

**SURVIVORSHIP OF NEW YORK CITY'S DIAMONDBACK TERRAPINS:
DETERMINING IMPACTS ON SURVIVAL OF NESTING FEMALES IN
JAMAICA BAY, NY**

by

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Submitted in partial fulfillment of the requirements for the degree of
Master of Art in Biology in the Graduate Division of
Queens College of The City University of New York

December 2018

Approved by: _____

Date: _____

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ACKNOWLEDGEMENTS

Thank you to my advisors, Dr. José Anadón and Dr. Russell Burke, for giving me the opportunity to learn so much over the past year. I would not be where I am today without the experience and knowledge I have gained through this project. I am beyond grateful. Dr. Anadón, thank you for supporting me as your student, having faith in me, and for your continued reassurance while working through this process. Dr. Burke, thank you for your guidance, allowing me to take part in your Jamaica Bay terrapin project, and encouraging me present at this year's herpetology conference. It may have been a small event for some but was major milestone for me. Alexandra Kanonik, thank you for your vast terrapin knowledge, advice when organizing the terrapin database, and always being available to answer my turtle related questions. A special thanks to all the Jamaica Bay Terrapin Research volunteers throughout the years, whose participation in the data collection and enthusiasm for terrapins made this project possible. Thank you to the population biologists at IMEDEA, who gave me the foundational knowledge of mark recapture analysis from which I was able to build on in the past year.

I would like to thank my family and friends for their love and their continued support throughout my life and for everything that I do. Finally, to my fiancé Jason, thank you for always being my rock, listening to my complaints, and supporting my college career.

ABSTRACT

The diamondback terrapin (*Malaclemys terrapin*), a long-lived turtle species of the eastern coast of the United States, is a charismatic and distinctive species known for its status as the only emydid turtle that strictly resides in coastal brackish waters. The state of the diamondback terrapin varies locally but many populations face declines due to environmental stressors attributed to the effects of human activity. Jamaica Bay, an urban estuary located in southern New York City, is home to at least two female diamondback terrapin populations. These populations nest seasonally on Ruler's Bar Hassock and John F. Kennedy airport (JFK), just 4.5 kilometers apart. Jamaica Bay terrapin populations are subjected to a highly urbanized environment with a long history of pollution and habitat degradation. Yearly monitoring has led to a greater understanding of their behavioral and reproductive characteristics, but little is known about their population vital rates including survival, a key parameter in long-lived species. Our objectives here were to 1) estimate survival and detection rate of female diamondback terrapins across years and between the two adjacent populations, and 2) test the impact of water quality, hurricanes, and injuries on survival to better understand the primary threats to female terrapin populations. We analyzed long-term mark-recapture data using an age classified structure within the Cormack-Jolly-Seber model to estimate survival rates. Apparent survival for Ruler's Bar female terrapins was high at 0.92 but declined over a 15-year period, while survival for JFK females was constant at 0.92. Water quality, represented by mean nitrogen levels, did not affect female terrapin survival in either population while models including the effect of Hurricane Sandy (2012) supported a decline in survival to 0.85 for two years following the storm in Ruler's Bar.

Injuries were analyzed for Ruler's Bar using a multistate approach to estimate survival and transition between injury states. Survival estimates for injury states were constant at 0.92 for individuals with no injuries and 0.88 for major injuries. The results support a distinction in survival patterns between the populations as well as the apparent impact of severe storms and major injuries. Survival determinations are crucial to understanding the status of the breeding female terrapin population and can aid in the development of local environmental and conservation policies.

INTRODUCTION

Malaclemys terrapin

The Diamondback terrapin holds a unique role in North American estuarine environments as the only species of the family Emydidae that lives exclusively in salt marshes and mangroves along the eastern and Gulf coasts, from Cape Cod to Corpus Cristi, Texas (Ernst and Lovich 2009). The Diamondback terrapin is considered a keystone species because of its role in controlling invertebrate populations that feed on salt marsh vegetation (*Spartina*) and the importance of its eggs in nutrient movement from water to land (Browne et al. 2015). Across their broad latitudinal range, terrapins vary in their life history with females reaching maturity at about 8 years of age for females and 5 years for males in northern populations (Roosenburg 1991; Ernst and Lovich 2009). Diamondback terrapins have a strong affinity to brackish waters with all stages of their life occurring in or near their natal estuarine area. Adult terrapins breed, feed, and overwinter within estuarine or brackish waters. Females use adjacent upland sandy areas during the nesting season which is between April and August throughout their territory (Ernst and Lovich 2009). Terrapin diets vary based on prey availability associated with each habitat and they often take advantage of a wide variety of food, with a propensity for mollusks and crustaceans (Hart and Lee, 2007). Their link to brackish waters has left them exposed to coastal development and vulnerable to associated anthropogenic effects such as habitat degradation and exploitation. Over the years, human impacts have threatened the viability of many populations and have left them subject to fragmentation and extinction (Roosenburg 1991; Butler et al. 2006).

Historical Population Threats

Diamondback terrapins experienced significant exploitation in the late 19th and early 20th century when terrapin meat was overharvested as a food source (Roosenburg 1991). Mass harvesting of adult terrapins resulted in significant population declines and the near extirpation of many populations. Terrapin populations have since had time to recover from years of overharvesting after the trend for terrapin meat as a popular delicacy diminished (Ernst and Lovich 2009). Since 1990, New York State has regulated the direct harvest of diamondback terrapins and has recently ended the issuing of permits in 2018. Despite these efforts, additional threats continue to endanger terrapin populations over the years as coastal development increases.

Road mortality of nesting females is an issue in regions where roads cross through nesting habitat. Terrapins prefer nesting areas with sandy soils and sparse vegetation which is consequently available on the sides of most roads (Szerlag and McRobert 2006). This problem has had a substantial impact on terrapins, especially in New Jersey where over 4,000 road kills were found between 1989 and 1995 (Wood and Herlands 1997). Management options for this threat include the use of barriers to prevent animals from crossing and signs to alert drivers of the potential for animal crossings. In addition to vehicle collisions, terrapin by-catch has been a primary threat to terrapins for decades (Butler et al. 2006). Incidental capture in recreational crab-traps pose the greatest risk for juveniles and adult males that can easily fit through funnel openings (Hart and Crowder 2011). Several studies have estimated high mortality rates based on by-catch data and considered the increase in mortality as the likely cause of population decline (Roosenburg et al. 1997; Hoyle and Gibbons 2000; Tucker et al. 2001). By-catch due to crab trapping

has also been linked to changes in demography and sex ratio in a declining population in South Carolina, which saw an increase in the proportion of older females and a higher ratio of females to males (Dorcas et al. 2007).

Local Populations of *Malaclemys terrapin*

Jamaica Bay, an urban estuary located along the southeast region of New York City, is home to at least two primary populations of nesting female diamondback terrapins. These populations are located just 4.5 kilometers apart, one nesting on Ruler's Bar Hassock and another nesting at John. F. Kennedy Airport. These two populations appear to have different dynamics occurring that may determine their future viability. In 2009, the number of nesting females at JFK increased significantly, indicating that the population grew rapidly in the years prior (Zostant et al. 2018; Burke and Francoeur 2014). This event gained the attention of local management and the focus shifted towards determining the cause for the substantial change in the population. Current data indicates that JFK females are on average smaller and perhaps younger than Ruler's Bar females, possibly attributed to the successful recruitment of new individuals into the JFK population (Zonstant et al. 2018). On the other hand, females at Ruler's bar do not have the same positive outlook. Yearly monitoring has shown that the number of nests per year in Ruler's Bar have declined significantly (Burke, pers. comm.). In addition, females appear to be, on average, larger and perhaps older than JFK females (Zostant et al. 2018). This could be an early indication of declining recruitment and future population numbers. Declined recruitment in a population, means a greater reliance on the survival of older females to maintain population viability (King and Ludlam. 2015)

Local Population Threats

Mortality due to roadway incidents and crab-trapping is not commonly reported in Jamaica Bay compared to other locations but the bay itself is still a prime example of many other anthropogenic and environmental hazards threatening terrapin populations. Potential threats in this area include pollution, coastal storms, motor boat activity, and raccoon predation. Characteristic of urban estuaries, water quality within Jamaica Bay is an ongoing issue with several waste water treatment plants primarily responsible for nitrogen loading through wastewater discharge (Sanderson et al. 2016). High nitrogen loading is a major contributor to the eutrophication, algal blooms, and the subsequent hypoxic events that have been recorded in Jamaica Bay in recent years (Wallace et al. 2014; Marsooli et al. 2018). Such conditions can create a serious physiological obstacle for aquatic animals through the degradation of water quality and alteration of food sources, especially during summer months (Baldwin et al. 2005). The effects of pollution on terrapin health is not well understood. However, toxin producing algal blooms are believed to be responsible for the mass mortality of terrapins in the waters of Long Island, NY (Hattenrath-Lehmann et al. 2017). In addition, some work has been done investigating the influence of heavy metals and persistent organic pollutants (Burger 2002; Basile et al. 2010). In Jamaica Bay, excess nitrogen leads to algal blooms of primarily sea lettuce (*Ulva* spp.) which covers mud flats and vegetation, overwhelms typical food sources, and in doing so can alter trophic food webs (Wallace and Gobler 2014; Mackenzie 2005). Consequently, *Ulva* often becomes one of the primary food sources in a terrapin's diet (Erasmus et al. 2012; Zostant et al. 2018). Despite little information on the direct effects, it is apparent that urbanization and pollution has had considerable impact on terrapin habitat in Jamaica Bay. Nitrogen loading may be one of

the primary causes of much of the salt marsh decline seen in the past decades (Sanderson et al. 2016). Significant loss of marshland has occurred since 1974 with overall losses averaging about 38% of all Jamaica Bay marsh islands (Hartig et al. 2002). Current estimates found that natural salt marshes have continued to decrease over time trend with a loss of 21 hectares between 2003 and 2013 (Campbell et al. 2017).

Catastrophic natural disturbances, such as hurricanes, can cause both short and long-term effects to ecosystem structure and coastal wildlife. Specifically, disturbance events can lead to direct mortality, injuries, alterations to habitat or refugia, and changes in food supply (Wunderle and Wiley 1996). Although hurricanes have important conservation implications, their impact on wildlife has not been thoroughly studied and few studies have specifically looked at the impact of hurricanes on eastern turtle species (Wunderle and Wiley 1996; Baldwin et al. 2005; Gibbons et al. 2001; Dodd et al. 2006). Hurricane Sandy occurred in late October of 2012, after the terrapin nesting season, with a subsequent Nor'easter that brought a significant drop-in temperature. Diamondback terrapins rely on salt marshes for critical foraging and overwintering habitat (Browne et al. 2015). The effect of Hurricane Sandy on salt marshes was variable depending on the health and location of the marsh island. Substantial vegetation, mudflat, and sand was lost from marsh islands particularly on the west side of Jamaica Bay (Wang et al. 2017; Campbell et al. 2017). In contrast, JoCo Marsh which is located near JFK Airport to the east, did not appear to experience any depletion of vegetation or sediment (Campbell et al. 2017). In response to this loss, some marsh islands, including Ruler's Bar, were restored in 2013 but did not show evidence of a stable recovery or revegetation that year (Campbell et al. 2017). Hurricane Sandy occurred when terrapins become less active in

the colder months which makes it difficult to evaluate the impact of the storm. However, direct mortality, injuries, habitat disturbance, and changes in resources are likely possibilities for Jamaica Bay terrapins that were vulnerable to this storm.

Motor boats are a significant threat to terrapin survival as a major cause of terrapin injury and mortality. Likewise, motorboats have become a larger physical threat as recreational and commercial boat traffic increases with urban development (Lester et al. 2013). Terrapins that experience collisions with motorboats sustain injuries that include missing portions of the carapace and plastron and large impact scars across the carapace. Unfortunately, terrapin basking behavior and their lack of response to boat sounds routinely leaves them exposed to passing motorboats (Cecala et al. 2008; Lester et al. 2013). Female terrapins are more likely to be hit by a passing boat, with a greater portion of adult females compared to males bearing scars attributed to propeller damage (Roosenburg 1991; Cecala et al 2008). This is likely a product of their larger size and greater difficulty when to swim away quickly from an approaching boat. Terrestrial predators such as the common racoon (*Procyon lotor*), are also a main cause of adult injury and mortality. Raccoon populations on Ruler's Bar were small prior to development on the island and are believed to have flourished due to their ability to adapt to urbanization (Ner and Burke 2008). Consequently, raccoons are known to be the leading predator of adult terrapins and terrapin eggs (Feinburg and Burke 2003; Baldwin et al. 2005). Adult female terrapins that bear evidence of a raccoon encounter often have severed or dislocated hind limbs and destruction of adjacent scutes (Seigel 1980; Hart and McIvor 2008). Although predation is a natural occurrence, pressure from an

overabundant raccoon community may be detrimental to the viability of terrapin populations.

Life History

Turtle species have evolved life history strategies that require high adult survival rates to offset delayed reproduction and high nest predation (Congdon et al. 1993; Iverson et al. 1991). Species with low reproductive rates and high adult survival may be particularly sensitive to even small changes in mortality (Enneson and Litzgus 2008). Furthermore, slight reductions in adult survival in many long-lived species can have the largest proportional impact on population growth (Crawford et al. 2014; Enneson and Litzgus 2008; Heppell 1998). Long-lived species such as the diamondback terrapin present unique obstacles for monitoring and research efforts. Individuals can reach a lifespan of nearly 40 years which drives the need for persistent and long-term monitoring to adequately estimate population parameters and assess population trends (Ernst and Lovich 2009). Adult biased structure and delayed reproduction makes terrapin populations highly sensitive to disturbances that alter survivorship, particularly of adults. Survival may also vary based on individual characteristics such as sex, size, or age as well as vary as a function of environmental variables. As a result, conservation implications for this work are significant. Quantitative estimates of population vital rates (e.g., survivorship) as well as the assessment of external covariates are key to understanding population dynamics and to the development of local population management policies.

Objectives

We analyzed long-term mark-recapture data of female diamondback terrapins to estimate survival of two adjacent populations in Jamaica Bay, NY. Data used in this analysis were collected yearly as part of two on going mark recapture studies in Ruler's Bar and JFK Airport, corresponding to 16 years and 8 years of data, respectfully. Our analysis of these populations included two primary objectives. First, to analyze the data using mark recapture modeling to estimate apparent survival of adult females between years and populations in Jamaica Bay, NY. Second, to test the impact of external covariates that were hypothesized to influence survival, including water quality, Hurricane Sandy, and major injuries. We look to highlight the potential impacts on female terrapin survival and provide information on the current status of the reproductive females in Jamaica Bay.

MATERIALS AND METHODS

Study Sites

Jamaica Bay (40.6178 N, 73.8425 W), an estuary within New York City, encompasses approximately 5,300 hectares of wetlands and open water bordered by the boroughs of Queens and Brooklyn (Sanderson et al. 2016). It is a highly urbanized water body with a watershed that includes residential, commercial, and industrial land. The land portion of Jamaica Bay is comprised of several salt marsh islands and parts of the surrounding mainland coast. The collective area of Jamaica Bay is included within the Gateway National Recreation Area and is home to the Jamaica Bay Wildlife Refuge

(JBWR), both of which are managed by the National Parks Service (NPS). Mark-recapture work was conducted at two primary sites within Jamaica Bay, Ruler's Bar Hassock and John F. Kennedy Airport.

Of the several tidal marshland islands that belong to the Jamaica Bay Wildlife Refuge, Ruler's Bar Hassock (40°36'58.68"N, 73°50' 07.63"W) is the largest central island, spanning about 458 hectares. Ruler's Bar is also the only island inhabited and connected by a bridge to the mainland. The primary study area is the immediate region surrounding the West Pond, one of two man-made freshwater ponds on Ruler's Bar (Ner and Burke 2008). The habitat consists of salt marshes dominated by *Spartina alterniflora* as well as sandy beaches, mixed grasslands, and shrubland that make up the high ground. West pond is one the main attractions in the JBWR and is designed with gravel trails to accommodate visitors. As a result, female diamondback terrapins are found nesting on gravel trails, near installed benches, the beaches flanking the refuge, as well as the surrounding vegetated areas.

John F. Kennedy airport (40°38'23"N 073°46'44"W) lies in the eastern coast of Jamaica Bay, spanning 1,740 hectares and about 4.5 kilometers from Ruler's Bar Hassock (Sanderson et al. 2016). The land itself was once dominated by marsh land but has since been filled, developed, and expanded into the bay. Despite the highly altered environment, the southernmost area of JFK airport is bordered by Joco Marsh, known to be the largest and healthiest marsh system in the bay (Campbell et al. 2017). The nesting habitat at JFK consists of sandy soil with sparse vegetation that is well above the tides. Female terrapins are typically found on or near the active airport runway adjacent to JoCo Marsh. Runway disturbances are a constant concern for JFK wildlife management and

preventing runway delays and terrapin mortality has been a focus of their efforts (Zostant el al. 2018).

Figure 1 Diamondback terrapin nesting and mark-recapture locations in Jamaica Bay, NY.



Mark Recapture Study

Mark-recapture work involving adult female diamondback terrapins in Jamaica Bay has been ongoing for both Ruler's Bar and JFK, with the initiation of the Ruler's Bar study in 1998. Consistent marking of female terrapins began in 2003, during regular intervals coinciding with the nesting season in late May to early August. The mark-recapture study concerning JFK females started in 2011 when terrapins were found nesting near active runways, making the population a concern for airport management. In both studies, each female terrapin captured was individually marked and measured before it was returned to its capture location. Two forms of identification were used; a Passive Integrated Transponder (PIT) tag which was injected into the body and a notch filed into one of the marginal scutes of the carapace corresponding to the yearly cohort. Beginning in 2006, detailed information on body condition was collected for Ruler's Bar females. Observations for abnormalities and injuries were documented by depicting any noticeable morphological issues on the shell or body on a diagram and providing a corresponding written description. Throughout monitoring seasons, coverage of study areas was consistent, but effort devoted to capturing terrapins varied each season based on the number of workers or volunteers participating in the project.

Cormack-Jolly-Seber Modeling Assumptions

We constructed encounter histories for each individual from 16 years of mark-recapture data for Ruler's Bar (2003-2018) and 8 years for JFK (2011-2017) to estimate female survival as well as evaluate the effects of external covariates. The Cormack-Jolly-Seber (CJS) open-population module (Lebreton et al. 1992) implemented in Program MARK (v. 8.2) (White and Burnham 1999) was selected to analyze both populations

separately, with parameter estimates constrained between 1 and 0 using a logit link function. Survivorship determinations are dependent on subsequent recaptures of individuals that were PIT tagged for identification during their first capture. Population parameters were determined directly through model selection by means of maximum likelihood estimation. Specifically, parameter values were found that maximize the probability of the data observed (Lebreton et al. 1992). Estimated survival and recapture probability parameters are defined as follows:

Φ : the probability that an individual at time t survives until $t+1$.

P : the probability that an individual is recaptured at time t given that is present at time t .

The primary assumptions of the Cormack-Jolly-Seber open population model puts forth a means of testing model fit. The basic assumptions include: 1) Every animal alive at time t has an equal chance of being captured in that sample; 2) Every marked animal alive in the population at a given sample time has an equal chance of survival until the next sampling occasion; 3) Marked animals do not lose their marks and marks are not overlooked; 4) Sampling periods are short; and 5) All emigration from the population is permanent (Amstrup et al. 2005).

Goodness of Fit Testing

Goodness of fit testing is an essential process of mark recapture analysis to ensure the selection of the appropriate base model. Without this integral step, low precision and inflated deviance will lead to the selection of unsuitable models with biased estimates (Lebreton et al. 1992). Goodness of fit of the most parameterized fully time dependent

model $[\phi(t) p(t)]$ was evaluated using the program U-Care which provided a series of contingency tables for each sampling occasion (Choquet et al. 2009). U-Care utilizes 4 component tests (Test3.SR, Test3.M, Test2.CT and Test2.CM) to assess violations of assumptions of the CJS model. The primary tests assessing the homogeneity assumption of the CJS model are Test 2.CT and Test 3.SR. Test 2.CT determines if marked animals meet the assumption of equal catchability while sub-test Test 3.SR specifically detects transience in which there is an excess of “non-recaptured” individuals within a newly marked group (Pradel et al. 1997). Namely, not all marked animals alive at (t) have the same probability of surviving to $(t + 1)$ and the probability of future captures depends on whether the animal was marked on or before occasion t . If Test3.SR is significantly affected ($p < 0.000$), analysis methods utilized a time since marking model $[\phi(2a^*t) p(t)]$ by including extra parameters to differentiate the first-year survival from the survival in subsequent recapture occasions (Pradel et al., 1997; Perret et al. 2003). Residual deviation is then accounted for by adjusting the variance inflation factor or $\hat{c} (x^2/df)$. This is calculated to scale the model deviance based on the sum of the three other component tests (3.SM, 2 C.T, 2 C.M), divided by their sum of degrees of freedom (Lebreton et al. 1992).

Modeling Procedures – Cormack-Jolly-Seber Modeling

Following goodness of fit evaluation, we constructed models that were based on deductive hypotheses that were biologically rational. First, we followed a modeling approach by beginning with the fully saturated model with time-dependence in both survival and capture $(\phi(t) p(t))$, and then fitting reduced parameter models to identify the main structure that described constant or between year variation in detection rate

(Lebreton et al. 1992). Once the supported structure for recapture rate was found, we tested whether survival was time-varying (t), constant (.) or following a linear trend in time (T) (Table 1). These models were used as reference models for analyzing environmental effects. We then examined the influence of covariates that were suspected to influence the variability of survival by constructing a set of linear models including the effect of water quality and Hurricane Sandy as additional parameters in the constant model [$\phi(2a) p(t)$] (Table 1).

Water quality was treated as a quantitative variable over time by including average nitrogen concentration as an additional parameter. The effect of Hurricane Sandy was explored in multiple ways. We tested the effect of the storm over the year it occurred (2012) as well as the possibility of a residual effect over the following year (2013-2014). Long-term changes in survival pre and post Hurricane Sandy were also tested. The effect of the hurricane was modeled by using a dummy variable in which years influenced by the hurricane and years not impacted were treated as two categories. All covariates were modeled with interactive or additive effects. Interactive effects include an additional parameter representing an interaction between main variables and additive effects represent parallel variation on survival (Lebreton et al. 1992).

The adjusted Akaike Information Criterion ($AIC = -2\ln(L) + 2k$) or QAICc was used to assess the relative probabilities of the candidate models with the lowest QAICc value and highest QAICc weight indicating the most parsimonious model (Burnham and Anderson 2002). The principle of parsimony follows the trade-off between number of parameters and the deviance of the model. Specifically, a model with too many parameters and high uncertainty is not ideal while only significant parameters should be

included in the model (Lebreton et al. 1992). We used the threshold $\Delta AIC > 2$ to distinguished between two models. If models have a ΔAIC less than 2, they have approximately equal support given the data (Burnham and Anderson 2002). If $2 < \Delta AIC < 7$, there is considerable support for a real difference between models and if $\Delta AIC > 7$, then there is strong support for a real difference between models.

Table 1 Notations and definitions of the effects tested on survival and recapture probabilities in Cormack-Jolly-Seber Models. Effects with interactions are indicated a (*) and additive effects with a (+).

Model Notation	Definition
$\phi(.) p(.)$	Survival probability are constant over time, and capture probabilities are constant over time
$\phi(.) p(t)$	Survival probabilities are constant over time, and capture probabilities vary over time
$\phi(t) p(.)$	Survival probabilities vary over time, and capture probabilities are constant over time
$\phi(t) p(t)$	Survival probabilities vary over time, and capture probabilities vary over time
$\phi(2a) p(.)$	Survival varies based on time since marking, and capture probabilities are constant
$\phi(2a) p(t)$	Survival varies based on time since marking, capture probabilities vary over time
$\phi(2a) p(.)$	Survival varies based on time since marking, capture probabilities vary over time
$\phi(2a*t) p(t)$	Survival varies based on the interaction of time since marking with time, capture probabilities over time
$\phi(2a*t) p(.)$	Survival varies based on the interaction of time since marking with time, capture probabilities are constant
$\phi(2a*HS) p(t)$	Survival varies based on the interaction of time since marking and Hurricane Sandy, capture probabilities vary over time
$\phi(2a+HS) p(t)$	Survival varies based on time since marking with the additive effect of Hurricane Sandy, capture vary probabilities over time
$\phi(2a*HS1y) p(t)$	Survival varies based on the interaction of time since marking and Hurricane Sandy with residual 1-year effect, capture probabilities vary over time
$\phi(2a+HS1y) p(t)$	Survival varies based on time since marking with the additive effect of Hurricane Sandy with residual 1-year effect, capture probabilities vary over time
$\phi(2a*HS \text{ pre/post}) p(t)$	Survival varies based on the additive effect of time before and after Hurricane Sandy, capture probabilities vary over time
$\phi(2a+HS \text{ pre/post}) p(t)$	Survival varies based on time before and after Hurricane Sandy, capture probabilities vary over time

$\phi(2a*NO3/NO2) p(t)$	Survival varies based on the interaction of time since marking and water quality Sandy, capture probabilities vary over time
$\phi(2a+NO3/NO2) p(t)$	Survival varies based on time since marking with the additive effect of water quality, capture vary probabilities over time
$\phi(2a*T) p(t)$	Survival varies based on the interaction of a linear trend and time since marking, capture probabilities vary over time
$\phi(2a+T) p(t)$	Survival varies based on additive effect of a linear trend and time since marking, capture probabilities vary over time

We used the analysis of deviance (ANODEV) to calculate the amount of variance explained by the external covariate which demonstrates the extent or significance of the effect being tested (Skalski et al. 1993). This provides a means of evaluating each hypothesis by comparing the fit of nested models. ANODEV also provides an alternative to model averaging by allowing a clear identification of the significance of factors when model uncertainty is present. The importance of the covariate is evaluated by comparing the deviance of the covariate model, the global model [$\phi(t) p(t)$], and constant model [$\phi(.) p(t)$] (Table 2). When ANODEV showed a significant relationship or trend between survival and a covariate, we evaluated the fraction of temporal variation explained by the external covariate by deriving the squared correlation coefficient or R^2_{dev} through the following calculation (Skalski et al. 1993; Grosbois et al. 2008):

$$R^2_{dev} = \frac{dev(constant\ model) - dev(covariate\ model)}{dev(constant\ model) - dev(global\ model)}$$

Table 2 ANODEV model selection.

Model	Model formula	Description
Constant Model	$f(\phi)=a$	Model with the fewest number of parameters that explains the baseline level in the comparison
Global Model	$f(\phi)=a(t)$	Model with the largest number of parameters that explains the total deviance
Covariate Model	$f(\phi)=a + b*x$	Model with the covariate being tested

Transience Estimation

The presence of transience within the data means there is an excess of individuals captured for the first time, released, and never recaptured in the following occasions. An estimate of the proportion of transient individuals may give insight into the percentage of individuals temporarily emigrating from the study area. To estimate the proportion of transient individuals in the sample, the methods of Pradel et al. (1997) were employed with initial survival between t and $t + 1$ related to the proportion of transients among newly marked individuals. Proportion of transient individuals in each sample for a given interval were calculated by dividing the estimated survival for the occasion with both residents [$\phi(2a)$] by the apparent survival of residents over the same interval (ϕ). The equation for portion of transients in the marked sample is as follows:

$$\tau = 1 - \frac{\phi(2a)}{\phi}$$

Injuries Analysis- Multistate Modeling

Recapture data between 2009 and 2018 were selected for injury analysis based on the years when thorough records on physical condition were collected. During each capture, abnormalities in appearance were depicted in a diagram to show the extent of the injury along with a corresponding written description. Data on injuries were then sorted by injury type and summed to determine the total number of injured individuals. To estimate survival, injuries were further classified into two states or groups, State 1 which included individuals without severe injuries and State 2 including those described as having extensive damage to their shell or limbs. Extensive damage was considered to include any missing limbs as well as damage to 3 or more marginal scutes and 2 or more

adjacent vertebral or costal scutes (Cecala et al. 2008; Lester et al. 2013). Injury information was not extensively recorded in JFK and did not provide enough data for comparative analysis.

To determine if survivorship differed between injured and non-injured terrapins, Multistate models in Program MARK (v. 8.2) were used to test the influence of state, capture, and transition between the 2 injury states (Brownie et al. 1993; White et al. 2006). Multistate models include three parameters defined as:

S: probability that an individual in a given state at time t survives until time $t + 1$

P: probability that a marked individual is recaptured at time t in a given state

Ψ : probability that an individual in a given state at time t is in state s at time $t + 1$

The Multistate model is considered an extension of the Cormack-Jolly-Seber model.

Multistate models allow individuals to move between states, indicated by their transition probabilities. We constructed encounter histories from 10 years of injury data reflecting recaptures in either state, State 1 or 2. Models were then constructed assuming either constant (.) survivorship or variable (t) survivorship within injury states, detection rates, and transition rates. Transition from state 2 to 1 was fixed, to model the situation in which terrapins remain within a major injury state if their first capture is within State 2.

Goodness of fit testing for multistate modeling is conducted the same as the Cormack-Jolly-Seber model. In this case, goodness of fit was evaluated through U-Care to assess the fit of the data to the Jolly MoVe (JMV) model which allows encounter probability to vary by a previous state (Pradel et al. 2003). Component tests 3G.SR, M.ITEC, and WBWA, detect transients, trap-dependence and the memory of past states,

respectfully. Related to previous to previous testing, a transient model is warranted if Test 3G.SR is significantly affected, and residual deviation is accounted for by adjusting the variance inflation factor (\hat{c}) (Lebreton et al. 1992).

RESULTS

Total Captures and Recaptures

Demographic parameters were estimated from 686 individuals recaptured at Ruler's Bar from 2003 to 2018, corresponding to a total of 1,078 individual female terrapins marked. The number of individual female diamondback terrapins captured in RB ranged yearly from 48 to 394 during the 16-year period (Figure 2). The proportion of turtles recaptured each year after their initial tagging varied from 17% to a high of 87%. JFK had more individuals captured within a shorter study period (2011-2018) with 3,130 total individuals marked and 1,015 individuals recaptured. The number of female terrapins captured per year ranged from 147 to 1201 over 8 years (Figure 3). Recapture proportions in each occasion in JFK ranged from 7% to 52%. Of the individuals recaptured and marked in Ruler's Bar, only 3 were recaptured in JFK in later occasions. Similarly, only 8 terrapins were recaptured in Ruler's bar after first capture in JFK, constituting less than 1% of recaptures in both populations.

Figure 2 Number of individual female Diamondback terrapins (*Malaclemys terrapin*) captured each year and number of recaptures each year in Ruler's Bar (2003-2018).

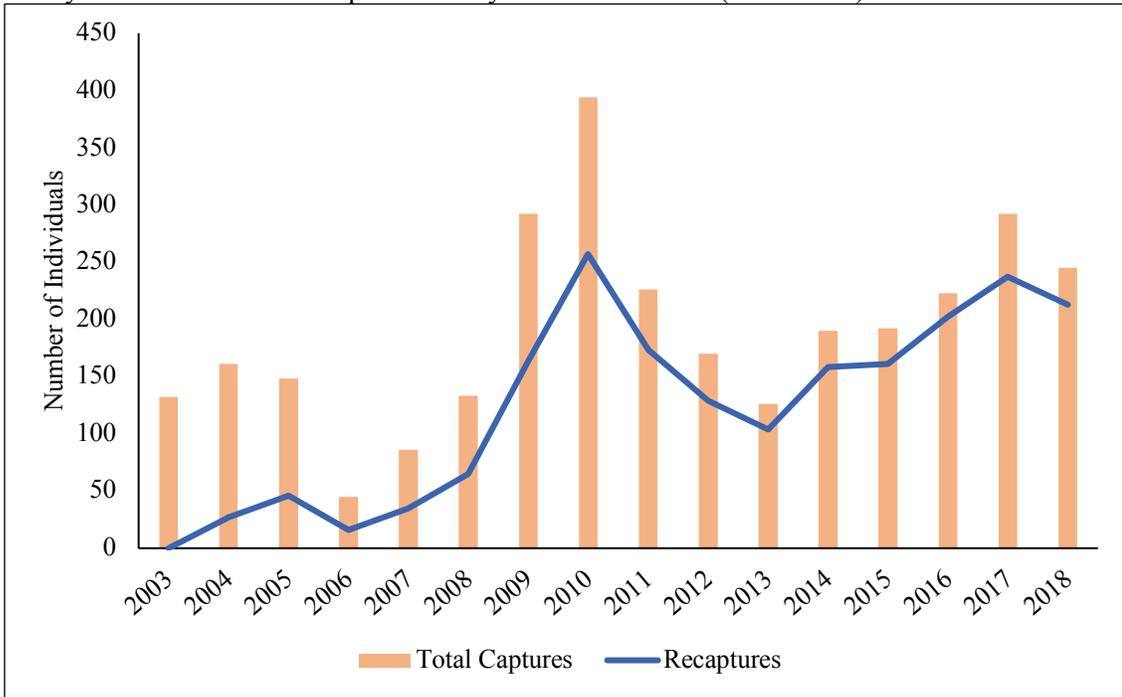
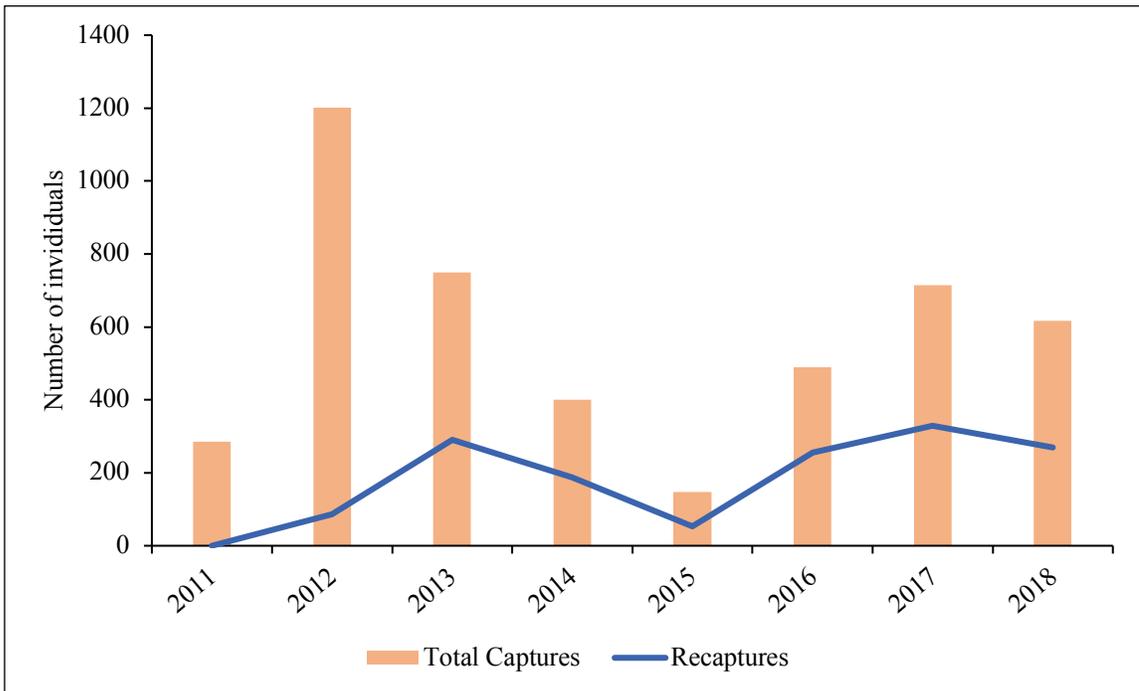


Figure 3 Number of individual female Diamondback terrapins (*Malaclemys terrapin*) captured each year and number of recaptures each year in JFK Airport (2011-2018).



Goodness of Fit and Model Selection

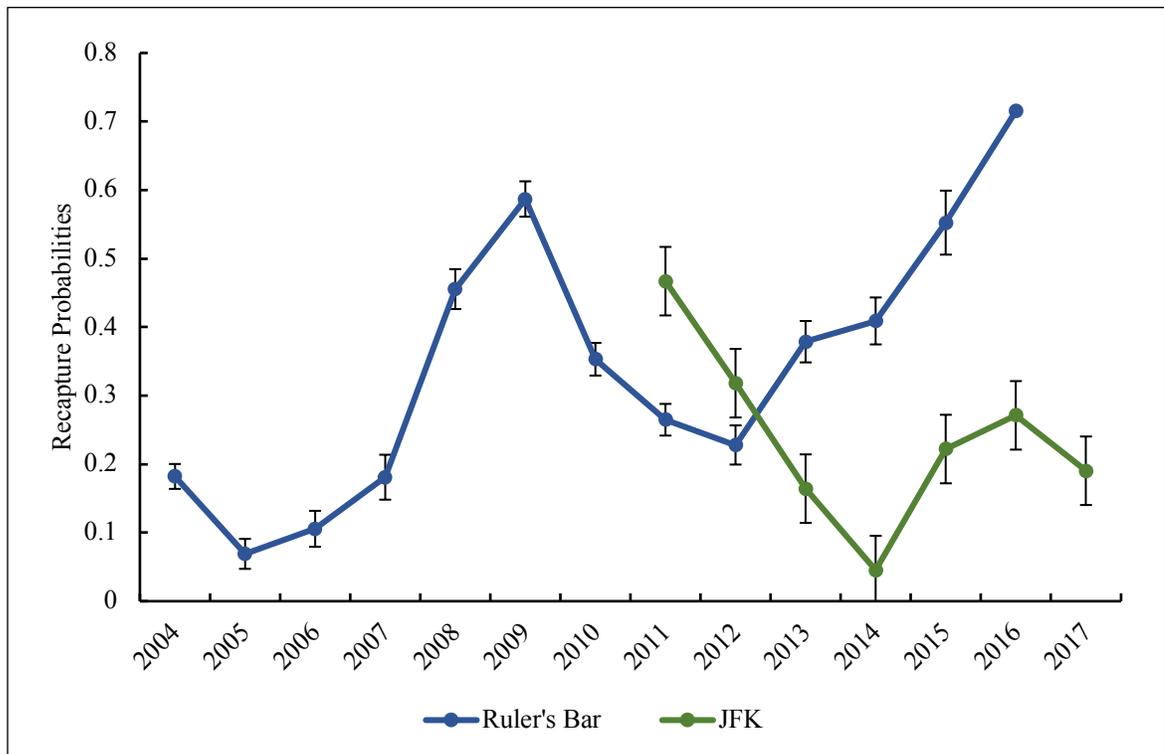
Goodness of fit testing showed evidenced of lack of fit to the Cormack-Jolly-Seber Model for both Ruler's Bar ($\chi^2(116) = 204.56, P < 0.0001$) and JFK ($\chi^2(33) = 84.66, P < 0.0001$). Examination of the component Test 3.SR confirmed that a significant transient effect was present in both Ruler's Bar ($\chi^2(14) = 64.14, P < 0.0001$) and JFK ($\chi^2(6) = 51.1297, P < 0.0001$). Therefore, individuals did not have the same probability of surviving from t to $t+1$ in either population because newly marked terrapins are less likely to be seen again than previously marked individuals. Transient individuals may considerably reduce the estimation of apparent survival when pooled with resident individuals. To avoid this negative bias, a time-since-marking (TSM) model was applied to the global model [$\phi(2a^*t) p(t)$], and all models going forward (Pradel et al. 1997). The TSM model produces two estimates of apparent survival, a separate set of values for the initial event of marking (representing both transient and resident individuals) and another set distinguishing successive recaptures (representing only resident individuals). To avoid further overparameterization of models, we chose to correct for over dispersion of the data and account for residual variation by adjusting the variance inflation factor (\hat{c}) for Ruler's Bar ($\hat{c} = 103.33/79 = 1.37$) and JFK ($\hat{c} = 33.529/1.24 = 1.24$). A \hat{c} well under 3 indicates that the model will reliably describe the data and estimates are likely to be valid (White & Burnham 1999).

Recapture Probability

The best supported model for Ruler's Bar estimated time dependent variation for recapture probability (QAICc w=0.42) (Table 3). Capture probability varied greatly between years or capture occasions in Ruler's Bar with estimates ranging between 0.052

(95% confidence interval (CI) = 0.029-0.11) and 0.62 (95% CI = 0.55-0.69) (Figure 4). Recapture rate also appeared higher in the last 5 years compared to the initiation of the study with probabilities remaining above 0.35. JFK recapture probability was also time varying (Table 4). JFK recapture probabilities varied greatly between capture years but remained very low with estimates below 0.50 throughout all years. Specific estimates ranged from 0.04 (95% CI = 0.032-0.059) to 0.46 (95% CI = 0.37-0.55) (Figure 4).

Figure 4 Recapture probability of female Diamondback terrapins (*Malaclemys terrapin*) captured each year at Ruler’s Bar (2004-2017) and JFK Airport (2012-2017).



Survival Probability

The best supported model for Ruler’s Bar estimated apparent survival as a function of the interaction between time since marking and a linear trend over time (QAICc w=0.42) (Table 3). Model $[\phi(2a*T)p(t)]$, specifies a gradual decrease in survival from 0.92 in 2004 (95% CI = 0.88-0.95) to 0.89 (95% CI = 0.86-0.92) in 2018 (Figure 5).

This indicates a decrease of about 0.16% each year. The interaction effect between time since marking and a trend appears to be significant as the additive model $[\phi(2a+T)p(t)]$ did not perform as well (QAICw=0.074) (Table 3). Some model uncertainty exists within the candidate models with two models showing equal support with a $\Delta QIC < 2$. The second-best model $[\phi(2a+HS1y) p(t)]$, displayed a $\Delta QAIC$ well below 2, indicating equal support along with the linear trend model. This model estimated survival as constant over time but with a decrease to 0.85 (95% CI = 0.76-0.91 over two years (2012-2014) following Hurricane Sandy (QAICc w=0.38) (Table 3). The model including an additive variable just over the year the storm occurred (2012-2013) also performed well within the candidate model set but did not explain enough variation in survival to be placed within the top models (QAICw=0.036) (Table 3). Both the additive and interactive effect of average nitrogen levels as an indicator of Jamaica Bay water quality did not produce a supported model that adequately explained yearly variation in survival.

The JFK data supported constant apparent survival for resident females (QAICc w=0.27) (Table 4). For model $[\phi(2a) p(t)]$, survival of residents was estimated at 0.92 (95% CI = 0.89-0.95) (Figure 5). The second-best model $[\phi(2a+HS1y) p(t)]$, showed equal supported with an $AIC < 2$ but did not account for enough deviance to be ranked above the constant survival (Table 4). Additional models including Hurricane Sandy and water quality were not favorable over the constant model.

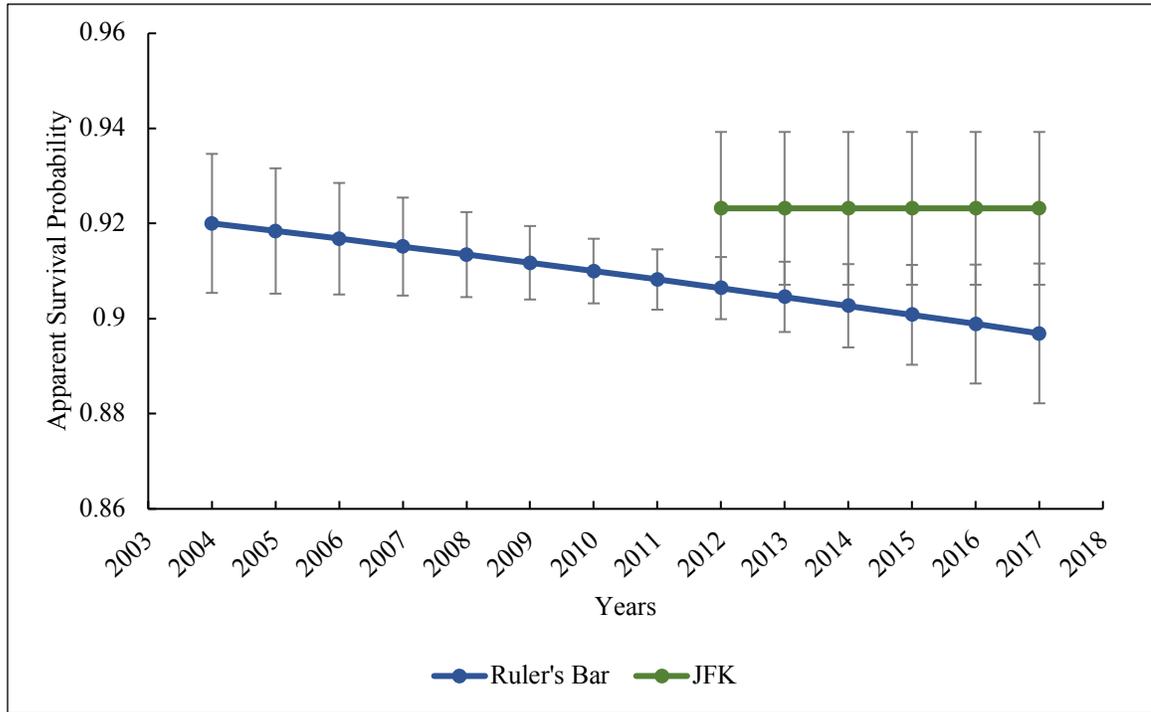
Table 3 Model selection of Cormack-Jolly-Seber models of apparent survival and recapture probability for adult females in Ruler’s Bar. Phi (ϕ) indicates apparent survival and p indicates recapture probability. Parameters were modeled as a function of time (t), trend (T), Hurricane Sandy (HS), and constant over time (.). “2a” indicates a two-age or transient model structure used. “ * ” = interaction between the effects tested. “ + ” = no interaction considered between effects tested (additive). $\hat{C} = 1.37$. Best model is in **bold**.

Model	Parameters	QAICc	Δ QAIC	QAICw	Deviance
$\phi(2a * T) p(t)$	19	6224.345	0	0.42416	1848.091
$\phi(2a + HS1y).p(t)$	18	6224.578	0.2327	0.37757	1850.351
$\phi(2a * HS1y) p(t)$	18	6226.442	2.0971	0.13357	1850.188
$\phi(2a + T) p(t)$	18	6227.614	3.2687	0.07435	1853.387
$\phi(2a+HS).p(t)$	18	6229.292	4.9469	0.03575	1855.065
$\phi(2a*HS).p(t)$	19	6230.672	6.3267	0.01794	1854.417
$\phi(2a+HS \text{ pre/post}).p(t)$	18	6231.373	7.0279	0.01263	1857.146
$\phi(2a*HS \text{ pre/post}).p(t)$	19	6231.538	7.1932	0.01163	1855.284
$\phi(2a*NO3/NO2).p(t)$	19	6236.147	11.802	0.00116	1859.893
$\phi(2a).p(t)$	17	6238.402	14.057	0.00038	1866.201
$\phi(2a+NO3/NO2).p(t)$	18	6240.175	15.83	0.00015	1865.948
$\phi(2a*t).p(t)$	43	6240.61	16.2651	0.00012	1815.260
$\phi(.) p(t)$	16	6253.123	28.7783	0	1882.947
$\phi(t) p(t)$	29	6257.352	33.0065	0	1860.744
$\phi(2a*t).p(.)$	20	6554.192	329.8471	0	2175.909
$\phi(t) p(.)$	11	6585.547	361.2021	0	2225.471
$\phi(2a).p(.)$	3	6629.746	405.401	0	2285.756
$\phi(.) p(.)$	2	6672.063	447.7183	0	2330.077

Table 4 Model selection of Cormack-Jolly-Seber models of apparent survival and recapture probability for adult females in JFK. Phi (ϕ) indicates apparent survival and p indicates recapture probability. Parameters were modeled as a function of time (t), trend (T), Hurricane Sandy (HS), and constant over time (.). “2a” indicates a two-age or transient model structure used. “*” = interaction between the effects tested. “+” = no interaction considered between effects tested (additive). $\hat{C} = 1.24$. Best model is in **bold**.

Model	Parameters	QAICc	Δ QAIC	QAICw	Deviance
$\phi(2a) p(t)$	9	6929.7710	0	0.272	174.4488
$\phi(2a + HS1y) p(t)$	10	6930.1225	.3515	0.228	172.7902
$\phi(2a+ HS) p(t)$	10	6931.6322	1.8612	0.107	174.2999
$\phi(2a* HS1y) p(t)$	11	6932.1104	2.3394	0.084	172.7671
$\phi(2a* HS) p(t)$	11	6932.3729	2.6019	0.074	173.0295
$\phi(2a* T) p(t)$	11	6932.6544	2.8834	0.062	173.3111
$\phi(2a* NO3/NO2) p(t)$	11	6933.0025	3.2315	0.052	173.6592
$\phi(2a* t) p(t)$	18	6939.3452	9.5742	0.002	165.8960
$\phi(.) p(t)$	8	6966.8168	37.0458	0.000	213.5036
$\phi(t) p(t)$	13	6969.2541	39.4831	0.000	205.8856
$\phi(2a* t) p(.)$	12	7167.1366	237.3656	0.000	405.7812
$\phi(t) p(.)$	6	7193.9426	264.1716	0.000	444.6446
$\phi(2a) p(.)$	3	7250.2320	320.4610	0.000	506.9490
$\phi(.) p(.)$	2	6932.6544	2.8834	0.000	533.2421

Figure 5 Estimates of apparent survival of the top models for residents of Ruler’s Bar [$\phi(2a^*T)$ p(t)] and JFK [$\phi(2a)$ p(t)].



ANODEV or analysis of deviance determines the amount of variance explained by a covariate through comparison of the deviance between the covariate, global, and constant models. ANODEV evaluation of the potential effects of external covariates revealed that the additive effect of Hurricane Sandy explained a significant amount of the survival variability in Ruler’s Bar. The model with an effect just one year following the storm year [$\phi(2a+HS)$ p(t)], explained enough deviance to be significant (p-value=0.0139). Through R^2 calculations, we estimated that Hurricane Sandy explained 21.9% of the survival variation (Table 5). The additive effect over two years following the storm [$\phi(2a+HS)$ 1y p(t)] was strongly supported and significantly affected survival (p-value=0.0025). This variable accounted for large portion of the variance in survival at 31.4% (Table 5). Models estimating an additive long-term change in survival post-Hurricane Sandy also appeared marginally significant (p-value=0.0285). The additive

and interactive effect of water quality were not supported and did not show a significant impact on survival variation (p-value=0.205). ANODEV analysis for Ruler’s Bar is summarized in Table 5.

Table 5 Ruler’s Bar ANODEV statistical tests performed to assess the significance of the relationship between temporal variation of survival estimates and external covariates (Hurricane Sandy, Water quality, Trend) Significance is displayed by model F statistic (F-anodev) as well as p-value significance level (P-anodev). The squared correlation coefficient (R^2_{dev}) displays the fraction or percentage of deviance explained by the covariate tested. “+”, additive effect; “*”, interaction effect. Best model is in **bold**.

Model	Deviance	Parameters	F-anodev	R ²	p-value
$\phi(2a+ T) p(t)$	1853.387	18	8.4025	0.239	0.0077
$\phi(2a* T) p(t)$	1848.091	19	6.6195	0.339	0.0051
$\phi(2a+ HS)$	1855.065	18	6.9942	0.219	0.0139
$\phi(2a* HS) p(t)$	1854.417	19	3.6112	0.231	0.0426
$\phi(2a + HS1y) p(t)$	1850.351	18	11.2924	0.314	0.0025
$\phi(2a* HS1y) p(t)$	1850.188	19	5.5016	0.314	0.0108
$\phi(2a +HS b/a) p(t)$	1857.146	18	9.055		0.0285
$\phi(2a * HS b/a) p(t)$	1855.284	19	3.2732		0.0553
$\phi(2a+ NO3/NO2)p(t)$	1865.948	18	0.1247		0.7269
$\phi(2a* NO3/NO2)p(t)$	1859.893	19	1.6961		0.2047

ANODEV procedures revealed that neither the hurricane or water quality appears to be significant in explaining survival in the JFK population. Most models performed marginally well in terms of AIC, although not with a QAIC < 2 that would have confirmed equal support. The effect of the hurricane over the two years was supported by the AIC but did not perform better than the constant model in explaining a significant portion of the deviance (p-value=0.2028). Overall, all external variables did not explain

enough deviance compared to constant model, given the additional parameters included.

ANODEV analysis for JFK is summarized in Table 6.

Table 6 JFK ANODEV statistical tests performed to assess the significance of the relationship between temporal variation of survival estimates and external covariates (Hurricane Sandy, Water quality) Significance is displayed by model F statistic (F-anodev) as well as p-value significance level (P-anodev). “ + ”, additive effect; “ * ”, interaction effect.

Model	Deviance	Parameters	F-anodev	p-value
$\phi(2a+ T) p(t)$	6931.0464	10	0.7518	0.4112
$\phi(2a* T) p(t)$	6932.6544	11	0.5370	0.6068
$\phi(2a+ HS)$	6931.6322	10	0.1417	0.7164
$\phi(2a* HS) p(t)$	6932.3729	11	0.6964	0.5299
$\phi(2a + HS1y) p(t)$	6930.1225	10	1.9246	0.2028
$\phi(2a* HS1y) p(t)$	6932.1104	11	0,8567	0.4647
$\phi(2a+ NO3/NO2)p(t)$	6931.4543	10	0.3178	0.5884
$\phi(2a* NO3/NO2)p(t)$	6933.0025	11	0.3560	0.7125

Transient Individuals

The lower survival and recapture probabilities of newly marked female terrapins over their first year highlighted the importance of rigorous goodness of fit testing and the selection of the appropriate starting model to avoid bias. Ruler’s bar females in their first capture year had lower survival rates from 0.91 to 0.54 over 16 years. JFK survival over the first capture occasion was also estimated much lower than residents at 0.67. These values would have substantially decreased resident survival and in turn would not have accurately reported the apparent survival of the resident population. The proportion of transient individuals temporarily emigrating out of the study area found in Ruler’s Bar was estimated to be on average about 17% of newly tagged females. JFK appears to have

a larger proportion of transience with about 27% of newly marked individuals temporarily dispersing out of the study area over the 8-year study period.

Ruler's Bar Injuries

Between 2009-2018, 156 individuals out of 874 ($156/874 = 17.8\%$) Ruler's Bar terrapins captured were observed to have some form of major injury. Among those injured, just over 5 times as many individuals had major shell damage ($n=137$) to their carapace or plastron compared to those with missing or dislocated limbs ($n=26$). Corresponding percentages of those injured, were 15.6% ($137/874$) of those with major shell damage compared to 2.9% ($26/874$) of those with limb injuries out of the total individuals. Few terrapins had both shell damage and major limb injuries ($n=7$). Typical carapace injuries for females in Ruler's Bar included missing pieces or entire marginal scutes, missing portions of main costal or vertebral scutes, extensive scarring across multiple scutes, as well as widespread shell infection and necrosis. Limb injuries include broken or misaligned bulging bones, missing whole limbs or missing part of a limb.

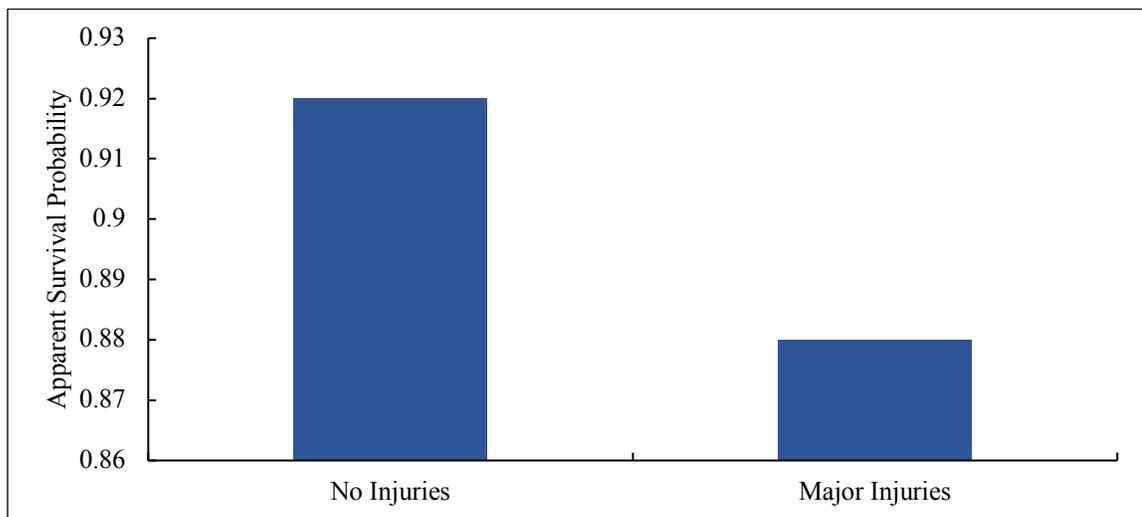
Goodness of fit testing indicated lack of fit due to transience (Test 3G.SR, $\chi^2(14) = 49.140$, $P < 0.0001$). A time since marking model (TSM) was constructed again and the variance inflation factor (\hat{c}) was adjusted ($\hat{c} = 1.30$). Among the models tested for survival after major injuries, the strongest support was found for the model with constant apparent survival (QAICw= 0.89) (Table 7). Survival estimates were lower for individuals with major injuries between the two injury states (Figure 5). Apparent survival (S) of residents in Ruler's Bar was constant at 0.92 (95% CI = 0.895-0.932) for individuals with no major injuries and 0.88 (95% CI = 0.836-0.926) for severe injuries

(Figure 6). In addition, transition to a major injury state (Ψ) did not appear to change over time and was estimated as low at 0.037.

Table 7 Model selection of multistate models of apparent survival and recapture probability, and transition between states for adult females in Ruler’s Bar. S (ϕ) indicates apparent survival, P indicates recapture probability, and Psi (Ψ) indicates transition rate. Parameters were modeled as a function of time (t) and constant over time (.). $\hat{C} = 1.30$.

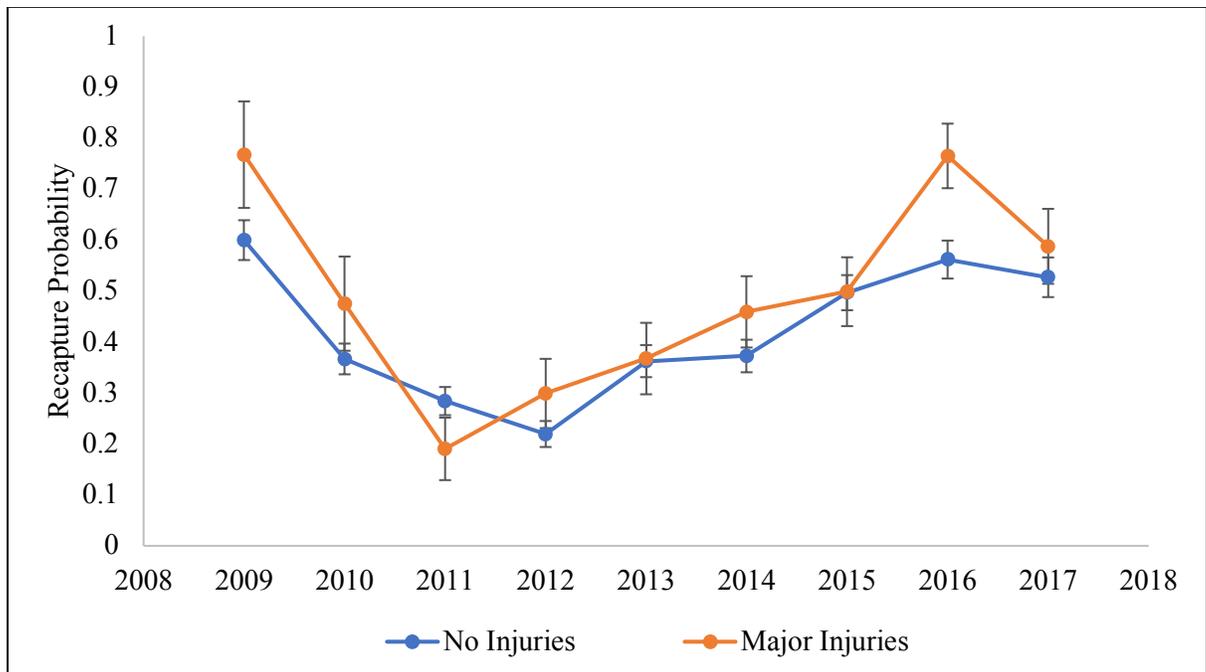
S	P	Ψ	Parameters	QAICc	Δ QAIC	QAICw	Deviance
(.)	(t)	(.)	23	6131.2552	0	0.896	2207.5732
(.)	(t)	(t)	30	6136.1744	4.9192	0.076	2198.1260
(t)	(t)	(.)	48	6138.3971	7.1419	0.025	2162.9569
(t)	(t)	(t)	55	6143.5587	12.3035	0.001	2153.3998
(t)	(.)	(.)	26	6211.0148	79.7596	0.000	2281.1877
(t)	(.)	(t)	33	6211.7563	80.5011	0.000	2267.5211
(.)	(.)	(.)	7	6268.4015	137.1463	0.000	2377.1969
(.)	(.)	(t)	14	6269.3104	138.0552	0.000	2363.9582

Figure 6 Estimates of apparent survival (S) for non-injured and injured terrapin females in Ruler’s Bar (2009-2018). No injuries (State 1). Major Injuries (State 2).



Recapture rate varied over time for both states, with those with major injuries having higher recapture in most years (Figure 7). Recapture probability for individuals without severe injuries (State 1) ranged from 0.22 (95% CI = 0.17-0.27) to 0.60 (95% CI = 0.52-0.67). Major injuries (State 2) ranged from 0.20 (95% CI = 0.097-0.34) to 0.77 (95% CI = 0.51-0.91) (Figure 7).

Figure 7 Recapture probability of female Diamondback terrapins (*Malaclemys terrapin*) captured each year at Ruler's Bar (2004-2017) in either injury state. No injuries (State 1). Major Injuries (State 2).



DISCUSSION

Survival and Recapture Probabilities

Using long-term data and mark-recapture analysis we estimated adult female survival probabilities for the first time for two primary diamondback terrapin populations in the New York City area. Turtles are long-lived animals that display high adult

survivorship, delayed reproductive maturity as well as low nest and hatchling survivorship (Ernst and Lovich 2009). High and constant survival (>90%) is key to the continued viability and persistence of turtle population, especially for adult females (Iverson et al 1991). Therefore, estimates of population vital rates are crucial in understand population change over time and evaluating management options. Ruler's Bar data showed strong support for two models: one indicating a steady decline in survival from 0.92 to 0.89 over 15 years and another estimating constant survival at 0.92 with a decline to 0.85 in the two years post-Hurricane Sandy. In contrast, the JFK population showed strong support for high and constant survival over time at 0.92, a trait exhibited by most turtle species (Shine and Iverson 1995). Overall, mean survival rates of both female terrapin populations were within average values for this species presented in the literature, ranging from 0.84 (Tucker et al. 2001) to 0.96 (Mitro 2003). Despite similar rates of survival in both populations, there is a clear difference in their pattern of survival over the study years. This distinction can be an indication the current stability of the JFK population while the definitive cause of the declining survival in Ruler's Bar females remains uncertain. The conservation implications for declining survival in this population are significant, even if it is by a small percentage (Crawford et al. 2014). Ruler's Bar experiences high nest mortality due to raccoon predation which could mean a greater reliance on high and constant female survival to maintain population growth. Decreasing female survival and high nest mortality will lead to a decline in population growth and local extinction.

Pollution remains a threat in Jamaica Bay although our models did not detect a relationship between nitrogen loading and terrapin survival. Jamaica Bay has a diverse

contaminant environment including heavy metals, pesticides, and sewage effluents. These factors can affect food resources, contaminate marsh systems, and bioaccumulate in the tissues of individuals (Sanderson et al. 2016). The impact of these pollutants on terrapins has not been thoroughly studied. Further information on the effects of these pollutants on terrapins as well as consistent environmental monitoring would be needed to determine relationships with trends seen at Ruler's Bar. The possible threat of pollutants is system wide and would likely impact both populations. This effect would not exclusively explain the different survival patterns found in the two populations, as models suggest one is constant and the other may be declining over time.

Severe coastal storms could lead to direct mortality and injury from storm debris, alteration of habitats, and changes in food availability in localized regions (Dodd et al. 2006). These factors may be responsible for the decline in survival in Ruler's Bar post-Hurricane Sandy. Mortality of terrapins can often go undetected and no measure of direct mortality was conducted after the storm. However, several female terrapins that survived the storm were found with severe shell damage in 2013 (Burke and Francoeur, 2014). In addition, habitat disturbance was significant with a loss of vegetation and sediment of tidal marsh islands particularly on the west side of Jamaica Bay (Wang et al. 2017; Campbell et al. 2017). Besides direct mortality, features of terrapin ecology could be behind the exact process that reduced their survivorship. Temporary loss of prime habitat and changes in food availability could lead to females to seek resources elsewhere and take advantage of alternative nesting areas. It is possible that terrapins surviving the storm experienced diminished physical condition and would have had to allocate more energy towards healing injuries or overcoming infection as well as seeking alternative

foraging areas. In the case of JFK females, the effect of Hurricane Sandy was not significant and therefore not supported. The exact cause behind this finding is uncertain but several factors that differentiate the populations may be responsible. JFK females appear to be younger and are perhaps better able to overcome injuries. The quality of their nearby habitat may be another factor. JoCo marsh, the salt marsh adjacent to JFK, surprisingly saw an increase in vegetation post-Hurricane Sandy due to movement of wrack (Campbell et al. 2014). JoCo may have been resilient to storm surge in part due to its already healthy condition and location on the far east side of the bay (Campbell et al. 2014). This could mean that terrapins had a reliable local refugia while enduring the storm resulting in less mortality and injury. In addition, a lack of habitat disturbance could indicate that foraging and over wintering areas remained unchanged and individuals did not expend energy in seeking resources elsewhere. The apparent healthy status of the JFK population demonstrates that it may be a good reference site and provide baseline data for future work in Jamaica Bay.

Declines in terrapin survival are typically attributed to an increase in human activity, usually involving direct mortality caused to crab trapping and road collisions (Witczak et al. 2014; Tucker et al. 2001; Crawford et al. 2014). Mortality due to these threats are not widely reported in Jamaica Bay and may not be attributable to the decreasing trend in survival in Ruler's Bar. Jamaica Bay terrapin populations are not sheltered from predation and motorboat activity. Injury rates in Ruler's Bar fall within average levels between 11% to 20% (Rosenburg 1991; Hart and McIvor 2006; Cecela et al. 2008; Crawford et al. 2014). Cecala et al. (2008) found that survival was lower for both males and female terrapins with major injuries. We found similar results, with

survival about 4% lower for injured terrapins. Transition estimates to an injured state were constant indicating that injury rate is not changing over time. Surprisingly, recapture rate of injured terrapins was higher in most years. This could be a product of their reduced physical condition leading them to nest in accessible open areas. Their injuries may also inhibit their ability to escape capture by volunteers and researchers. Injuries in Ruler's Bar appear to be caused by both motorboat activity and raccoon predation. Motorboat injuries are typically characterized by large scars across the carapace or missing pieces of marginal scutes (Cecala et al. 2008). Injuries caused by raccoons are indicated by damage to limbs, tails, and even the back of the carapace (Hart and McIvor 2008; Feinburg and Burke 2003). Unfortunately, it is often difficult to determine the exact cause of injury. Barnacles play a significant role in the degradation and infection of scutes (Seigel 1983). Healed carapace injuries and infected wounds need to be studied carefully to distinguish between the cause of injury. If motorboat activity is suspected of being the primary origin of carapace injury, the possibility of increasing boat traffic as the source of declining survival could be explored.

Temporary Emigration

Goodness of fit testing is simple evaluation of model adherence to underlying assumptions, but it also reveals aspects of the data that may be of biological interest. The presence of transient individuals is not commonly reported in diamondback terrapin populations. In this case, the presence of transient individuals poses a small particularity when constructing Cormack-Jolly-Seber models but generates questions regarding the behavior of the species and may provide insight about the dynamics of two populations (Sasso et al. 2006). A possible explanation for the presence of transient animals could be

an issue with the tagging method, if newly tagged individuals are easily detected by predators or the injected tag causes injury and infection. Such complications in terrapin tagging has not been found in this study or indicated in previous studies. On the other hand, if animals first captured are less likely to be seen again this reveals a meaningful aspect of their ecology, the existence of temporary emigrants. Furthermore, if females are temporarily emigrating from their foraging and nesting area, then where are they emigrating to and why? In the case of Ruler's Bar and JFK, movement between the populations appears to be minimal with only a few individuals found in both locations. If this is truly the case, female terrapins are perhaps traveling to and from smaller populations that nest elsewhere in Jamaica Bay.

Future Work

Long term studies of marked populations are essential to answering fundamental questions regarding population biology. In addition, the life history of the diamondback terrapin suggests that additional mortality due to injuries and even small decreases in survival are not factors that can be sustained over time (Crawford et al. 2014). The implications for the future of Ruler's Bar are straightforward. Declining survival of reproductive females for a species that relies on high adult survival will mean declining populations numbers and possible extirpation. Local management should attempt to pinpoint the cause of decline, whether it be one factor or a synergistic effect of multiple variables.

Future recapture studies including males and juvenile terrapins will be critical in better understanding the dynamics of the population. Data collected on males will not only allow direct estimates of survival for this segment of the population but also provide

further information on injury rates. This will allow for the direct comparison with females to determine if survival varies between groups and to determine if females are more prone to injuries than males. Very little information is known about juvenile terrapins regarding survivorship and population numbers. Therefore, expanded recapture efforts would provide one of the first direct estimates of juvenile survival. With the additional information on juveniles and males we will be able to make predictions of the future of the terrapin populations. Finally, population modeling can help us determine the impact of variations in survival on population growth and abundance. A population model will also allow us to assess the response in population growth to various management strategies. This will allow for informed conservation policies in the future that may be necessary in preventing population decline.

CONCLUSIONS

- The objectives of this thesis were to estimate and compare the survival of adult female diamondback terrapins in two Jamaica Bay populations as well as test the impact of possible threats to survival. These threats including water quality, hurricanes, and major injuries.
- This goal was carried out using long-term recapture data of nesting females in two Jamaica Bay female populations. We used mark recapture data analysis through Cormack-Jolly-Seber and Multistate Models to estimate survival and recapture probabilities as well as evaluate the potential impacts on survival in Jamaica Bay terrapins.

- Analysis showed a current distinction in the pattern of survival between the two Jamaica Bay populations. Ruler's Bar females show a declining trend in survival from 0.92 to 0.89 over the study period while JFK survival has remained constant over time at 0.92.
- Models including the effect of Hurricane Sandy showed a decrease in survival to 0.84 over the two years following the storm in Ruler's Bar but this effect was not supported for JFK. The effect of water quality (nitrogen levels) was not significant in explaining any variation in survival in either population. Finally, a significant portion of females in Ruler's Bar showed signs of major injuries (17.8%). Females with severe injuries also had lower survival at 0.88 compared to those without injuries at 0.92.
- The decline in survival in the two years after Hurricane Sandy could be attributed to direct mortality, injuries caused by storm debris, and alteration of resources. This decline was not seen in JFK females. JFK females are younger and perhaps more resilient to the direct effects of major storms and are better able to cope with injuries. In addition, the healthier marsh system at JFK may provide better protective habitat for terrapins.
- The conservation implications for declining survival in Ruler's Bar are significant. Declines even by a small percentage can have major effects on population growth. Ruler's Bar may also be experiencing declining recruitment due to high nest predation by raccoons. Reduced female survival in a population relying on high and constant survival to maintain growth can lead to local extirpation.

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