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Temporal and Spatial Variation in Survivorship of Diamondback Terrapins (*Malaclemys terrapin*)

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Abstract. – The diamondback terrapin (*Malaclemys terrapin*) is a species of conservation concern that has experienced noticeable declines throughout its range. Mark–recapture studies have been conducted on terrapins at Kiawah Island, South Carolina, since 1983, and during the early 1990s, this population began to decline. Our objectives were to evaluate current spatial and temporal variation in survivorship and compare current estimates of survivorship with those calculated from 1983 to 1999 in a previous study. We used an 11-year data set (2003 to 2013) in a capture–mark–recapture analysis to estimate the survivorship of terrapins in 5 creeks. Among creeks, annual survivorship estimates ranged from 61% to 82% with no difference between the sexes. Survivorship was lower than that documented for this population in the early 1990s. Recent anthropogenic habitat modification, such as the construction of docks, roads, and housing developments, as well as activities such as crab-trapping, likely play a role in low annual survivorship. Results from this long-term study are essential for understanding terrapin population status and can inform conservation and coastal ecosystem management.

Key Words. – Diamondback terrapin; turtle; mark–recapture; population decline; long-term study; Kiawah Island; South Carolina; habitat modification

Anthropogenic activities often result in major declines or extirpations of animal species (McKinney 2006; Hamer and McDonnell 2008). Extirpation of species is closely linked to ecosystem collapse (Jackson et al. 2001), and the local elimination of turtles may be especially detrimental to aquatic ecosystems. Turtles represent a substantial proportion of faunal biomass and serve as herbivores, carnivores, scavengers, prey, and vectors for seed dispersal within their habitats (Congdon and Gibbons 1989; Gibbons et al. 2001). Several anthropogenic activities have led to the decline of diamondback terrapins (*Malaclemys terrapin*), the only species in the family Emydidae that strictly inhabits brackish environments throughout its geographic range (Tucker et al. 2001; Mitro 2003; Baldwin et al. 2005; Avissar 2006; Dorcas et al. 2007; Ernst and Lovich 2009). Crab trapping, both recreational and commercial, has been a primary factor linked to terrapin population declines (Roosenburg et al. 1997; Wood 1997; Dorcas et al. 2007; Grosse et al. 2009). Additionally, the creation of roads threatens nesting females, whereas the presence of human-subsidized predators increases mortality of eggs and hatchlings (Burger 1976; Riley et al. 1998; Szerlag-Egger and McRobert 2007).

Declines in the terrapin population at Kiawah Island, South Carolina, have been documented over the past 3 decades. Gibbons et al. (2001) described high site fidelity and limited dispersal of terrapins among creeks and was the first to document declines in the population. Tucker et al. (2001) examined this population from 1983 to 1999 and found average annual survivorship among all creeks to be 83.5% (SE = 0.045) for males and 84.0% (SE = 0.054) for females. Low annual survivorship estimates, such as those reported by Tucker et al. (2001), suggest the terrapin population is declining. Dorcas et al. (2007) studied the population at the Kiawah Island from 1983 to 2004, documented a population decline, and found changes in demography (shift toward older, larger turtles and a female-biased population) consistent with declines resulting from mortality in crab traps. Increased recreational activities, crab trapping, and land-use change in this rapidly developing area may be causing continued declines in this population of terrapins; however, estimates of annual survivorship of this population have not been quantified since 2000 (Tucker et al. 2001; Cecala et al. 2008). Given the high site-fidelity of terrapins for particular creeks (Gibbons et al. 2001; Szerlag-Egger and McRobert 2007), demographic parameters may exhibit spatial variability; thus continued estimates of survivorship are particularly important for monitoring the current status of this imperiled population. Determination of temporal variation in creek-specific demographic parameters may allow for a better interpretation of where declines are occurring and provide insight into causes of declines.

Our primary objective was to develop current estimates of survivorship of the Kiawah terrapin population. Our specific aims were to 1) quantify spatial and temporal patterns of survivorship in the Kiawah terrapin population from 2003 to 2013, and 2) compare current estimates of survivorship to those calculated from 1983 to 1999 by Tucker et al. (2001).

METHODS

Study Site. — Data collection was conducted northwest of Kiawah Island, South Carolina (80°08′W, 32°36′N), in tributaries of the Kiawah River. Kiawah Island terrapin populations have been surveyed regularly since 1983 (Gibbons et al. 2001; Dorcas et al. 2007). Sampling took place in 5 separate creeks: Terrapin Creek (1983–2013), Oyster Creek (1986–2013), Fiddler Creek (1987–2013), Stingray Slough (1990–2013), and Sandy Creek (1992–2013). Habitat immediately surrounding tidal creeks is dominated by *Spartina alterniflora* salt marsh. For a detailed description of the study site, see Gibbons and Harrison (1981), Lovich and Gibbons (1990), Lovich et al. (1991), Zimmerman (1992), Tucker et al. (1995), Hoyle and Gibbons (2000), and Gibbons et al. (2001).

Data Collection. — From 1983 to 2001, turtles were sampled at regular intervals during summer months, and beginning in 2003, sampling was conducted biannually, in May and October. Our data set includes only sampling from 2003 to 2013, when trapping techniques and sampling intensity and frequency were more consistent. We used trammel nets and seines to capture terrapins during low tide (Lovich and Gibbons 1990; Tucker et al. 1995). Lovich and Gibbons (1990) studied this same terrapin population from 1983 to 1990 and found that, although these sampling techniques have the potential to be sex biased, recapture probability for males and females was the same. Each turtle captured was individually marked (Sexton 1959) and measured before it was returned to its capture site. Survivorship determinations were based on continual recaptures of individuals that were marked for identification. In addition, recapture validation was supplemented with information on the individual's sex, carapace and plastron length, shell depth, and body mass between captures. Age was determined when possible by counting growth rings on the carapace and plastron (Roosenburg et al. 1997). To determine sex, we used overall body size and shape, tail length, and the position of the cloaca. In females, the cloaca is positioned anterior to the rear carapace margin, and in males, the cloaca sits posterior to the carapace margin.

Data Analysis. — We used the Cormack-Jolly-Seber (CJS) module of program MARK (v. 6.0; White and Burnham 1999) to quantify spatial and temporal patterns of survivorship at each creek. We constructed encounter histories for each turtle (based on years the creek was sampled) to assess potential differences in survivorship of males and females at each of the 5 creeks. We used a top-down approach to determine survival (Lebreton et al. 1992; Muths et al. 2006). First, keeping survivorship (ϕ) constant over time, we evaluated models that varied in capture probability (p). Specifically, we evaluated models where capture probability was held constant, varied by sex, varied by time, and varied by an interaction of sex and time. We did not include creeks as an attribute group because given our sampling methods, we did not expect location of the creek to influence our ability to capture terrapins. Once we determined the best parameterization for p, we included it in subsequent models examining temporal and sex-specific variation in probability of survival. Specifically, we evaluated the following 8 models of survivorship: 1) constant probability of survivorship over time, 2) variation in survivorship by year, 3) by sex, 4) by creek, 5) by sex and creek, 6) by year and sex, 7) by year and creek, and 8) by year, creek, and sex.

To select the model that best fit our data, we used Akaike's Information Criteria (Akaike 1973) adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). To test for overdispersion in our data, we performed a bootstrap goodness-of-fit test on the most parameterized model and calculated a c-hat index for correction (Burnham and Anderson 2002). More specifically, we ran 1000 simulations and then corrected for overdispersion by adjusting the c-hat to 1.18 (observed c-hat divided by the mean of simulated c-hats), resulting in $QAIC_c$-values. We examined $\Delta QAIC_c$- and Akaike-weights to evaluate the strength of evidence for each model; the model with the lowest $QAIC_c$-value, and greatest $QAIC_c$-weight (w) was considered the model that best fit our data (Burnham and Anderson 2002).

RESULTS

From 2003 to 2011, we sampled the 5 main creeks on Kiawah Island 22–38 times each (Table 1). We captured 477 terrapins (representing 1089 terrapin capture events). The number of individuals captured per creek ranged from 2 to 228 (Table 1).

The top model for capture probability was sex-specific ($QAIC_c$ $w = 0.693$; Table 2). Capture probability was 0.367 for males (95% CI = 0.32–0.42) and 0.293 for females (95% CI = 0.24–0.36). Among the eight models tested for survivorship (Table 3), the model with the highest support indicated that terrapin survivorship varied among creeks ($QAIC_c$ $w = 0.664$; Table 3, Fig. 1). Mean annual survivorship from 2003 to 2013 in Oyster Creek was estimated to be 82.1% (95% CI = 0.76–0.87). Fiddler Creek mean annual survivorship was 77.9% (95% CI = 0.72–0.83). Sandy Creek had the third highest mean annual survivorship estimate at 71.4% (95% CI = 0.66–0.76). Mean annual survivorship for Stingray Slough was estimated to be 66.4% (95% CI = 0.50–0.79), and that of

Table 1. Number of sampling events and individual turtles that were captured per creek between 2003 and 2013 at Kiawah Island, SC.

Creek	No. of individual sampling events	No. of individual turtles captured
Fiddler Creek	38	89
Sandy Creek	31	145
Oyster Creek	36	228
Stingray Slough	22	13
Terrapin Creek	22	2
Sum	155	477

Terrapin Creek was 60.5% (95% CI = 0.30–0.85). Terrapin Creek survivorship estimates were based on two individuals (Table 1), which resulted in high degree of uncertainty surrounding the mean estimate.

To fulfill our second objective of comparing our results to those of Tucker et al. (2001), we examined survivorship estimates based on our sex- and creek-specific survivorship model (Model 5, ''ϕ (creek, sex), *p* (sex)'' in Table 3). Mean annual survivorship rates for males were estimated to be 68.5% (95% CI = 0.62–0.75) in Sandy Creek, 82.8% (95% CI = 0.69–0.83) in Fiddler Creek, and 82.0% (95% CI = 0.75–0.87) in Oyster Creek. Female mean annual survivorship was estimated to be 77.7% (95% CI = 0.68–0.85) in Sandy Creek, 80.5% (95% CI = 0.68–0.89) in Fiddler Creek, and 82.8% (95% CI = 0.70–0.91) in Oyster Creek. Our sample size was too low (Table 1) for Terrapin Creek to make a comparison between sexes between our study and that of Tucker et al. (2001). Sampling in Stingray Slough began in 1990 and, therefore, was not part of the Tucker et al. (2001) study (Table 4).

DISCUSSION

During the 11 yrs (2003–2013) of biannual surveys of Kiawah Island, mean survivorship of terrapins at the 5 main creeks was low compared with other estimates for this species and ranged from 60.5% to 82.1%. Our findings suggest that the terrapin population of Kiawah is experiencing continued and possibly even accelerated declines, congruent with findings of Gibbons et al. (2001), Tucker et al. (2001), and Dorcas et al. (2007). Also, we found that overall capture probability was relatively low and was influenced by sex, with females having a slightly lower probability of capture than males.

Tucker et al. (2001) studied the same Kiawah Island terrapin population from 1983 to 1999 and found that annual male survivorship among the 5 creeks ranged 79%–90% and that of females ranged 75%–97%. In the sex- and creek-specific survivorship model from 2003 to 2012, survivorship estimates were comparable to those of Tucker et al. (2001) with the exception of Sandy Creek, with estimates that were 20% lower on average (Table 4). Although the model used by Tucker et al. (2001) does not best reflect our data (Table 3), it is further indication of

Table 2. Model set analyzing the effect of time and sex on capture probability using Cormack-Jolly-Seber models. The best-supported model is indicated in bold.

Model	$QAIC_c$	$\Delta QAIC_c$[a]	w[b]	Model likelihood	K[c]
ϕ[d] (.)[e], *p*[f] (sex)	**2,040.53**	**0.00**	**0.69**	**1.00**	**3**
ϕ (.), *p* (.)	2,042.98	2.45	0.20	0.29	2
ϕ (.), *p* (time)	2,044.33	3.81	0.10	0.15	11
ϕ (.), *p* (time, sex)	2,054.70	14.17	0.00	0.00	21

[a] Difference in $QAIC_c$ relative to the top model.
[b] $QAIC_c$ weight.
[c] Number of parameters in the model.
[d] Probability of survivorship.
[e] Constant probability of survivorship.
[f] Probability of capture, which varies by inclusion of the following covariates: creek, sex, year, or interactions of each.

Table 3. Model set analyzing effects of time and sex on survivorship and recapture rate at Fiddler, Sandy, Oyster, Stingray, and Terrapin Creeks using Cormack-Jolly-Seber models. The best-supported model is indicated in bold.

Model	$QAIC_c$	$\Delta QAIC_c$[a]	w[b]	Model likelihood	K[c]
ϕ[d] (creek), *p*[e] (sex)	**1,725.82**	**0.00**	**0.66**	**1.00**	**7**
ϕ (year), *p* (sex)	1,728.54	2.73	0.17	0.26	12
ϕ (.)[f], *p* (sex)	1,730.18	4.36	0.07	0.11	3
ϕ (sex), *p* (sex)	1,730.90	5.08	0.05	0.08	4
ϕ (creek, sex), *p* (sex)	1,731.46	5.64	0.04	0.06	12
ϕ (year, sex), *p* (sex)	1,774.21	21.39	0.00	0.00	22
ϕ (year, sex, creek), *p* (sex)	1,799.80	73.99	0.00	0.00	84
ϕ (year, sex, creek), *p* (sex, year)	1,821.98	96.16	0.00	0.00	100

[a] Difference in $QAIC_c$ relative to the top model.
[b] $QAIC_c$ weight.
[c] Number of parameters in the model.
[d] Probability of survivorship, which varies by inclusion of the following covariates: creek, sex, year, or interactions of each.
[e] Capture probability, which varies by sex for each model.
[f] Constant probability of survivorship.

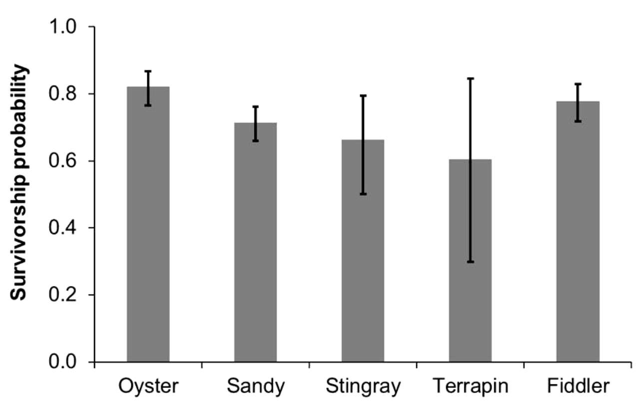

Figure 1. Annual survivorship (ϕ) estimates from 2003 to 2013 in Oyster, Sandy, Stingray, Terrapin, and Fiddler Creeks, generated using Cormack-Jolly-Seber models in Program MARK. Bars represent 95% confidence intervals. Terrapin Creek survivorship estimates are based on 2 individuals, which resulted in high degree of uncertainty surrounding the mean estimate.

Table 4. Comparison of sex- and creek-specific mean annual survivorship estimates in the present study to mean estimates of Tucker et al. (2001) with 95% confidence intervals in parentheses.

Creek	Sex	Present study	Tucker et al.
Sandy	Male	0.685 (0.62–0.75)	0.901 (0.55–0.99)
Creek	Female	0.777 (0.68–0.85)	0.971 (0.04–1.00)
Stingray	Male	0.640 (0.43–0.81)	—[a]
Slough	Female	0.699 (0.44–0.87)	—
Terrapin	Male	*[b]	0.830 (0.74–0.90)
Creek	Female	0.682(0.34–0.90)	0.847 (0.70–0.93)
Fiddler	Male	0.768 (0.69–0.83)	0.819 (0.79–0.85)
Creek	Female	0.805 (0.68–0.89)	0.792 (0.75–0.83)
Oyster	Male	0.820 (0.75–0.87)	0.788 (0.72–0.85)
Creek	Female	0.828 (0.70–0.91)	0.748 (0.66–0.82)

[a] —, estimate not provided.
[b] *, no males captured.

continued declines in survivorship over time in the Kiawah Island terrapin population.

Annual survivorship of most adult chelonians is estimated to be ≥ 90% (Iverson 1991). Few studies have specifically estimated annual survivorship of terrapin populations. Mitro (2003) studied female survivorship and recruitment in a Rhode Island terrapin population and found that, between 1990 and 2000, annual adult female survivorship decreased from 96% to 94%. Hart (2005) studied terrapin populations in Florida and estimated annual survivorship to be 79%. Hart et al. (2007) later estimated survivorship of terrapins inhabiting the Everglades National Park to be 79%. Tucker et al. (2001) studied the same population of terrapins as in our study and estimated average annual survivorship across creeks to be 83%, which ranked in the lower 30% percentile of the 25 chelonian annual survivorship estimates reported by Shine and Iverson (1995). Compared with each of these studies, most of our survivorship estimates are low, and we documented a sharper decline in annual survivorship rates than that observed by Mitro (2003) over a 10-yr period in Rhode Island. For terrapin populations, which exhibit delayed sexual maturity and high site fidelity (Gibbons 1987; Congdon et al. 1993; Szerlag-Egger and McRobert 2007; Hart and Lee 2008), low adult survivorship can lead to local population extinctions (Roosenburg 1991).

Terrapins at Kiawah Island show high creek fidelity (Tucker et al. 2001), and this ''isolation'' in conjunction with population declines may make it difficult for terrapins to naturally repopulate a site, even if threats are removed. As a result, we are beginning to see extirpation of populations on a creek-by-creek basis. Based on the number of terrapins captured in the last 5 yrs, terrapin populations in Stingray Slough and Terrapin Creek are very small. When we first started sampling Terrapin Creek, we had 38 captures in 1983, 52 in 1984, and 97 in 1986. Similarly, when sampling began in Stingray Slough, we captured 42 terrapins in 1990, 36 in 1991, and 71 in 1992. Only 2 terrapins have been captured in Terrapin Creek since 2003, despite intensive biannual sampling. Similarly, only 3 terrapins were captured in Stingray Slough in 2009, the last year terrapins were captured in that creek.

Various factors may be responsible for the continued decline of the Kiawah Island terrapin population since studies of this population began in 1983. During 1983, a dock was installed within the area of our 5 study creeks, giving humans increased access to terrapin habitat for crab trapping and other activities (Tucker et al. 2001). Grosse et al. (2009) documented 94 dead terrapins in a single trap in a Georgia tidal marsh. It is conceivable that a single crab trap could be equally devastating to the Kiawah Island population. The risk of terrapins entering a crab trap is much higher in the spring and summer months when terrapins are more active, yet this is also the time when crab trapping intensity is highest, to target molting female crabs (Harden and Willard 2012). Concurrently, with the increased urbanization of Kiawah Island, females may be experiencing lower survivorship as a result of road mortality during nesting excursions (Szerlag-Egger and McRobert 2007). The continued development of waterfront property promotes the establishment of human-subsidized predators, which may also contribute to observed declines in the population (Burger 1976; Riley et al. 1998).

CONCLUSIONS

Turtles typically reach sexual maturity late in life and, thus, depend on high adult survivorship to maintain populations. Therefore, long-term sampling is critical to understanding survivorship and recruitment trends (Gibbons 1987; Congdon et al. 1993; Hart and Lee 2008). Survivorship in all 5 tidal creeks from 2003 to 2013 was found to be relatively low compared with other studies (Tucker et al. 2001; Mitro 2003; Hart 2005; Hart et al. 2007), indicating that the terrapins inhabiting the tidal creeks at Kiawah might benefit from protection from anthropogenic activities. Although our study does not identify specific threats, based on previous research, crab trapping has been found to be detrimental to terrapin populations (Dorcas et al. 2007) and is likely one of the primary reasons for documented declines. Removal of abandoned crab pots and the installation of bycatch reduction devices may help decrease terrapin mortality in crab traps (Dorcas et al. 2007; Hart and Crowder 2011), but regulations that limit crabbing in critical areas at certain times of the year also may be necessary to prevent further declines and eventually allow populations to recover.

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