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Demography and Ecology of Mangrove Diamondback Terrapins in a Wilderness Area of Everglades National Park, Florida, USA

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Diamondback Terrapins (*Malaclemys terrapin*) are distributed in brackish water habitats along the U.S. east coast from Massachusetts to Texas, but many populations may be in decline. Whereas ample morphological, behavioral, and reproductive information has been collected for terrapins living in temperate salt marsh habitats, comparatively little is known about mangrove terrapins. To understand population structure of mangrove *M. terrapin* living in a wilderness area, we conducted a capture–recapture study in the remote, protected Big Sable Creek complex of Everglades National Park, Florida. The goals of the study were to collect baseline demographic data and to compare population structure and growth rates of mangrove terrapins with what is known for more well studied salt marsh terrapins in locations that experience human-imposed threats. We marked 300 terrapins; the sex ratio was 1 female:1.2 males. Considerable sexual size dimorphism was apparent, with reproductively mature females three times larger (by mass) than mature males. Eighty percent of females and 94% of males were classified as mature, based on straight plastron length (SPL). For a subset of terrapins not yet at maximum size ($n = 39$), we measured growth as a change in straight carapace length over time of 0.3–26.4 mm/yr for females ($n = 26$) and 0.9–14.5 mm/yr for males ($n = 13$). Our study presents the first demographic data on mangrove *M. terrapin* in the coastal Everglades.

HUMAN-induced disturbances threaten the viability and persistence of many vertebrate populations, including turtles. Populations of *Malaclemys terrapin* are no exception, as their coastal range predisposes them to interactions with humans; terrapins inhabit brackish water along the U.S. east coast from Massachusetts to Texas (Ernst et al., 1994). Evaluation of the potential impacts of human disturbances can be aided by studies of populations subject to minimal human activity. Considered a species of special concern in many states throughout the Atlantic and Gulf coasts, the terrapin is also currently listed as endangered in Massachusetts (Watters, unpubl.) and threatened in Rhode Island (August et al., 2001). Demographic data have been collected over the past several decades for terrapins living in temperate salt marsh habitats; the sites where studies were conducted were often heavily impacted by threats including fishing pressure (Roosenburg et al., 1997; Wood, 1997; Roosenburg and Green, 2000) and roadkill (Wood and Herlands, 1997; Szerlag and McRobert, 2006). With the exception of periodic surveys in the Florida Keys by A. Carr, Jr. (1946) and R. Wood (1992) and recent work by B. K. Mealey (B. K. Mealey, pers. comm.), comparatively little is known about terrapins that occupy creeks within dense subtropical mangrove habitats in wilderness areas.

Several research reports from the 1900s presented careful descriptions of unique morphological characters of mangrove terrapins (i.e., bulbous and keeled vertebrals) from different locations in southern Florida and throughout the Florida Keys (Hay, 1904; Fowler, 1906; Carr, 1946; Wood, 1992). However, such descriptions were based on very few individuals, and no data from systematic surveys of mangrove terrapins have been published. Terrapins in salt marsh habitats have been well studied in Massachusetts (Auger and Giavannone, 1979; Auger, 1989), Maryland (Roosenburg, 1991; Roosenburg and Green, 2000), South Carolina (Lovich and Gibbons, 1990; Tucker et al., 1995, 1997, 2001; Gibbons et al., 2001), and Florida (Seigel, 1980a, 1980b, 1980c, 1983, 1984, 1993; Butler et al., 2004, 2006). Comparisons of available data for north Florida terrapins suggest that female terrapins reach sexual maturity at a plastron length (PL) of 135 mm or 4–5 years, and males mature at 95 mm PL at age 2–3 yrs (Seigel, 1984). These sizes at maturity are similar to the sizes reported for female northern terrapins (132 mm [Montevecchi and Burger, 1975]) and South Carolina terrapins (138 mm [Lovich and Gibbons, 1990; Gibbons et al., 2001]).

Because the overall status of terrapins remains unclear and human pressures are mounting in all coastal environments, we sought to address how ecologically and morphometrically different subtropical mangrove terrapins are from their temperate salt marsh relatives. We initiated a capture–recapture study in an unimpacted, protected wilderness site within Everglades National Park (ENP). Specifically, we present baseline data on mangrove *M. terrapin* body size, population structure, sex ratio, injuries, and growth for comparisons with terrapin populations living in less protected and more heavily human-impacted (i.e., by fishing pressure, roadkill) study sites. We include the first calculations of growth rates for wild mangrove terrapins for individuals sampled in the Big Sable Creek (BSC) complex. This information will contribute to an understanding of mangrove terrapin population structure in a protected population that experiences little anthropogenic pressure.

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MATERIALS AND METHODS

Study site.—The BSC complex is located in southwest Florida within ENP, at the northwest edge of the Cape Sable peninsula (Fig. 1). The site is dominated by red mangroves (*Rhizophora mangle*) and is situated within the protected wilderness area of the southwest coastal Everglades. The study area is approximately 2.1 km from N to S, and 1.6 km from E to W, or just under 4 km^2. Maximum tidal range on spring tides is approximately 2.5 m, and tides in this complex are semidiurnal, with saline Gulf water penetrating into headwater streams (Morisawa, 1968) on high tides. The site is a mosaic of intertidal mudflats and mangrove forests bissected by subtidal creeks. No detectable freshwater inflow results in near marine salinity of 27.7–34.2 ppt (Silverman, 2006) year-round.

Data collection.—To define the exact study area, we first surveyed the entire BSC complex and then refined search areas to waters navigable during low tides. For terrapin sampling, we conducted five sampling trips to the BSC complex (Table 1; Fig. 1) from November 2001 through October 2003 and worked throughout navigable creeks within the complex around new moons to take advantage of spring tides (i.e., highest high and lowest low tides). We hypothesized that such tides would provide strong tidal currents that entrained terrapins in subtidal waters, concentrating animals on falling tides. All terrapin captures were made by the same team members (KMH, GLH). During the first sampling trip to the site, we used both commercial crab pots and dip nets to capture terrapins, but thereafter used only dip nets. On all trips, dip netting was most successful during a two-hour window around both diurnal and nocturnal low tides.

Upon capture, we determined gender by examining position of cloacal opening and tail thickness; males have longer tails with the cloacal opening situated posterior of the shell margin (Lovich and Gibbons, 1990). For each terrapin we also noted anomalies in appearance and assigned a unique capture number. We measured straight line and curved carapace and plastron lengths and widths to the nearest 0.1 cm (SCH = straight carapace height; SCL = straight carapace length; SCW = straight carapace width; CCL = curved carapace length; CCW = curved carapace width; SPL = straight plastron length; SPW = straight plastron width). We used a flexible tape for over the curve carapace measurements and Forestry Suppliers calipers for straight carapace and plastron measurements. We recorded mass to the nearest 1 g with an OHaus™ digital scale. As well, we noted injuries, distinguishing marks, and recapture events. We estimated age by counting rings on the plastral scutes (Cagle, 1939), and categorized each individual as either mature or juvenile according to Seigel's (1984) plastron length determination (≥95 mm = mature male, ≥135 mm = mature female). Because Seigel's (1984) work was the most geographically proximal to our study area, we rely on those estimates of size at maturity for classification of mature individuals in the BSC population. We also recorded a GPS location for each turtle's capture and recapture location. Finally, we uniquely marked each newly captured terrapin in four ways: by notching the marginal scutes; by inserting an individually numbered 9- or 10-digit alpha-numeric passively induced transponder (PIT) tag (Buhlmann and Tuberville, 1998); by taking head-on, dorsal, ventral, and side view photographs for photo-identification (with particular emphasis on capturing the unique pattern of each terrapin's plastron); by taking blood samples to be screened later for microsatellite DNA analysis. We used this redundant marking system to ensure no errors in identification. For consistency, one researcher (KMH) performed all the notching, PIT tagging, photographing, and blood sampling throughout the study. We re-measured recaptured terrapins. All terrapins were released to their original capture sites.

Little is known about terrapin growth rates in the wild. Because we measured SCL (taken down the dorsal midline from the nuchal notch to the distal tip of the posterior marginals) for each individual upon capture and recapture, we could determine changes in SCL over time. To calculate growth rates, we subtracted SCL at original capture from measurement at recapture to produce millimeters of growth. We then used this figure to calculate a growth rate per individual per year. In the case of multiple recaptures of an individual, only the initial capture and last recapture were used in our calculations. Here we present growth rates calculated for terrapins that displayed a change in SCL over time (i.e., zero values were eliminated). As well, because we noted anomalies in appearance upon each capture, we could determine the percentage of turtles that initially had or acquired injuries. Such anomalies included missing limbs, carapace damage, and tail damage. We then summed and counted the total number of injured animals over time. We sorted the data by injury type and gender for summary calculations and statistical analysis. We performed statistical analysis with SigmaStat 3.5 (Systat Software, San Jose, CA, 2006), referencing Zar (1999). We examined bias in sex ratio with Chi-square tests, differences in mean body measurements between genders using nonparametric Mann–Whitney *U*-tests, and differences in mean growth rates between genders with *t*-tests. Statistical significance was set at the $P < 0.05$ level.

RESULTS

Captures.—Repeated, systematic surveys of the study area creeks during both daylight and nighttime hours at low tides produced a total of 300 captures (139 females, 161 males). Over five sampling trips (November 2001–October 2003) we performed 29 total sampling days (Table 1). Number of captures varied by sampling trip, but ranged from 35–96 individuals (Table 1). The overall sex ratio of captures was 1.0(F):1.2(M), only slightly male-biased, and not significantly different from 1:1 ($\chi^2 = 1.622$, df = 1, $P = 0.204$). Although we captured 24 animals (13 females, 11 males) in crab pots on the first sampling trip (November 2001), the majority of terrapins were captured with dip nets (126 females, 150 males). Individual terrapins were often captured multiple times, with 54.3% of the marked terrapins being recaptured once, 24.7% recaptured twice, 12.0% recaptured three times, 6.0% recaptured four times, and 3.0% recaptured five times (Fig. 2). Our overall recapture rate was 40%, and some recapture locations were within meters of original capture sites in the same creek systems (data not shown). We also discovered that mangrove terrapins in BSC predominately used the upper headwater portions of the creeks (i.e., first-order streams). Average depth of surveyed areas within the complex during low tide sampling was 0.7 m. We observed a distinct lack of terrapin presence in the creeks that open out to large mudflats (i.e., creeks in the southern half of the complex) or that feed

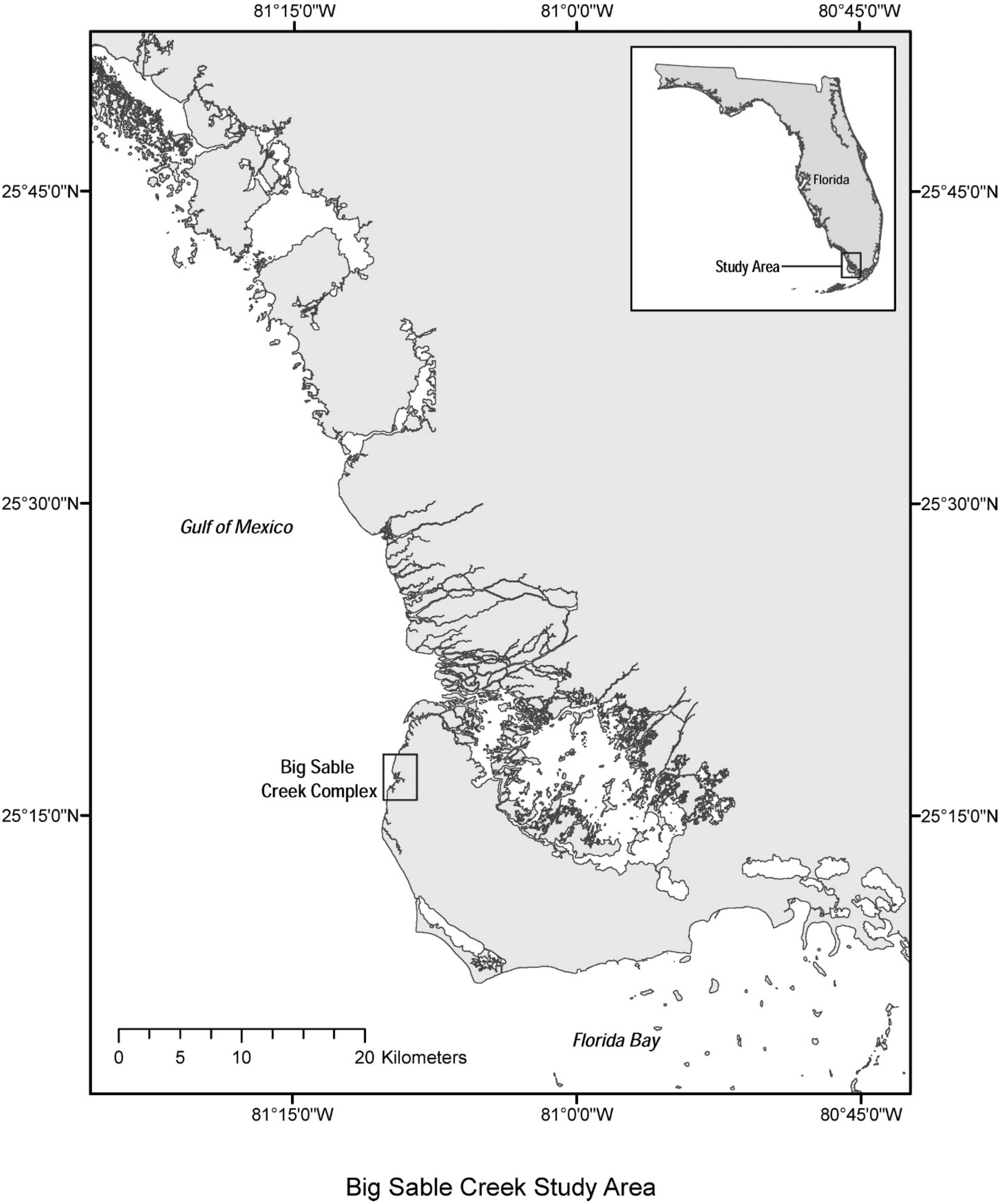

Fig. 1. Location of the Big Sable Creek study site (inset box) in southwest Florida. Approximate coordinates for the mouth of the complex are 25°16.780′N, 81°09.574′W.

Table 1. Capture Summary of Mangrove *Malaclemys terrapin* over Time in the Big Sable Creek Complex, Everglades National Park, Florida, with Sampling Effort.

Sampling period	1	2	3	4	5	Total
Midpoint date of trip	11/16/01	7/11/02	12/4/02	5/7/03	10/26/03	
Duration of sampling trip (# days)	3	5	6	6	9	29
Total # terrapins captured (F:M ratio)	50 (29F:21M)	96 (45F:51M)	64 (30F:34M)	35 (19F:16M)	55 (16F:39M)	300 (139F:161M)

directly into the Gulf (i.e., long creeks to the north of the BSC complex). Unique features of this headwater habitat include patchy areas of substantial submerged log cover (Hart, 2005), as well as fallen trees and intertidal mud banks used as basking areas (K. Hart, pers. obs.).

Size structure.—Mature adults comprise the vast majority of the animals in the sampled population, as 80% of females and 94% of males were mature according to straight plastron length (SPL) measurements (defined according to Seigel, 1984; Fig. 3). Sexual size dimorphism was also apparent in the population across all measurements (Table 2, Fig. 3). Females were on average three times larger (by mass) than males (Table 2). Because measurement data failed normality tests, we used nonparametric Mann–Whitney Rank Sum Tests to examine differences in mean values of all standard measurements between males and females. In all cases, the difference in the mean values between males and females was significantly greater than would be expected by chance ($P < 0.001$; Table 2).

Growth rate.—We detected changes in SCL over time (i.e., growth) for 39 individuals ($n = 26$ females; $n = 13$ males). All other recaptured turtles ($n = 21$) displayed no detectable change in SCL over time (thus their data were not included in growth rate calculations). Growth rate varied by gender (Table 3) and mean growth for the subset of females displaying a change in SCL was 5.9 mm/yr (SD = 6.8). For the subset of males displaying a change in SCL over time, mean growth was 3.0 mm/yr (SD = 3.6), and was not statistically different ($t = 1.39$, df = 37, $P = 0.1717$) from females.

Injuries.—We observed injuries on 47 individual terrapins (47/300 = 15.7%) in BSC. Nearly twice as many females ($n = 30$) as males ($n = 17$) had injuries and the sex ratio of injured terrapins was 1.8 (F):1.0 (M). We recorded injuries to the carapace, limbs, tail, head, jaw, and plastron (Table 4). The most common injuries were damage to the carapace and limbs, accounting for 53.2% of damage. Some animals (7/47 = 14.9%) had a combination of injuries.

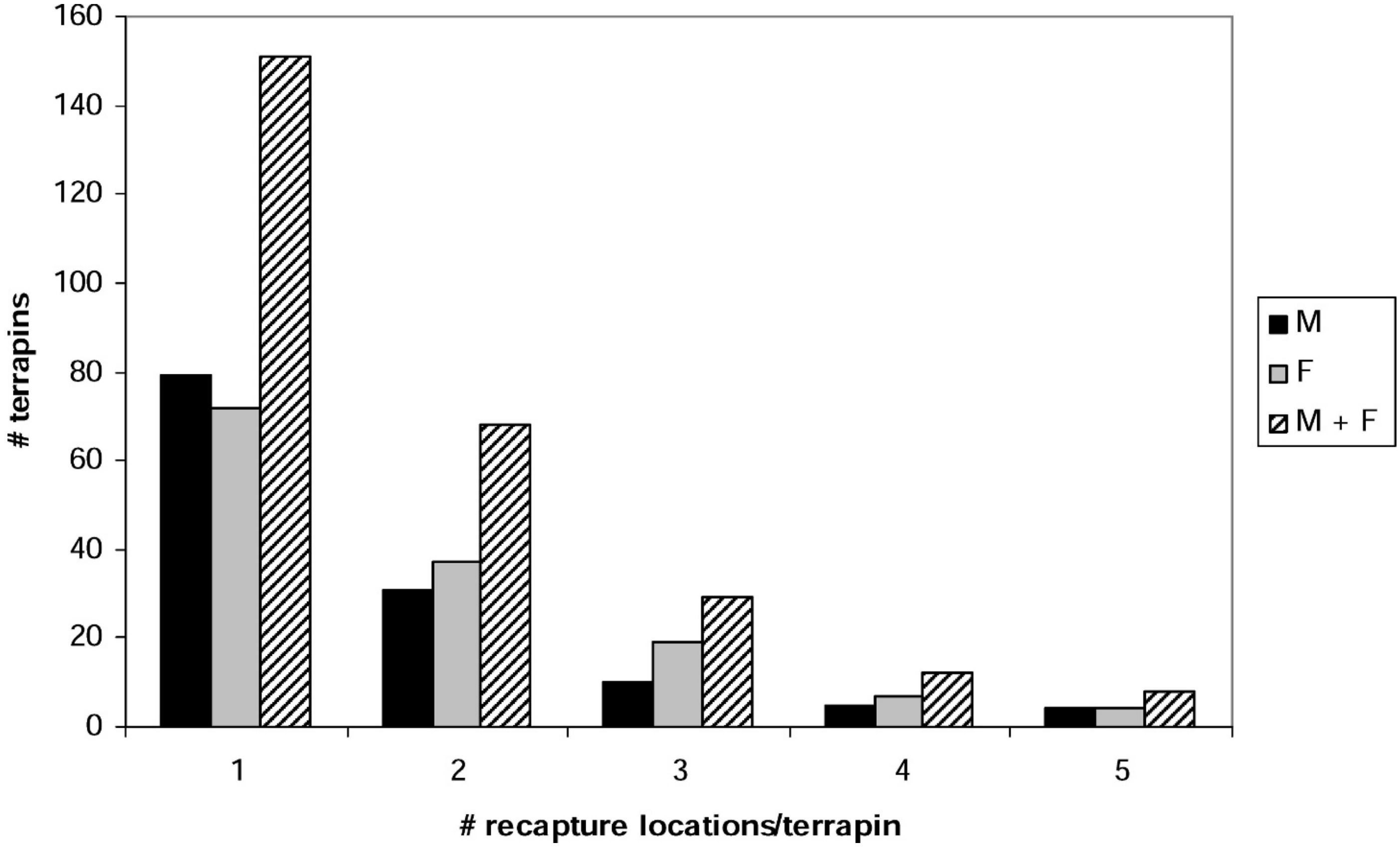

Fig. 2. Number of recapture events for each terrapin marked during the course of the *M. terrapin* capture–recapture study in the Big Sable Creek complex, Everglades National Park, Florida. M = males; F = females; M + F = males and females combined.

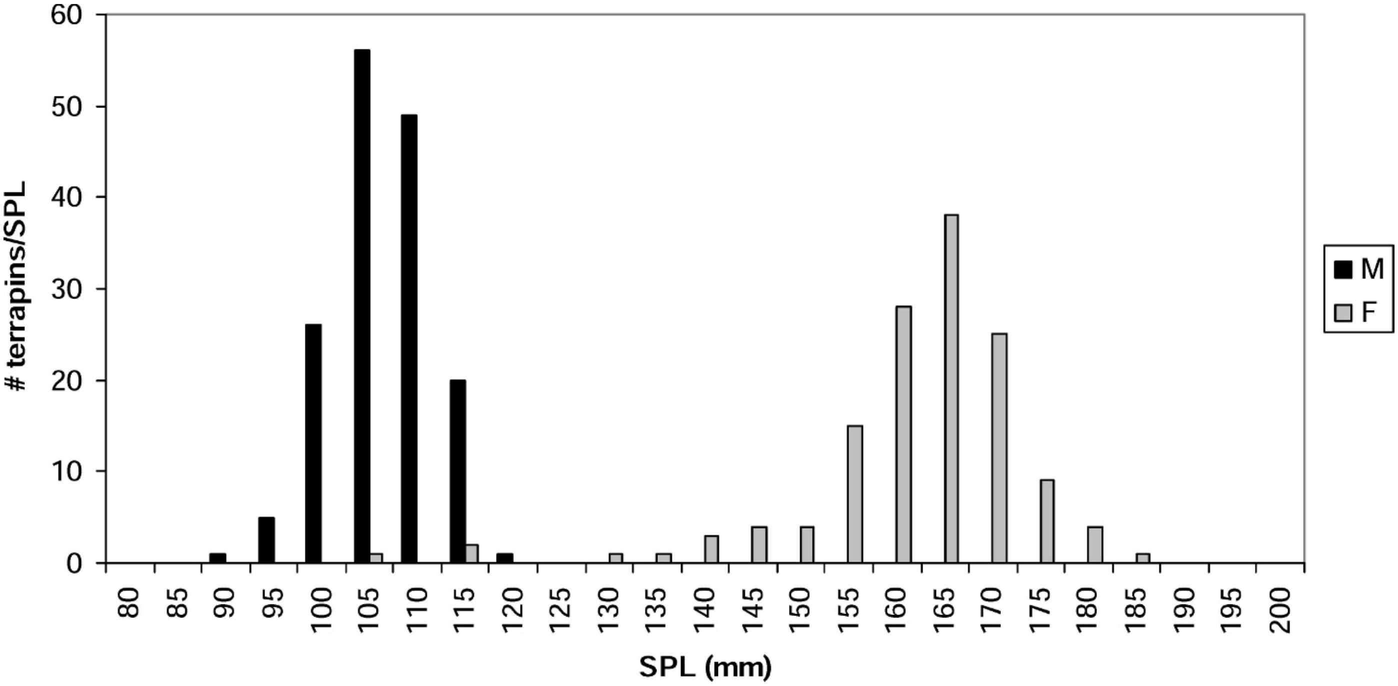

Fig. 3. Size–length frequency distribution illustrating the size (as measured through straight plastron length [SPL]) of male (M) and female (F) Diamondback Terrapins in the Big Sable Creek complex, Everglades National Park, Florida. Note: Seigel's (1984) classification of mature Florida turtles: ≥95 mm SPL are mature males and ≥135 mm are mature females.

DISCUSSION

We were able to recapture many marked individuals over time, which may be indicative of site fidelity. However, a more focused study is necessary to calculate metrics such as home range size and determine specific habitat use patterns. We also found that terrapins primarily occupied and consistently used the upper reaches of the narrow, relatively deeper, meandering creeks within the northern half of the BSC complex. The submerged logs in the upper reaches of the creeks are likely the remnants of old red mangrove trees. The habitat they provide was apparently created as a result of two major hurricanes, the Great Labor Day Hurricane of 1935 and Hurricane Donna in 1960 (Wanless et al., 1994). Such ''loggy'' habitats may provide food and refuge areas for terrapins; this finding, in particular, is important for understanding what may contribute to essential habitat for mangrove terrapins, and it may be one of several predictors of where to find additional terrapins in other areas throughout the BSC complex and in other local and/or regional mangrove habitats. Unlike their salt marsh relatives, mangrove terrapins seem to be found in areas with substantial in-water habitat structure (i.e., high log cover). To date, no such micro-habitat associations have been reported for terrapins living in more northern locations, perhaps because extensive herbaceous salt marshes are frequently distant from the nearest forested landscape.

The sex ratio in the adult terrapin population in BSC was approximately 1:1. Turtle populations with a 1:1 sex ratio are generally considered to be evolutionarily stable (Fisher, 1930). The only other population in the range of the terrapin with a reportedly equal sex ratio is from Sandy Neck, Massachusetts (Auger, 1989). This Massachusetts site is very close to the northern extreme of the species' range,

Table 2. Morphometric Data Summary Comparisons for Mangrove *Malaclemys terrapin* from the Big Sable Creek Complex, Everglades National Park, Florida. Numbers presented are mean measurements (SD). Abbreviations are as follows: SCH = straight carapace height; SCL = straight carapace length; SCW = straight carapace width; CCL = curved carapace length; CCW = curved carapace width; SPL = straight plastron length; SPW = straight plastron width. Mass is reported in grams (g) and measurements in cm; * = *P*-value < 0.001, representing statistically significant differences in measurements between genders.

	SCH	SCL	SCW	Mass	CCL	CCW	SPL	SPW
				Females (*n* = 139)				
Mean	7.7	18.1	13.6	1008.6	19.8	17.9	16.0	8.2
SD	0.6	1.4	1.0	204.8	1.6	1.4	1.2	0.7
Range	5.1–9.0	11.8–20.1	9.4–15.4	272.0–1458.0	11.7–22.0	11.3–21.0	10.3–18.5	5.2–9.5
				Males (*n* = 161)				
Mean	4.9	12.6	9.4	298.1	13.6	11.7	10.5	5.5
SD	0.3	0.7	0.5	45.2	0.7	0.6	0.5	0.3
Range	4.3–5.7	10.6–14.2	7.8–10.5	164.0–414.0	11.4–15.4	7.8–13.2	8.7–11.6	4.4–6.1
Mann–Whitney *U*-statistic	52.5*	238.0*	181.0*	197.5*	365.0*	181.5*	122.5*	295.0*

Table 3. Range and Mean Change in Straight Carapace Lengths (Growth) over Time for Mature Male and Female Mangrove *Malaclemys terrapin* upon Successive Recpatures in the Big Sable Creek Complex, Everglades National Park, Florida. Standard deviation (SD) is presented in parentheses, and SCL = straight carapace length.

Gender	SCL range (mm/yr)	Mean change in SCL (mm/yr)
Female (*n* = 26)	0.3–26.4	5.9 (6.8)
Male (*n* = 13)	0.9–14.5	3.0 (3.6)

Table 4. Summary of Injuries Observed on Mangrove *Malaclemys terrapin* Sampled in the Big Sable Creek Complex, Everglades National Park, Florida.

Injury location	# Females	# Males	Total # females and males	%
carapace	8	5	13	27.7
limb	5	7	12	25.5
tail	6	2	8	17.0
head	2	0	2	4.3
jaw	2	1	3	6.4
plastron	2	0	2	4.3
multiple injuries	5	2	7	14.9
Total	30	17	47	100.0

and the BSC site is close to the southern latitudinal extreme. Previous discussions of terrapin population structure have centered on variations in sex ratios reported from throughout the range. Seigel (1984) measured a strong female-bias in sex ratio in east central Florida, even during mating season when males would be more likely to be present for sampling. Roosenburg et al. (1997) also found a female bias in sex ratio in the Patuxent River, Maryland. However, Lovich and Gibbons (1990) found a male bias in sex ratio in South Carolina. As well, in northeastern Florida, Butler (2002) trapped male terrapins more frequently and reported a 1.0(F):1.33(M) male-biased sex ratio. As Butler et al. (2006) pointed out, possible differences in measured sex ratios include sampling gear bias, geographic variation in population biology, and gender bias in mortality source (i.e., fishing pressure such as incidental drowning in crab traps, which potentially kills more males than females [Roosenburg et al., 1997]). Another potential influence on sex ratios may stem from differences in nest temperature, a factor that affects gender of developing terrapin embryos (Bull, 1985; Janzen, 1995). However, knowing that the sex ratio in a wilderness population is nearly 1:1 may be instructive for comparisons with these more heavily impacted populations throughout the eastern Atlantic seaboard. For example, populations in the southeastern U.S. may have female-skewed sex ratios (Roosenburg et al., 1997), a feature that may result from higher mortality of males in crab pots (Roosenburg and Green, 2000; K. Hart, unpubl. data [North Carolina]; W. Roosenburg, pers. comm. [Maryland]).

Size structure.—The BSC population of terrapins was comprised mostly of adults. Although we do not present estimated ages of animals here because of the lack of a clear relationship between age and plastral growth lines for turtles (Brooks et al., 1997; Aresco and Guyer, 1998; Litzgus and Brooks, 1998a), our coarse estimates of age agreed with size at maturity estimates, indicating that the majority of terrapins sampled were adults. This may indicate that, first, our sampling strategy and location favored adults and adult habitat; it is possible that hatchling and juvenile terrapins use a habitat different from the near-marine salinity tidal creeks in which we sampled. The BSC study site is regularly flooded by full-strength seawater from the Gulf, with measured salinities in the range of 32 ppt (Silverman, 2006; K. Hart, unpubl. data); Dunson and Mazzotti (1989) determined that marine salinities were a limiting factor in the distribution of reptiles in Florida Bay. Additionally, Cowan (1981) found that terrapins could tolerate a wide range of salinities, but hatchlings had their highest growth rates at salinities of 9 ppt, and their growth stops completely at 21 ppt if a source of freshwater is not provided (Dunson and Mazzotti, 1989). Many areas occupied by mature terrapins in BSC routinely exceeded this upper salinity limit, yet we did capture and mark several small, approximately three-year old (i.e., juvenile) male and female terrapins. Second, it is also possible that the lack of young animals may indicate low or limited recruitment for this seemingly remote site. The BSC complex could represent a ''sink'' habitat (Pulliam, 1988) within the South Florida metapopulation of terrapins (Hart, 2005). Continued capture–recapture sampling and future analysis of microsatelite DNA variation to uncover mating links should resolve this important metapopulation dynamic.

Growth.—The mean annual growth (increase in SCL) detected for 39 male and female *M. terrapin* in BSC is similar to that measured for other emydid turtles. The calculated rates complement what is known of captive terrapin growth (Hildebrand, 1932). In general, chelonian growth rates are more rapid during the juvenile and subadult stages and decrease dramatically after attainment of sexual maturity (Wilbur, 1975; Charnov, 1986; Charnov et al., 1993; Shine and Iverson, 1995; Litzgus and Brooks, 1998b). Because all recaptured turtles in this study were mature, growth data presented here is indicative of slower adult growth rates. This information is useful because somatic growth functions are critical parameters for understanding the life history of a species and for developing management plans for wild populations (Bjorndal et al., 2001).

Injuries.—The average injury rate calculated for BSC terrapins (16%) is considerably higher than the observed rate in a North Carolina population (6%; K. Hart, unpubl. data), but close to the boat prop injury rate for a sampled population in Maryland (20%; Butler et al., 2006). Lovich and Gibbons (1990) reported missing feet on 12% of females and 8% of males in a South Carolina terrapin study and proposed that encounters with terrestrial mammals might be the cause. In a northeastern Florida study, 6% of both genders were missing feet or limbs whereas others had tail, jaw, and shell damage (J. Butler, pers. comm.). In BSC, we observed injuries such as missing limbs, missing parts of limbs (i.e., from the knee down), missing or damaged feet, broken tails, deep scrapes on the carapace, and jaw damage, all of which are consistent with damage from terrestrial predators such as raccoons (*Procyon lotor* [Linnaeus, 1758]), aquatic predators such as sharks (Elasmobranchii; Bonaparte, 1838) and crocodiles (*Crocodylus acutus* [Cuvier, 1807]), and potentially avian predators such as bald eagles (*Haliaeetus leucocephalus* [Linnaeus, 1766]). Although the remote BSC mangrove complex provides a habitat that has low risks of anthropogenic mortality, it may support populations of predators that pose potentially higher risks of natural mortality. In other locations throughout their range where terrapins are regularly closer to humans, predators might well have been reduced by anglers and hunters.

Conclusions.—As recreational use of the remote southwest Florida coast increases with the ever expanding human population, impacts on the coastal mangrove habitat will surely intensify. Although fishing guides and individuals have a long boat trip to the remote BSC area, the protection this considerable travel distance offers will not last. Undoubtedly more recreational anglers and outdoor enthusiasts will frequent the BSC area. As these activities increase in the future, so too will impacts on the environments visited. Strategies to minimize recreational boat traffic in the wilderness areas of the southwest coastal Everglades and to reduce accumulation of food waste and resulting scavengers (e.g., raccoons) should be initiated on beaches in the Cape Sable region to protect terrapins that live in and use this unique, and until very recently, unexplored mangrove habitat.

Multi-year studies of marked populations are essential for answering many questions fundamental to our understanding of population biology. For example, decade-long studies of seabird populations have begun to reveal trends in age-specific survival (Wooller et al., 1992). Continuing studies of manatees (*Trichechus manatus* [Linnaeus, 1758]) have revealed patterns in survival with respect to frequency and intensity of coastal storms (Langtimm et al., 1998; Langtimm and Beck, 2003), and long-term sea turtle studies revealed lower than expected adult survival rates in areas where human exploitation occurs (Bjorndal et al., 2003). The present ongoing *M. terrapin* study will continue to be an important source of information to test hypotheses about factors affecting not only survival, but also reproduction, movement patterns, genetic diversity, and other aspects of mangrove terrapin ecology and population dynamics. In the shorter term, this data set will also allow for determination of possible storm and hurricane effects on the population demography of this species through examination of capture–recapture data and continued marking efforts.

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