler, 2000; Burger, 1977). The extent of predation depends on the environment and vegetative cover. Grasses and shrubs growing on upland nesting areas provide cover for hatchlings from avian predators. On the other hand, too much cover makes nest construction difficult and can destroy existing nests (Roosenburg, 1994). In past studies, it was demonstrated that hatchlings immediately travel to the closest vegetative cover after emerging from the nest in order to escape avian predators (Burger, 1977). For this reason, diamondback terrapins are selective to nesting grounds with approximately 20% to 30% vegetative cover (Burger, 1977).

Ruminant predators seem to dominate nesting areas with approximately 50% vegetative cover. Raccoons not only target nests and hatchlings, they also attack the nesting adult female. Most predation occurs during the laying and hatching period, thus the rate of predation is not constant during the average 90-day incubation. The average nest success is low due to this predation, resulting in 1% to 3% survivorship of eggs to hatchlings (Angel, 1980). Nest predation varies from 50% to 90% and is density dependent (Roosenburg, 1994). Thus, the decreased nesting success access further exacerbates the problem of predation. Shoreline development and human encroachment may also artificially increase predation by animals that become acclimated to urbanization. Raccoons are a prime example of this association with human intrusion and are a least predating predator of terrapins and terrapin eggs. Raccoon numbers seem to increase due to lack of their natural predators, thus imposing a greater stress on hatching and nest mortality (Roosenburg, 1990).

Similarly, pollution is a contributing factor to the decline in terrapin numbers. Pollution deteriorates water quality and nesting sites. Chemical and sediment erosion runoff contaminates coastal areas and destroys food sources. Insecticides and herbicides also contribute to the decrease in number of terrapins. Large quantities of chlorinated hydrocarbons (stained in many pesticides) are stored in the body fat in the late summer and early fall and could cause death in turtles as they use this fat during hibernation (Ernst and Barbour, 1972).

Motorboats also pose a physical threat to diamondback terrapins. Propeller damage inflicts fatal wounds primarily to adult female terrapins as they bask at the surface. The higher frequency of propeller cuts among females is likely due to their larger size, and hence a reduced ability to escape incoming boats (Roosenburg, 1990). Although we have not observed prop damange first hand in Florida bay, it is common (10%) in our study sites on the Texas gulf coast.

Aside from these ancillary causes, there are also continuing direct reductions in terrapins due to human activities. There remains an active meat fishery in many states. Thus, the commercial harvest of the last century continues, albeit with occasional regulations. There are also direct harvests that are not related to terrapin meat consumption. The most significant to diamondback terrapin mortality rates is crabbing. Private land owners, as well as commercial fishermen, set crab pots that have the potential to severely impact terrapins. Juveniles of both sexes and adult male terrapins, because of their smaller size, are most frequently caught in crab pots. Females remain vulnerable until approximately age seven when they reach sufficient size at sexual maturity. Terrapins have an innate curiosity to investigate, and the presence of a terrapin in a crab pot may be the perfect attraction for additional turtles (Roosenburg, 1950). The greatest tragedy in terrapin mortality results from abandoned or infrequently checked crab pots. In 1989, an abandoned crab pot (or ghost pot) was discovered with the entire shells of 49 terrapins and the partial remains of others. This single crab pot represented an estimated mortality of 1.0% to 2.8% of the entire Patuxent River population (Roosenburg, 1990). Likewise in 1988, one of us (M. Forstner) located a single "ghost pot" which contained, at minimum, 27 individuals as partial remains (right plastron bridge elements were used in the assessment). This specific locality in Texas is now believed to be completely extirpated of terrapins; none have been recovered at this site in the subsequent 4 years of surveys.

Conservation Management Data From Florida Bay

The Florida Fish and Wildlife Conservation Commission classified all five subspecies of diamondback terrapin occurring in Florida (Figure 20.1) as "imperiled taxa" (Millsap et al., 1990). To manage and conserve an endangered animal such as diamondback terrapins, the dynamics of their populations must be understood. As a result we have sought information regarding population size, structure, and dispersive events in the Florida Bay populations by examining ornate diamondback terrapin and mound-feeding diamondback terrapin which can ultimately be related back to fecundity and dispersal. Issues of fecundity are easily directly
determined; however, dispersal appears to be much more difficult to examine in diamondback terrapins. There are many reasons for turtle dispersal including mating, nesting, search for food and fresh water, avoidance of habitat alteration, and natural disasters such as hurricanes or droughts.

Before one can determine if terrapins are migrating and emigrating, one must first understand the distribution of individual turtles. Likewise, in much the same way as it is necessary to qualify activities impacting terrapins, it is absolutely imperative that populations be surveyed, and where possible, subject to mark-recapture estimates to gain an estimate of numerical size. Mark and recapture study not only help to assess population size, structure, and distribution, they are also useful in assessing diamondback terrapin population demographics and biology. One of the first studies derived an estimate of 2000 terrapins for one area of Chesapeake Bay (Roosenburg, 1990) and 4700 terrapins specifically within the Patuxent River area (Roosenburg, 1992). Based on extensive mark and recapture studies between 1994 and 2001, we estimate population sizes for ornate diamondback terrapin in Everglades National Park at 1300 terrapins and mangrove diamondback terrapin the Middle Keys at 650 and 200 in the Lower Keys (Persson et al., 2000).

Although there are many criticisms of the various algorithmic methods applied to estimate a given population from recapture data, we believe that our estimates are very close to the true values based upon a number of criteria. We routinely recapture a significant portion of individuals on each field survey, with recapture rates ranging from a low of 40% upward to nearly 60% depending on the study sites (Forstner et al., 2000). We have remained active in seeking new unexplored populations in the system and extensively examine areas adjacent to our primary study sites (without contradicting our conclusions on the relative size of the populations under study). The figures support the contention that population size of diamondback terrapins in south Florida remains greatly reduced from a century ago. These estimates are also the first piece of circumstantial evidence regarding the extremely sedentary nature of terrapins in Florida Bay.

Reports have indicated minor dispersal of terrapins correlated with mating (Seigel, 1980a). Typically, the male locates and pursues the female until she is responsive to copulation. Female terrapins are philopatric, returning to the same nesting site year after year. The longest documented female dispersal for nesting occurred in Sandy Neck, Cape Cod, Massachusetts (Auger and Giovannone, 1979). The terrapin traveled 1600 m from mating to nesting site. In our experience, this is an extremely large terrapin travel distance; the average female dispersal for nesting reported elsewhere lies between 10 m and 100 m (Burger and Montvecchi, 1975; Roosenburg, 1994) indicating that they remain within their isolated populations. Studies in north Florida have located one important nesting beach for the Carolina diamondback terrapin. Problems determining the time of day when nesting occurred, locating nests, identifying predators and vegetation on the beach were completed by Butler (2000). Nesting beach details remain confidential to protect nesting female terrapins. In our study populations in Florida Bay, nesting has not been observed to any significant degree, nor have any hatched nests been located. We have located predatory nests (presumably by black rats [Rattus rattus]) on several sites. We have also radiographed gravid females and subsequently radio-tracked them, but were unsuccessful in locating the nesting sites they used. Currently, there is little known about the nesting biology of south Florida terrapin populations, but it would appear that they nest within several hundred meters of their normal habitat in the lagoons.

Previous mark and recapture studies indicate that diamondback terrapins move very little within their range. The minimal movement that does occur is along shorelines and is distance-dependent. Our current data support this pattern as well. We have had only two individuals move between islands (<1000 m) out of nearly 2000 marked individuals at sites throughout the system. Thus, our data support the idea that terrapins are sedentary.

We have also utilized radio telemetry in an ongoing study to assist in determining home ranges and daily activity patterns of terrapins. The 22 individuals (13 males and 9 females) whom we have followed for periods up to 2 years have shown movement around the island/lagoon habitats, but no dispersal from the sites. We were able to track females consistently, whereas tracking males was more difficult. In no case did the average movement distance exceed 1000 m per recapture.

We have also begun examining of the underlying population genetic structure found within and among study sites in Florida Bay and the Florida Keys. Genetic data that describe the underlying structure of animal populations are extremely valuable, if not critical, to the development of a sound management plan (Avise, 1994; 1995; 1996; Moritz, 1994b). Movement of animals from one population to another is the most important factor in maintaining genetic homogeneity of species throughout their range. When populations become isolated and gene flow is reduced, evolutionary processes such as genetic drift or selection can alter genetic composition of isolated populations.
(Putumya, 1988). Population studies of diamondback terrapins throughout their range have indicated that there is considerable geographic variation in life history characteristics (Segal, 1984) among populations, suggesting that migration on a wide scale does not occur. However, molecular studies of mitochondrial DNA (mtDNA) of terrapin populations indicate that genetic uniformity exists except for a break near Merritt Island, Florida (Lamb and Avise, 1993). This genetic "break" divides the northern populations, M.t. terrapin, M.t. centra, and M.t. terpsis from the southern Gulf populations, M.t. rhizophorum, M.t. macropitana, M.t. pileata, and M.t. littoralis (Lamb and Avise, 1992). Miller (2001) has indicated that there is very limited mtDNA variation across the entirety of the range of diamondback terrapins. Nuclear genetic markers called microsatellites are both co-dominantly inherited and hypervariable, thus they can provide information about both male and female dispersal over time and potentially increase our resolution at the population level. In our continuing work, we have found unique alleles in separate study sites. These preliminary data indicate that the populations are very stable with little interpopulational migration over time.

Finally, we recently completed a study that further emphasizes the low dispersal rates in this species. The study sought to determine the effects of hurricanes on terrapin populations. Miller (2001) examined a terrapin population before and after hurricane Georges passed over the study area on 26 September 1998. For a period of 4 months, the number of terrapins we found was dramatically decreased from pre-hurricane numbers; afterward we began to find the turtles more regularly. In fact, 6 months after the hurricane, we were able to recapture individuals at approximately the same rates as before the storm. We were recapturing the same individuals as were present prior to the storm. The same turtles were relocated often within meters of their original capture sites, despite dramatic habitat damage due to strong winds and high seas. We do not know where the individuals were during the months immediately after the storm, but we do know that the same individuals were returning to the site where they were present before the storms. We failed to detect any evidence that the storm's effects led to dispersal of individuals either away from or into the pre-hurricane population of the island.

With these documented findings, several questions pertaining to the biology and life history patterns of diamondback terrapins are raised. Are diamondback terrapin subspecies valid? The morphological characters appear to be quite variable within our insular populations. Likewise, despite very low mitochondrial variation, we have found variability at neutral nuclear genetic markers. Unfortunately, rather than resolving life history characteristics, this leads to further questions. If terrapins maintain such evident site fidelity, how do they maintain genetic homozygosity? Most importantly for conservation and management efforts, how do they establish new populations? Given the size fidelity we have observed, how have they reestablished previously extirpated populations? Or indeed, have they actually reestablished new populations or are the current populations the result of the few individuals left on the islands after the market hunting? This last speculation would at least partially explain the current genetic results. Only with future research, public education, and outreach programs as part of the overall conservation efforts, can we hope to properly manage this species in the wild.

Conclusions

In several ways, diamondback terrapin populations represent a unique situation in turtle biology. Direct human depredation of diamondback terrapins dramatically reduced their populations early in the last century. Current human depredations are similarly affecting turtles worldwide. Anecdotal evidence would suggest that terrapins were able to recover some of their population size over a 20-year period (Ballachey, 1988), but the evidence is not explicit on this issue. It may have been that historically uncultivated populations were discovered and fully utilized, mimicking a recovery. In any case, we have good evidence that the populations we study today went through the bottleneck event of 70 years ago. Thus, they provide an example of what we might expect if we were to guide the other 200 species of turtles currently at risk worldwide through the current bottleneck event. The populations can recover and we have documented apparently stable diamondback terrapin populations, with even some of the same individuals, several decades in the Lower Keys using data from previous terrapin studies conducted in 1982 by Wood (unpubl. data).

However, additional anthropogenic impacts can undo the recovery efforts. In particular with terrapins, our evidence and that of many other researchers support the idea that terrapins are philopatric within a very restricted home range. Hence, many extremely local effects (e.g., crabbing) can have long-term consequences. The terrapin populations of Florida Bay are currently persisting in only the most heavily utilized and impacted estuarine systems in the United States; thus they can tolerate significant outwardly deleterious effects on their habitat and appear to remain healthy. Unknown to us is the long-term viability of
those populations. The evidence from diamondback terrapins indicates that preventing overharvest of the adults for the meat trade is simply the first step in rectifying the decline. It will require rectifying the deleterious direct and indirect anthropogenic effects that occur far beyond that first step if we are to ensure long-term viable populations in the wild. The good news, at least for diamondback terrapins, is that with harvest restraints enforced, the populations have demonstrated the capacity to rebound and maintain themselves subsequently for a period now stretching to more than 70 years. This piece of evidence alone is enough to enhance our efforts to revise and enforce direct adult harvest quotas for this and any other impacted turtle species both in Florida and worldwide. Given limitations to harvest, the populations can then stabilize and even potentially recover given the habitat and time to do so.

Turtles represent a worldwide industry and require reasonable guidelines for both direct and indirect impacts in order to remain intact as viable populations in the wild. This is true across Europe, Asia, and South America. In their recovery, Florida’s diamondback terrapins should be similar to the iconic nature of the alligator for endangered species (Chapter 16) in that they represent an example of a species which was able to recover from serious declines in the past given only nominal protection and enforcing reasonable harvest laws.

Acknowledgments

We extend our special appreciation to the Everglades National Park, Florida Fish and Wildlife Conservation Commission and the Florida Keys National Refuges for granting permits and allowing access to protected areas for this study. For valuable comments on the manuscript we are indebted to K. Babbitt, W. Landier, W. Meshake and several anonymous reviewers. A very special thank you to the Batchelor Family for their financial support and advice during this project. Our sincerest gratitude to the USGS Species at Risk awarded to MKJS and BKM. Thanks to AVID, Inc. for equipment support, scanners and PIT tags. Hats off to the staff of the Department of Environmental Sciences at the Miami Museum of Science for their dedication and participation in this project.