

Malaclemys terrapin Hatchlings: Variation in Seasonal Emergence

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This thesis titled

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ABSTRACT

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Malaclemys terrapin Hatchlings: Variation in Seasonal Emergence

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The Diamond-backed Terrapin, *Malaclemys terrapin*, displays facultative emergence at its northern distribution, whereby some turtles hatch and depart from the nest in the fall before the onset of winter and others overwinter within the nest and emerge the following spring. A long-term demography study at the Paul S. Sarbanes Ecosystem Restoration Project at Poplar Island, Maryland allowed for the comparison of fall and spring emergent nest success and hatchling survival. Data from 2006-2014 revealed that though fall emergence was more common, had higher within-nest survival, and produced larger hatchlings, spring emergent hatchlings had higher survival probability up to three years of age. Furthermore, I investigated individual hatchling righting behavior, aquatic and terrestrial burst speed, and aquatic and terrestrial endurance as fitness proxies that correspond to survivorship differences between fall and spring emergent hatchlings from the 2014 nesting season. Spring emergent hatchlings moved faster and longer than fall emergent hatchlings on both land and water. This spring advantage in speed and endurance could contribute to higher survival by aiding in predator avoidance and foraging abilities. Fall and spring hatchlings emerge into very different biophysical and predator environments. The corresponding performance and survivorship in Poplar Island terrapins suggests that seasonal variation may allow for the persistence of facultative emergence as a strategy in temperate turtle species.

DEDICATION

To my friends and family, near and far:

You were there during the good times

and when turtles grew tedious.

ACKNOWLEDGMENTS

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CHAPTER 1: SEASONAL EMERGENCE AND SURVIVORSHIP VARIATION IN
MALACLEMYS TERRAPIN HATCHLINGS

Abstract

Variation in the timing of hatchling emergence is common among turtles but also can vary within a species. *Malaclemys terrapin*, the Diamond-backed Terrapin, displays facultative emergence in populations at its northern distribution when some turtles hatch and depart from the nest in the fall before the onset of winter, and other hatchlings overwinter within the nest and emerge the following spring. In this study, we assess fitness metrics associated with fall and spring emergence across life cycle stages to understand why *M. terrapin* emerge facultatively in the fall or spring. We compare nest emergence data from 2006-2014 and demographic data from 2008-2014 to describe the underlying selective pressures that may result in fitness differences between emergence strategies. Our work was conducted on the Paul S. Sarbanes Ecosystem Restoration Project at Poplar Island, Maryland, from 2006 to 2014, an island where raccoons and foxes are absent and thus turtle nest survival is unprecedentedly high. We investigate whether fall or spring is more productive for hatchling *M. terrapin* emergence. Furthermore, we investigate whether body size varies between individuals with different emergence seasons. Lastly, we investigate whether survivorship differs between seasons of emergence. On Poplar Island, the average percentage of fall emerging nests (53%) is greater than spring emergence (25%) while the average percentage of unsuccessful nests is 22%. Fall hatchlings accounted for 69% of 5,533 marked individuals while 31% emerged in the spring. We recaptured 212 marked hatchlings, of which 56% were fall and

44% were spring emerging. A higher percentage of total spring emergent hatchlings were recaptured (fall: 3.13%, spring: 5.32%). Fall emergent nests had a higher within-nest survivorship at 74% on average, with spring emergent nests displaying a 65% average within-nest survival (ANOVA, $F_{(1,475)} = 9.7356$, $P < 0.002$). Hatchling height and mass also differed between fall and spring emergent hatchlings (MANOVA, *Pillai's Test* = 0.04575, $F_{(4,1157)} = 13.8675$, $P < 0.001$) with spring emergent hatchlings being smaller on average. When modeled in MARK, estimated survivorship (ϕ) values indicated that spring emergent hatchlings have a higher survivorship than fall emergent hatchlings ($\phi_{\text{fall}} = 0.4013$ and $\phi_{\text{spring}} = 0.4678$), with season present as an independent variable in the best fit model (LRT, $\chi^2_{(1)} = 5.065$, $P < 0.05$). Though fall emergence is the more common strategy, has a higher within-nest survivorship, and produces larger hatchlings, spring emergent hatchlings have higher survival probability during the first two years in life, but similar survival rates beyond age three. We believe this could be due in part to seasonal differences in predation pressures, however, specific factors that influence the difference in *M. terrapin* survivorship between emergent seasons have yet to be determined.

Introduction

In temperate regions, the emergence timing of hatchling turtles from nests varies among species and generally follows one of two patterns: fall emergence or delayed emergence (Costanzo et al. 2008). Fall emergence occurs when turtles hatch and depart from the nest before the onset of winter, while delayed spring emergence occurs when fall hatchlings overwinter within the nest and emerge the following spring. Facultative delayed emergence also occurs within a few species where both fall and spring

emergence is observed (Costanzo et al. 2008). Environmental variation between emergence seasons differs with regard to climatic and predator conditions, allowing for differing selective pressures for fall and spring hatchlings. Hatchling turtles have high mortality rates (Janzen et al. 2000) and conditions encountered upon emergence can directly affect survival during their most vulnerable life stage.

Malaclemys terrapin, the Diamond-backed Terrapin, is an emydid turtle and is the only turtle in North America that specializes in brackish water habitats (Hart and Lee 2006). Their range spans from Cape Cod, Massachusetts to Corpus Christi, Texas along the Atlantic coast and the Gulf of Mexico, resulting in one of the largest ranges of all North American turtles (Hart et al. 2014; Ernst and Lovich 2009). In their northern distribution, *M. terrapin* display a facultative emergence strategy (Baker et al. 2006) while toward the southern region they only emerge in the fall. Within a single cohort displaying facultative emergence, many clutches emerge in the fall while the other clutches overwinter within their natal nests and emerge in the spring (Roosenburg et al. 2003; Gibbons 2013). Though it is rare, some observed nests have had some individuals emerge in the fall while other individuals from the same clutch delay emergence (Graham 2009; Baker et al. 2006). *M. terrapin* also displays an ontogenetic change in habitat use. Hatchlings live predominantly in shallow water and fringe marsh habitats that allow for terrestrial movement throughout their juvenile stage (Roosenburg et al. 1999; 2003; 2004). *M. terrapin* hatchlings hibernate underground as opposed to underwater like adult terrapins and the hatchlings of many other species (Carr 1952; Draud et al. 2004; Carroll and Ultsch 2007). After approximately three years of age, terrapins take on a fully aquatic

lifestyle with the exception of female nesting (Yearicks et al. 1981; Roosenburg 1994; Gibbons et al. 2001). This preference for semi-terrestrial habitats and terrestrial hibernacula is poorly understood and may be common in hatchlings of aquatic turtles.

On the Paul S. Sarbanes Ecosystem Restoration Project at Poplar Island (hereafter Poplar Island) in Talbot County, Maryland, the *M. terrapin* population displays facultative emergence with hatchlings from the same nesting season emerging in both the fall and the spring. The restoration project at Poplar Island uses dredge material from the Baltimore Approach Shipping Channel to rebuild an island in the Chesapeake Bay that once existed as part of an archipelago, restoring native salt marsh and upland forest habitats for local species. Soon after the beginning of the project, *M. terrapin* began nesting upon sandy beaches created using native sand from the site (Figure 2). The lack of mammalian predators on Poplar Island allows for high survival rates of both nests and individual *M. terrapin* after emergence (Roosenburg et al. 2014) and thus provides an excellent opportunity to study hatchling overwintering ecology.

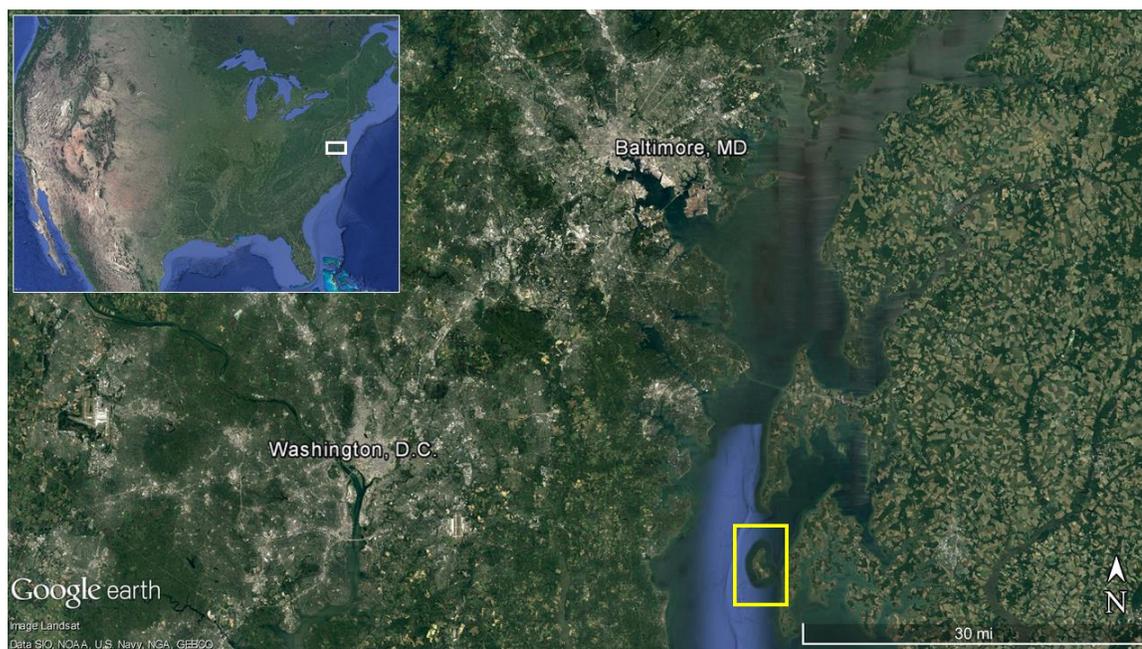


Figure 1. Poplar Island, MD location shown in yellow in relation to Baltimore, MD, and Washington, D.C. ($39^{\circ}02'20.83''$ N $76^{\circ}36'38.74''$ W. Google Earth. December 31, 1969. October 8, 2016).



Figure 2. Image of Poplar Island. Highlighted in red are the nesting areas where emergent hatchlings are collected. Cell names are labeled in white (38°45'45.82" N 76°22'36.00" W. Google Earth. October 19, 2013. June 7, 2016).

In this study, we analyze Poplar Island nesting data from 2006 to 2014 to describe variation in *M. terrapin* hatchling emergence season. The number of nests and the number of hatchlings exhibiting each emergence strategy allows for comparison of emergence strategies and the nest success between seasons. Hatchling size measurements at emergence allow for the investigation of seasonal morphological differences that may affect fitness. Additionally, we analyze seven years of *M. terrapin* mark-recapture data from hatchlings marked by year and by emergence season from 2008-2014 on Poplar Island to investigate whether survivorship differs between seasons of emergence. We investigate three questions: (1) is one emergence time (fall or spring) more productive in

terms of hatchling *M. terrapin* nest success and within nest survivorship? (2) Does *M. terrapin* size vary between emergent seasons? (3) Does juvenile *M. terrapin* survivorship vary between their emergent seasons as hatchlings?

Materials and Methods

Study Site

Poplar Island is located in the Chesapeake Bay in Talbot County, Maryland. Poplar Island is part of an archipelago, approximately 56 kilometers south of Baltimore, Maryland, and four kilometers west of the mainland at Sherwood, Maryland (Figure 1). This restoration effort, led by the U.S. Army Corps of Engineers and the Maryland Port Authority, plans to restore the island to its original size, to provide a deposit site for Chesapeake Bay dredge material, and to create wetland and upland habitats for local species (Burton; Bailey 2011). Upon project completion, the island is expected to utilize 52 million cubic meters of dredged sediment contained by 10,700 meters of internal and bordering dikes (CENAB 2014).

Poplar Island was created by first laying a perimeter dike with stone revetment and then subdividing the island interior into “cells” to be filled with dredged material. There are a total of six large interior cells on the island (Figure 2), each sub-divided into smaller cells. With the pending expansion, 298 hectares will be restored into salt marsh and an additional 340 hectares will continue to be built up and restored to upland forest and meadow habitat native to the eastern coastal plain while 56 hectares will be comprised of embayment areas which lead into wetlands (CENAB 2014). Poplar Island

currently provides terrestrial habitat for local and migrating birds as well as aquatic habitats for crabs, fish, and *M. terrapin* (Maryland Port Association 2014).

Malaclemys terrapin prefer sandy beaches for nesting, which are found along the eastern side of Poplar Island in Cell 3, Cell 5, and the Notch, as well as along sandy cross dikes throughout the island (Figure 2; Roosenburg et al. 2014). Hatchling and young juvenile terrapins on Poplar Island are generally found in tidal marshes, while older juveniles and adults are fully aquatic (Yearicks et al. 1981; Roosenburg 1994). *M. terrapin* on Poplar Island nest from May to August and hatchlings display facultative emergence, leaving their nests in both the fall and the spring.

Data collection was completed under scientific collecting permits issued by The Maryland Department of Natural Resources to W.M.R. approving all methods from 2006 to 2014. Animal care protocol was approved by the Ohio University Institutional Animal Care and Use Committee (IACUC numbers L02-06; Protocols 13-L-023).

Seasonal Nest Distribution and Within-Nest Success

To locate *M. terrapin* nests, sandy areas on Poplar Island (Figure 2) were monitored daily from May to August each year from 2006 to 2014 for signs of nesting such as terrapin tracks, disturbed substrate, and displaced sand on vegetation. Nests were located and excavated to establish the presence of eggs. The location of each nest was identified and recorded using a Garmin eTrex GPS (Roosenburg et al. 2003). The number of eggs was counted in nests less than 24 hours old, indicated by pink, translucent eggs. After egg number was recorded, the eggs were replaced in the nest cavity, the nest was refilled, and a 1.25cm wire mesh held by four survey flags was placed over the nest to

protect it from avian predators and mark its presence. After approximately 50 days of incubation, aluminum flashing (with a 0.5-0.75 meter circumference and 20 cm height) was inserted around the nest with a 1.25cm wire mesh secured on top (Roosenburg et al. 2003). Emerging hatchlings were captured in the ring and protected from avian predators by the wire mesh.

Hatchling *M. terrapin* throughout Poplar Island were collected upon emergence between August and October each fall and hatchlings in nests allowed to overwinter in the Notch and Cell 5 were collected between April and May in the spring. In all years except 2014, overwintering nests outside of the Notch and Cell 5 were excavated in the fall. Due to logistical constraints, spring nests were excavated on a single day rather than allowing overwintering hatchlings to emerge naturally. This occurred during all years except for spring emergence in 2013 and 2015 when we monitored overwintering nests weekly and collected hatchlings upon emergence. At the end of each emergence season, we excavated each nest to determine the number of fall and spring emergent hatchlings, dead hatchlings, and dead eggs present. The total numbers of fall emergent, spring emergent, failed nests, and nests of unknown fate were recorded each year.

The frequency of emergence strategies was calculated as a proportion of the total number of nests and hatchling for each year and across all years. Within-nest survivorship was calculated as the number of hatchlings produced by each nest divided by the total number of eggs in the clutch. Within-nest survivorship of arcsine square root transformed data was compared between emergence seasons using a 2-way ANOVA with emergence season and year as independent variables. Only nests from the Notch and Cell

5 were included due to the fall collection of all nests outside of these areas on most years. Depredated nests, completely failed nests, and nests with unknown fate were excluded from the analysis.

Hatchling Size

All hatchlings were transported to an onsite laboratory and each was marked with a set of notches specific to its cohort and emergence season in its marginal scutes as well as with a Northwest Marine Technologies[®] coded wire tag. The individually numbered coded wire tags used for presence and absence identification were subcutaneously injected in the right rear limb using a 25-gauge needle. For each marked hatchling, plastron length, carapace length, width, height, and mass were recorded before it was released on site. In reptiles, many studies support the hypothesis that natural selection favors larger body size (Janzen et al. 2000) allowing for body size to be used as a fitness proxy. Hatchling size was natural log transformed and compared between seasons of emergence using a 2-way MANOVA with plastron length, width, height, and mass as dependent variables and emergence season and year as independent variables. Due to significant clutch effects on size in this population (Tokash 2016) the mean sizes for each nest were used in this analysis.

Juvenile and Adult Survivorship

Juvenile and adult *M. terrapin* were captured during daily aquatic sampling throughout Poplar Island from May to August from 2008-2014. Fyke nets and baited turtle traps were set in place Monday, checked daily, and removed on Friday each week. Juvenile and adult *M. terrapin* that were collected from the nets, traps, and on land were

transported to the onsite laboratory for processing. Researchers recorded plastron length, carapace length, width, height, head width, and mass for each individual. Each individual was marked with a monel tag (National Band and Tag Company) placed in the 9th right marginal scute and a Biomark, Inc. Passive Integrated Transponder injected into the loose skin in the right inguinal area. Marked hatchlings from 2006 to 2014 were identified out of the captured individuals by using a Northwest Marine Technologies[®] V-Detector to detect the coded wire tag. These individuals marked as hatchlings from 2008 to 2014 were identified as spring or fall emergent by the notch codes present on their marginal scutes (Roosenburg et al. 2003). Marked hatchlings that emerged before 2008 were identified to the year of hatchling by the marginal scute notch codes present. Individuals were released at the site of collection each day.

Apparent survivorship (ϕ) from fall and spring emergent hatchlings from 2008 to 2014 was estimated using MARK. Only individuals marked as hatchlings with known emergence seasons were included in this analysis. Each individual was marked present for each year in which it was recaptured one or more times and absent if the individual was not recaptured. Season of emergence (fall or spring) was used as an individual covariate in the analysis. Individuals found dead upon emergence or nest excavation were excluded from the analysis. Age and time dependent survival and recapture models were tested. For all models, recapture (ρ) did not differ between fall and spring while survivorship (ϕ) was always tested with emergence season as an independent variable to investigate whether a difference between emergence seasons existed. The best fit model determined by the corrected Akaike's Information Criterion (AICc) was selected and was

tested against a null model which did not include emergence season as a variable using a Likelihood Ratio Test (LRT) to determine whether season played a significant role in survivorship.

Results

Seasonal Nest Distribution and Within-Nest Survivorship

On average, 78% of the marked Notch and Cell 5 nests on Poplar Island produced hatchlings. Fall emergence was observed in 53% of marked nests from 2006-2014, while 25% of the nests overwintered and emerged the following spring. Of these, 3% of nests produced both fall and spring emergent hatchlings. The remaining 22% of nests failed to produce hatchlings or had an unknown fate (Table 1) for many reasons such as predation, tidal inundation, or wash outs due to heavy rain.

Table 1

Number of Nests in the Notch and Cell 5 from 2006 to 2014

| <i>Year</i> | <i>2006</i> | <i>2007</i> | <i>2008</i> | <i>2009</i> | <i>2010</i> | <i>2011</i> | <i>2012</i> | <i>2013</i> | <i>2014</i> | <i>Total</i> |
|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|--------------|
| Total | 146 | 170 | 183 | 159 | 124 | 178 | 172 | 130 | 104 | 1,366 |
| Fall | 49 | 92 | 113 | 68 | 77 | 134 | 62 | 66 | 56 | 717 |
| Spring | 33 | 50 | 40 | 66 | 21 | 22 | 40 | 45 | 28 | 345 |
| Both | 1 | 0 | 1 | 4 | 4 | 4 | 12 | 1 | 8 | 44 |
| Unsucc. | 64 | 28 | 30 | 25 | 26 | 22 | 70 | 19 | 20 | 304 |

Note: Unsuccessful nests include fully depredated nests, failed nests, overwintering nests that did not emerge, and nests of unknown fate. Nests designated as Both had individuals emerge in both the fall and spring.

Out of the 5,533 marked hatchlings from 2008 to 2014, 69% of the total emerged hatchlings came from fall emergent nests and 31% emerged in the spring (Table 2). There were 211 of the marked hatchlings recaptured, out of which 56% of these recaptured individuals were fall emergent hatchlings and 44% emerged in the spring. This resulted in 3.13% of the total fall releases being recaptured, while 5.32% of the total spring releases were recaptured.

Table 2

Numbers of Marked Hatchlings Released on Poplar Island from 2008 to 2013

| <i>Year</i> | <i>2008</i> | <i>2009</i> | <i>2010</i> | <i>2011</i> | <i>2012</i> | <i>2013</i> | <i>Total</i> |
|---------------------------|-------------|-------------|-------------|-------------|-------------|-------------|--------------|
| Total Marked Hatchling # | 1,135 | 1,199 | 504 | 1,090 | 671 | 934 | 5,533 |
| Fall Marked Hatchling # | 713 | 660 | 430 | 988 | 399 | 612 | 3,802 |
| Spring Marked Hatchling # | 422 | 539 | 74 | 102 | 272 | 322 | 1,731 |

Within-nest survivorship differed by season of emergence (ANOVA, $F_{(1,475)} = 9.7356$, $P < 0.002$). Fall emergent nests had a within-nest survival of 74% on average, with the spring emergent nests displaying a 65% within-nest survival (Table 3). Within-nest survivorship also varied between years (ANOVA, $F_{(1,475)} = 8.5197$, $P < 0.004$). There was no significant season*year effect on within-nest survivorship (ANOVA, $F_{(1,475)} = 3.1639$, $P > 0.05$). Though within-nest survivorship was higher for fall emergent nests on average, spring emergent nests exhibited a higher mean within-nest survivorship in 2007 and 2008 (Figure 3).

Table 3

Mean Percent Within-Nest Survivorship in the Notch and Cell 5 from 2006 to 2014

| <i>Year</i> | <i>2006</i> | <i>2007</i> | <i>2008</i> | <i>2009</i> | <i>2010</i> | <i>2011</i> | <i>2012</i> | <i>2013</i> | <i>2014</i> | <i>All</i> |
|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|------------|
| Fall | 76% | 78% | 72% | 78% | 68% | 72% | 80% | 81% | 58% | 74% |
| Spring | 59% | 84% | 86% | 70% | 34% | 47% | 52% | 64% | 70% | 65% |

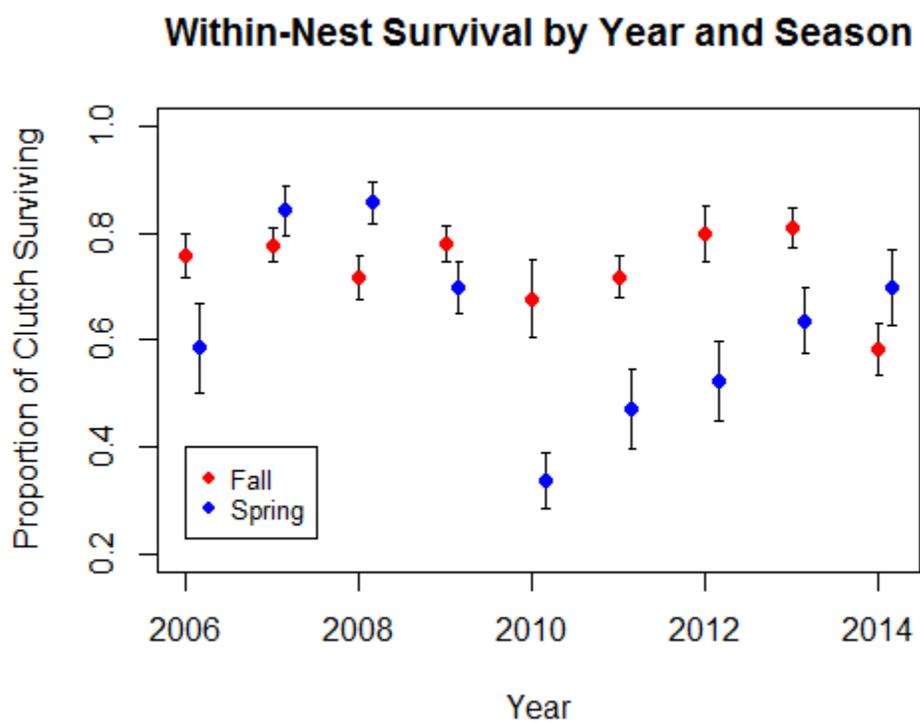


Figure 3. Within-nest survival as a proportion of surviving clutch is shown from 2006 to 2014. Mean fall values are in red and mean spring values are in blue. Standard error bars are shown.

Hatchling Size

Overall, seasonal difference in hatchling size exists between fall and spring emergent hatchlings (MANOVA, *Pillai's Test* = 0.04575, $F_{(4,1157)} = 13.8675$, $P < 0.001$). There was also a year (MANOVA, *Pillai's Test* = 0.07086, $F_{(4,1157)} = 22.0588$, $P < 0.001$) and a year*season (MANOVA, *Pillai's Test* = 0.012855, $F_{(4,1157)} = 3.7666$, $P < 0.005$) effect on hatchling size upon emergence. When the dependent variables were separated for individual analysis, hatchling height and mass differed between fall and spring emergent hatchlings (MANOVA, $F_{(1,1160)} = 26.2138$, $P < 0.001$ for height and $F_{(1,1160)} = 34.0768$, $P < 0.001$ for mass) with smaller spring emergent hatchlings on average (Table 4). Similarly, only height and mass had a significant year*season effect (MANOVA, $F_{(1,1160)} = 5.1462$, $P < 0.05$ for height and $F_{(1,1160)} = 11.3989$, $P < 0.001$ for mass). No seasonal difference was found for plastron length or hatchling width (MANOVA, $F_{(1,1160)} = 0.0108$, $P > 0.05$ for plastron length and $F_{(1,1160)} = 1.0059$, $P > 0.05$ for width). Though mass was similar each year (MANOVA, $F_{(1,1160)} = 1.6895$, $P > 0.05$), plastron length, width, and height differed by year (MANOVA, $F_{(1,1160)} = 42.3058$, $P < 0.001$, $F_{(1,1160)} = 17.0556$, $P < 0.001$, and $F_{(1,1160)} = 7.3190$, $P < 0.01$ respectively).

Juvenile and Adult Survivorship

There was an emergence season effect on hatchling survivorship (LRT, $\chi^2_{(1)} = 5.065$, $P < 0.05$). The best fit model indicated that during the first three years of life in which *M. terrapin* lives semi-terrestrially, fall and spring emergent hatchlings differ in survivorship with spring hatchlings surviving better (Table 5). There was no seasonal effect on survivorship from age four to seven, when *M. terrapin* begin their fully aquatic

behavior. Estimates of hatchling survivorship increased with age. In the best fit model, recapture probability was modeled as fully age dependent by nesting year and did not include season as a variable (Table 6).

Table 4

Mean Body Sizes of M. terrapin upon Emergence from 2006 to 2014

| <i>Year</i> | <i>Season</i> | <i>2006</i> | <i>2007</i> | <i>2008</i> | <i>2009</i> | <i>2010</i> | <i>2011</i> | <i>2012</i> | <i>2013</i> | <i>2014</i> |
|-------------|---------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| P. L. (mm) | Fall | 28.32 | 27.26 | 27.27 | 27.22 | 26.93 | 26.42 | 26.94 | 27.29 | 26.24 |
| | Spring | 27.44 | 27.66 | 27.53 | 27.24 | 26.84 | 26.27 | 26.73 | 26.17 | 26.64 |
| Width (mm) | Fall | 28.24 | 27.52 | 27.39 | 27.24 | 26.66 | 26.73 | 27.23 | 27.65 | 26.93 |
| | Spring | 27.65 | 27.86 | 27.42 | 27.27 | 26.87 | 26.15 | 27.25 | 26.60 | 27.19 |
| Height (mm) | Fall | 17.20 | 15.84 | 15.69 | 15.98 | 16.24 | 15.64 | 15.98 | 15.79 | 16.30 |
| | Spring | 16.20 | 15.96 | 15.74 | 15.41 | 15.64 | 15.20 | 15.23 | 15.44 | 15.79 |
| Mass (g) | Fall | 7.35 | 7.53 | 7.42 | 7.38 | 7.28 | 7.34 | 7.53 | 7.58 | 7.30 |
| | Spring | 7.07 | 7.25 | 7.04 | 7.14 | 6.75 | 6.50 | 6.92 | 6.31 | 6.80 |

Note: P.L. = plastron length. Mean body sizes were calculated using nest averages.

Table 5

Survivorship and Recapture Probability Estimates Predicted by the Model of Best Fit

| <i>Survivorship</i> | <i>Age Class</i> | <i>ϕ Estimate</i> | <i>Season</i> |
|---------------------|------------------|---|---------------|
| | Age 1-3 | 0.4013 (SE \pm 0.0533) | Fall |
| | | 0.4678 (SE \pm 0.0626) | Spring |
| | Age 3-7 | 0.7078 (SE \pm 0.1070) | Combined |
| <i>Recapture</i> | <i>Age Class</i> | <i>ρ Estimate</i> | <i>Season</i> |
| | Age 2 | 0.9331×10^{-3} (SE \pm 0.6704×10^{-3}) | Combined |
| | Age 3 | 0.01211 (SE \pm 0.005071) | Combined |
| | Age 4 | 0.1919 (SE \pm 0.03015) | Combined |
| | Age 5 | 0.5270 (SE \pm 0.06002) | Combined |
| | Age 6 | 0.3667 (SE \pm 0.08848) | Combined |
| | Age 7 | 0.1846 (SE \pm 0.08246) | Combined |

Table 6

AICc, $\Delta AICc$, and Model Likelihood Values of MARK Models

| | <i>AICc</i> | $\Delta AICc$ | <i>Model Likelihood</i> | <i>Phi Model Description</i> |
|------------|-------------|---------------|-------------------------|---|
| Model 1 | 2271.4491 | 0.0000 | 1.0000 | season*age _(1-3 yrs old) , age _(4-7 yrs old) |
| Model 2 | 2273.4531 | 2.0040 | 0.3672 | season*age _(1-3 yrs old) , season*age _(4-7 yrs old) |
| Null Model | 2274.5071 | 3.0580 | 0.2168 | age _(1-3 yrs old) , age _(4-7 yrs old) |

Note: A model description is provided for each model. A likelihood ratio test was used to test for the significance of the effect of season by comparing the model of best fit, Model 1, to the Null Model lacking the effects of season.

Discussion

The Poplar Island population of *M. terrapin* displays facultative emergence in which fall emergence is more common than emergence in the spring. Fall emergent nests also have greater within-nest survivorship than spring emergent nests. Although a greater number of fall emergent hatchlings successfully developed, emerged, and were recaptured, a higher proportion of spring emergent hatchlings were recaptured (fall: 3.13%, spring: 5.32%). This suggests that spring emergent hatchlings have greater survivorship than fall emergent hatchlings. When modeled in MARK, estimated ϕ values supported this observation. Survival for the first three years of life differs between fall and spring emergers (ϕ from 0.4013 and 0.4678 during fall and spring respectively) and increases in subsequent years to 0.7078. This shift is due to an ontogenetic habitat shift from a semi-terrestrial life stage into a fully aquatic life stage. Factors that influence survival such as predation change when this shift occurs. A higher survivorship suggests that there is increased immunity from predators during the aquatic life stage of older juveniles and adults.

Many avian species that prey upon hatchlings, including herons and cormorants, follow an annual schedule of migration and reproduction which could select for *M. terrapin* emergence. *M. terrapin* spring emergence occurs from late March to early May (Baker et al. 2006; W.M. Roosenburg, personal communication, December 12, 2014) which partially overlaps with the arrival of cormorants, herons, and other predatory birds in April and May (King et al. 2012). Early emerging spring hatchlings may be able to find shelter and develop a behavioral familiarity with a new habitat before many of the predators arrive. Fall emergence occurs in early August and continues to the beginning of November (Baker et al. 2006; W. M. Roosenburg, personal communication, December 12, 2014) when cormorant and heron fledglings have begun foraging. There are both great blue heron and cormorant rookeries in the Poplar Island Archipelago in addition to nesting egrets, night herons, and four species of sea gull. Most of the migratory bird predators depart mid-September through late October to overwinter south (King et al. 2012). These birds do not return to the island until late April when much of the spring emergence is complete. Consequently, this may lead to increased danger of fall emergent predation before the hatchlings hibernate for the winter. Survivorship may also be higher for spring emergent hatchlings because they reduce the possibility of encounters with predators. By staying underground in the fall, spring emergent individuals have removed weeks of exposure to predators that fall emergent individuals face (Costanzo et al. 2008).

Though fall emergent hatchlings may be more susceptible to predation, the beneficial within-nest survival (Table 3) may be why fall emergence is a more common strategy for *M. terrapin* even though spring individuals have higher rates of survival once

emerged (Table 5). Spring emergent nests may have a lower within-nest survivorship on average due to hazards associated with overwintering, such as dehydration and injury from cold (Reviewed in Costanzo et al. 2008). They may also have a lower within-nest survivorship due to the longer period of time before collection. This may have impacted the spring of 2013 and 2015, where researchers were able to be present on site during the emergence of overwintering individuals. Delayed collection allowed for the natural emergence of hatchlings, introducing error and allowing for a greater chance of hatchling escape. Hatchlings escaping due to a longer time span in the nesting environment would artificially lower within-nest survivorship. To reduce issues associated with this error, nests in which hatched egg shells but no hatchlings were found were counted as successful.

Along with seasonal differences, within-nest survival also differed among years. Some years had high levels of predation by deer mice, king snakes, or fox that arrived at Poplar Island when the Poplar Island Sound had frozen over during cold winters. Differences in weather patterns among years can also impact within-nest survival if atypical temperatures or precipitation are encountered for extended periods of time. For example, 2010 was abnormally hot and dry during the nesting season at Poplar Island (NOAA 2016). Within-nest survival was unusually low that year, especially for overwintering individuals (Figure 3). Available nesting sites have shifted throughout time on Poplar Island as vegetation spread and construction progressed. The dynamic nature of nesting sites allows for the creation of new nesting locations while old nesting spots may become less suitable.

Soil types within these varying nesting sites may also affect overwintering and success of *M. terrapin* nests by affecting the microhabitat present during development and hibernation. The availability of water exchange in nesting substrate can increase gas exchange allowing for greater oxygen availability, though moisture that is held in soils can act as a buffer from sudden changes in temperature (Reviewed in Costanzo et al. 2008). Sandy soil along beaches, which is the preferred nesting substrate of *M. terrapin* (Roosenburg et al. 2014), maintains a higher water potential (Roosenburg and Dennis 2005) and is less compact than many inland nesting sites. Inland nesting sites which contain soil with less sand could inhibit fall emergence due to the difficulty of breaking through the hard surface (Roosenburg et al. 2003). Sandy soils can also influence inoculative freezing in terrestrially hibernating turtles by allowing for the presence of ice nucleating agents in hibernacula. A study by Graham found that fall emerging nests on Poplar Island had both a lower bulk density and more inorganic ice nucleating agents than spring nests, which could allow for easier emergence in the fall and disadvantageous natal nest hibernacula (2009). Though soil types influence hibernation, there is little evidence that supports overwintering individuals avoid certain soil types for terrestrial hibernation (Reviewed in Costanzo et al. 2008).

Like the many complexities involved with survival and nest success, the seasonal size differences in hatchling *M. terrapin* are also influenced by a number of factors. At the time of emergence, spring hatchlings typically have a shallower height and a less mass than fall emergent hatchlings (Table 4). Hatchling height is likely a function of developing in an oval shaped egg and maturing into a dorsally compressed turtle after

hatching. At measurement upon emergence, flatter spring individuals have been out of the egg for months hibernating within their natal nest while fall individuals emerge within days of hatching and are still affected by the constraint of developing in an oval egg shape, potentially resulting in larger fall heights. Mass and height may also be seasonally different due to the greater presence of a yolk sac during fall emergence. Fall individuals are often observed with an external yolk sac upon emergence, whereas it is less common in spring emergent *M. terrapin*. Even after the plastron closes and the yolk is internalized, it has yet to be fully absorbed. The temporal difference in spring and fall emergence may allow for greater yolk absorption in spring hatchlings, resulting in a smaller height and mass. The seasonal difference in mass also suggests that hatchlings use up some of the residual lipids contained in the yolk while in the natal nest. This would allow for the development and maturation of tissues important for the neuromuscular mechanics of locomotion, potentially benefitting these spring hatchlings with higher survivorship. Furthermore, desiccation throughout the winter months also impacts hatchling height and mass.

As a result of the ontogenetic habitat shift observed for *M. terrapin*, the first three years of life have very low estimated recapture rates (Table 5). This was confirmed during sampling on Poplar Island, as 1-3 year olds were not commonly recaptured. The demographic sampling methods used in this study target aquatic habitats where *M. terrapin* spend the majority of their lives. Fyke nets and turtle traps were placed in salt marshes or in shallow open water habitats and were intended to capture older juveniles or adults. The nets and traps often have a mesh size that hatchling or young juvenile *M.*

terrapin would be able to slip through in the event that they entered a net or trap, along with other bycatch. Young juvenile *M. terrapin* have been most successfully recaptured by rolling over the rack under which they hide along the shorelines of salt marshes. After the third year of life when *M. terrapin* become more aquatic, the recapture rate greatly increases and then gradually decreases with each additional year (Table 5). This gradual decrease could be due to the mortality of marked individuals or to movement away from the sampling areas. However, these older age classes are underrepresented in this data set. Broadly, the trends noted in this study are also limited to the scope of a single study site. The proportion and effects of facultative emergence may vary among sites. The terrapin's large distribution allows for differences in emergence strategy with northern populations displaying facultative emergence and southern populations emerging from their nests in the fall. *M. terrapin* populations within their northern range may vary how facultative emergence is displayed as factors such as climate, predator presence, and nesting environment vary spatially and temporally across latitudes.

In summary, *M. terrapin* hatchlings in northern distributions, including the population on Poplar Island, display facultative emergence. Each year on Poplar Island, more nests emerge in the fall than in the spring. Fall emergent nests also have greater within-nest survivorship. This results in a greater number of hatchlings each fall than in the spring. Though fall emergence is the more common strategy, spring emergent hatchlings have a greater chance of survival. I believe this could be due in part to predation pressures such as increased predator presence and exposure in the fall, or to increased avoidance ability in spring emergent hatchlings. Further demographic studies

on additional species and at additional sites could provide insight as to whether spring emergence consistently has higher survivorship in turtles with facultative emergence. Though we predict predation plays an important role, specific factors that influence the difference in *M. terrapin* survivorship between emergent seasons have yet to be determined.

CHAPTER 2: PERFORMANCE OF *MALACLEMYS TERRAPIN* HATCHLINGS:
VARIATION IN SEASONAL EMERGENCE

Abstract

Variation in development and emergence timing is prevalent throughout turtle species. Temperate species typically develop during the warmer time of the year but emerge during either fall or spring. The Diamond-backed Terrapin (*Malaclemys terrapin*) is one of a few species that has a facultative emergence where some hatchlings emerge from their nest in the fall and others overwinter within their nest and emerge in the spring. I studied performance metrics of fall and spring emerging *M. terrapin* hatchlings on Poplar Island, Maryland, to evaluate why spring hatchlings have higher survivorship than those that emerge in the fall (Chapter 1). Hatchling performance metrics associated with seasonal emergence strategies that may lead to increased survival within their environment were previously uninvestigated. I examined individual hatchling righting behavior, aquatic and terrestrial burst speed, and aquatic and terrestrial endurance as fitness proxies that correspond to survivorship differences between fall and spring emergent hatchlings from the 2014 nesting season. I compared performance between fall and spring emergent hatchlings using ANCOVAs, MANOVAs, and linear mixed models (LMMs). To determine the significance of season of emergence, LMMs of best fit including season were compared to a null model lacking the influence of season using likelihood ratio tests (LRTs). It was found that spring emergent *M. terrapin* hatchlings had higher endurance and burst speed in both terrestrial and aquatic trials (LRT, $\chi^2_{(6)} = 19.8286$, $P < 0.0005$ for terrestrial burst speed, $\chi^2_{(6)} = 59.5301$, $P < 0.0001$ for aquatic

burst speed, $\chi^2_{(6)} = 225.2065$, $P < 0.0001$ for terrestrial endurance, and $\chi^2_{(4)} = 53.7214$, $P < 0.0001$ for aquatic endurance) with season acting as an explanatory variable within the best fit model for both terrestrial and aquatic endurance tests (LMM, $T_{(38,198)} = 2.2450$, $P < 0.05$ and $T_{(39,313)} = 3.2483$, $P < 0.005$, respectively). Righting behavior also differed between season of emergence, with fall emergent individuals having a shorter latency time and total time to right than spring emergent individuals (LRT, $\chi^2_{(6)} = 17.8304$, $P < 0.005$ and $\chi^2_{(6)} = 17.7480$, $P < 0.005$, respectively). The spring hatchling advantage in speed and endurance could contribute to higher spring survival by aiding in predator avoidance and foraging abilities. Spring hatchlings are also older and more developed than fall hatchlings upon emergence, potentially contributing to the pattern of increased locomotor abilities. The seasonal difference in righting behavior could be due to a difference in predator avoidance strategy, with fall emergent hatchlings righting themselves quickly to escape predation in warmer temperatures and spring emergent hatchlings remaining motionless in cooler temperatures to avoid the attention of predators. Fall and spring hatchlings emerge into very different biophysical and predator environments between the two seasons. These performance differences can translate into fitness differences that allow for the persistence of facultative emergence as a strategy in temperate turtle species.

Introduction

Variation in developmental and emergence timing is prevalent among turtle species (Chapter 1). Among temperate turtle species, development corresponds to the warm months of the year, however, emergence timing can vary (Constanzo 2008). Some

temperate species' hatchlings emerge exclusively in the fall (e.g. snapping turtles) and others overwinter and emerge in the spring (e.g. painted turtles). Relatively few temperate species have plastic emergence behavior with both fall and delayed spring emergence within the same population (Chapter 1). This strategy allows spring hatchlings to emerge at an older age than the fall hatchlings from the same nesting season. In species that display facultative emergence, the proportion of nests producing fall or spring emergent hatchlings vary annually (Lovich et al. 2014; Chapter 1) and little is known about the cues that trigger emergence or in situ overwintering (Graham 2009). Nonetheless, the cues that trigger emergence and the environmental conditions that affect fitness may differ also between fall and spring hatchlings.

Overwintering is suspected to be common in species that have seasonally variable emergent environments, extended nesting seasons, unfavorable food availability upon hatching, and higher survivorship for hatchlings that remain in the nest compared to typical fall emergence (Gibbons and Nelson 1978). Gibbons and Nelson (1978) hypothesized that delayed emergence will be favored in species with highly unpredictable fall environments, suggesting that spring hatchlings wait for a seasonal change indicating favorable conditions in the spring where the benefits of overwintering outweigh the costs. Baker et al. (2013) also found that emergence strategies often correspond to favorable conditions for the hatchlings, such as lowered risk of predation or advantageous temperatures for emerging ectotherms, further supporting the Gibbons and Nelson (1978) hypotheses.

Malaclemys terrapin, the Diamond-backed Terrapin, typically displays fall emergence in its southern range and facultative emergence in its northern range (Ultsch 2006; Gibbons 2013). Overwintering in populations has been noted in multiple studies along the Atlantic coast including in New York (Scholz 2007), New Jersey (Baker et al. 2006), and South Carolina (Hildebrand 1928), and has been suggested as far south as northern Florida though these data were inconclusive (Butler et al. 2004). *M. terrapin* hatchlings live semi-terrestrially, occupying the edges of brackish water marshes throughout the beginning of their juvenile stage (Roosenburg et al. 2003). As adults, *M. terrapin* are fully aquatic apart from female nesting activity (Yearicks et al. 1981; Roosenburg 1994; Gibbons et al. 2001).

On the Paul S. Sarbanes Ecosystem Restoration Project at Poplar Island (herein Poplar Island) in Talbot County, Maryland, spring emergent *M. terrapin* hatchlings have higher survivorship than individuals that emerge in the fall (Chapter 1). Factors that influence this difference in survival between emergent seasons are unknown. High performance abilities can potentially increase survivorship by enhancing predator avoidance and limiting exposure to high risk microhabitats such as those with severe temperatures; both are major sources of hatchling mortality (Janzen et al. 2000).

Classically, performance metrics have been used as fitness proxies (Van Berkum et al. 1989; Delmas et al. 2007). In the vulnerable hatchling life stage where turtles do not actively defend themselves, locomotor abilities such as righting, sprint speed, and endurance can increase survivorship by aiding in predator avoidance. Performance can be highly repeatable (Van Berkum et al. 1989; Holem et al. 2006) and plays a large role in

carrying out behaviors which are important for survival and reproduction. Performance has been studied in a wide array of taxa, including lizards (Bennett et al. 1984; Huey and Bennett 1987; Huey et al. 1989; Van Berkum et al. 1989), salamanders (Shaffer et al. 1990), mice (Dlugosz et al. 2009), and turtles (Dial 1987; Janzen et al. 2000; Rivera et al. 2010) and is an ecologically relevant trait that influences fitness (Van Berkum et al. 1989).

Many aspects of a turtle's ecology influence its locomotor performance. Dial (1987) examined *Caretta caretta* hatchling frenzy behavior and the energetics associated with the rapid journey from their nest to the surf. Dial found that anaerobic metabolism supports part of the energetic demands of the fast terrestrial burst speeds displayed by *C. caretta* during the hatchling frenzy. This is a physiological adaptation supporting a locomotor performance for predator avoidance in hatchlings (1987). Janzen et al. (2000) studied the selection of predators on size in hatchling *Trachemys scripta*. After a mark-recapture study using a drift fence with pitfall traps and field searches to relocate released individuals, Janzen et al. found that larger *T. scripta* hatchlings were more likely to be recaptured than small hatchlings (2000). They suggest that this size difference is due to differential mortality caused by size dependent predation, with larger individuals displaying locomotor capabilities that increased predator avoidance (Janzen et al. 2000).

Rivera et al. (2010) compared the hydrodynamic stability of a four-limbed rowing type of aquatic locomotion found in *Chrysemys picta* to forelimb flapping locomotion in other rigid-bodied tetrapods. This study suggests that aquatic stability is greater in animals like *C. picta* that use asynchronous rowing compared to synchronous rowing

used by sea turtles. Though turtles are not as stable in the water as other rigid-bodied tetrapods, their morphology allows for greater control over directionality. This suggests that the energetic costs associated with low stability may be less important than speed and maneuverability (Rivera et al. 2010). A multitude of factors such as energetics, size, locomotor style, and morphology can directly affect the locomotor performance of turtles.

In this study, I compare fall and spring emergent *M. terrapin* hatchling locomotor performance to determine if variation in ability exists between emergence seasons. Is *M. terrapin* hatchling performance repeatable? If so, do factors such as temperature or season of emergence influence locomotor performance repeatability? Repeatability between trials can indicate whether tests of performance are appropriate fitness proxies. Furthermore, do spring emergent *M. terrapin* hatchlings perform better than fall emergent hatchlings? If so, this could be an important factor influencing the survivorship difference between fall and spring emergence.

Materials and Methods

Study Site

Poplar Island is part of an archipelago in the Chesapeake Bay in Maryland (Figure 1). The Project at Poplar Island led by the U.S. Army Corps of Engineers and the Maryland Port Authority aims to provide a deposition site for dredged substrate from the Baltimore Approach Shipping Channel and to restore wetland and upland habitats (Burton; Bailey 2011). Poplar Island is protected by stone revetment dikes that surround six large containment cells. These cells house the dredged material and provide substrate

needed for habitat creation. Two areas of Poplar Island are sandy beaches. One is found in an area outside Cell 3 where a natural sandy beach has formed outside the perimeter dike and a second area is in Cell 5 and the Notch, a protected area where the perimeter dike is made of sand (Figure 2; Roosenburg et al. 2014). *M. terrapin* use these beaches for nesting and due to the lack of mammalian nest predators, nest success is high compared to nests found on the mainland (Roosenburg 1994). Because of this comparatively high nest success and the annual presence of facultative emergence, Poplar Island is an excellent system to study seasonal emergence strategies.

Hatchling Collection

I walked known nesting areas on Poplar Island (see Figure 2; Roosenburg et al. 2014) daily from May 12 to August 8, 2014 for signs of terrapin nests, including tracks, disturbed substrate, or displaced sand on vegetation. The nest presence was established by excavating the nest and exposing eggs. The GPS location of each nest was identified and recorded using a Garmin eTrex GPS (Roosenburg et al. 2014). A 1.25cm wire mesh held by four survey flags was placed over the nest to protect it from avian predators and mark its presence. After approximately 50 days of incubation, aluminum flashing (with a 0.5-0.75 meter circumference and 20 cm height) was inserted around the nest with a 1.25cm wire mesh secured on top (Roosenburg et al. 2014) to prevent avian hatchling predation. The rings trapped emerging hatchlings which were collected and brought to the lab for processing.

During processing, each hatchling's marginal scutes were notched specific to cohort and emergence season. Hatchlings were also marked with individually numbered

Northwest Marine Technologies[®] coded wire tags. These coded wire tags were subcutaneously injected in the right rear limb using a 25-gauge needle and were used for presence and absence identification during recapture. Plastron length, carapace length, width, height, and mass were recorded for each hatchling before they were released on site (Roosenburg et al. 2014).

Fall emergent hatchlings were collected between 4 August, 2014 and 3 September, 2014 and overwintering hatchlings between 6 April, 2015 and 22 May, 2015. Thirty-two individuals were randomly selected from each emergent season (a maximum of two individuals per clutch) and tested for righting behavior as well as aquatic and terrestrial burst speed starting within a few days of emergence. From these thirty-two individuals, I selected twenty from each season to undergo aquatic and terrestrial endurance trials. For this selection, one individual was randomly selected from each clutch, then an additional four individuals were selected from the remaining group to total twenty. Individuals with severe shell deformities or large unabsorbed yolk sacs were excluded from trials due to potential impacts on performance ability (Burger 1976). Collected hatchlings were housed in 5 gallon aquaria in a holding facility with minimal temperature control and natural lighting. They were fed TetraFauna ReptoMin Baby food pellets daily as soon as they started showing signs of feeding. I returned the hatchlings to the original site of capture after test completion.

Performance Metrics

Performance of spring and fall emergent *M. terrapin* hatchlings was tested to compare locomotor ability between seasons. The thirty-two hatchlings collected from

each season were tested at three temperatures: 20, 26, and 32°C. I placed hatchlings in a Percival® Scientific Inc. I-30 Series Incubator for a minimum of one hour prior to trials to adjust body temperature to the test temperatures (Ben-Ezra et al. 2008). Locomotor metrics included aquatic and terrestrial burst speed, aquatic and terrestrial endurance, and righting behavior.

Righting Behavior

To observe righting behavior, a 40cm x 20cm x 27cm glass tank was filled with 2cm of moist sand to mimic the natural environment and provide traction for righting (Elnitsky and Claussen 2006). To begin the test, each individual was placed on its carapace. Following hatchling placement, I immediately moved out of view to minimize interference. Behavior was filmed with a Panasonic LUMIX® DMC-TS3 camera at 30 frames per second (fps). Total righting time started immediately after placement and stopped after the individual had completely righted itself. Latency time was recorded as the time between placement and the initiation of righting (when the head or a limb came in contact with the substrate and body movement began). Time to right was recorded at the initiation of righting until the individual was upright and the plastron was flat on the substrate (Delmas et al. 2007). Total righting time was the sum of latency time and time to right for each individual. Three replicates were done, at least 15 minutes apart, for each individual at each temperature.

Burst Speed

For terrestrial burst speed, a 1.2m x 10cm x 10cm linear race track constructed out of ¼ inch Plexiglas was lined with a 2cm deep substrate of moist sand to provide traction

and simulate typical environmental conditions. I placed this track next to a 5cm x 5cm grid for spatial reference purposes. All trials were video recorded from above using a mounted Panasonic LUMIX[®] DMC-TS3 camera at 30 fps. For each trial, an individual was placed on one end of the track and chased to encourage maximum speed toward the opposite end of the track. Timing began when the hatchling crossed a starting line 10cm at the beginning of the track and stopped when it crossed the finish line, 10cm from the end of the track (Ben-Ezra et al. 2008). Velocity was determined by dividing the distance travelled by the time it took for each 10cm segment and the fastest velocity for each trial was used. I used the same experimental set up to determine aquatic burst speed. The track was filled with water approximately 7cm deep was placed on a 5cm x 5cm grid for spatial reference. Water temperature was maintained at the test temperature using a Neslab Endocal RTE-100 Refrigerated Bath/Circulator. Each individual underwent three trials, at least 15 minutes apart, at each temperature.

Endurance

I tested terrestrial endurance on a treadmill with three 44cm x 8cm lanes. Individuals were set on the treadmill set to a speed of 0.08m/s and tapped to initiate forward movement (Elinitsky and Claussen 2006). The hatchlings were timed until they failed to maintain speed and made contact with the back of the treadmill for thirty continuous seconds despite encouragement. Three trials were done on each individual, at least one day apart, for each temperature.

To test aquatic endurance, a recirculating flow tank with a 50cm x 10cm x 10cm testing chamber was constructed out of ¼ inch Plexiglas (Elinitsky and Claussen 2006;

Vogel and LaBarbera 1978). The water was set to a velocity of 0.09m/s and maintained at the testing temperature using a Neslab Endocal RTE-100 Refrigerated Bath/Circulator. Water velocity was confirmed by measuring the speed of neutrally buoyant object placed in the recirculating flow tank averaged over eight trials. An individual was placed in the contained test-space and tapped to encourage forward movement. The hatchlings were timed until they failed to maintain speed and made contact with the back of the test-space for thirty continuous seconds despite encouragement. Two trials were done on each individual, at least one day apart, for each temperature. All endurance trials were video recorded from above using a mounted Panasonic LUMIX® DMC-TS3 camera at 30 fps.

Analyses

Videos were analyzed using Tracker v.4.87 to obtain data from the recorded trials. I organized and manipulated all data in Microsoft Excel. The statistical tests were run in RStudio v.0.98.501. Intraclass correlation coefficients (ICCs) and Spearman's rank repeatability correlation tests were used to analyze repeatability of each individual's trials (Davy et al. 2014). Analyses were performed using the *psych* package ICC() function for interclass correlation coefficients (Revelle 2013) and the *stats* package cor.test() function for the Spearman's rank repeatability correlation tests (R Core Team 2014). The ICC tests were run on all trials for each performance and produced a value, ranging between zero and one, with higher values indicating greater repeatability. The alpha level $\alpha = 0.05$ was used for all ICC tests. Davy et al. (2014) suggested rank repeatability must be demonstrated alongside high ICC values in order for a performance to be considered a suitable gauge for fitness. Therefore, Spearman rank correlation coefficients (r_s) for each

pair of trials (T1:T2, T2:T3, and T1:T3) were utilized to determine whether rank orders of individuals within each emergent strategy are correlated between trials (Davy et al. 2014). More significant correlations among pairs of trials indicated greater repeatability. The alpha level $\alpha = 0.05$ for Spearman rank correlation coefficient tests was adjusted using the Bonferroni correction to $\alpha = 0.0167$. Performances that display greater repeatability are more suitable fitness proxies.

Two-way repeated measures ANCOVAs were run using the *stats* package `aov()` function to determine the relationship between burst speed and endurance performance and season of emergence (R Core Team 2014). Season and temperature were used as independent variables and body size was the covariate. The dependent variables included the velocity or time of each performance for each individual. A MANCOVA was used to analyze righting behavior in respect to season using the *stats* package `manova()` function (R Core Team 2014). Latency time and time to right were included as the dependent variables. Mean trial time for each individual was used. Season of emergence and temperature were the independent variables and body size was a covariate. Assumptions were checked for each statistical test to verify the validity of the results obtained. Linear mixed models (LMMs) were run using the *nlme* package `lme()` function to explain variation in performance due to season of emergence, testing temperature, body size, and interactions between these variables (Pinheiro et al. 2013). Season of emergence was included as a variable in every model. A random intercept effect for each individual was included in each model to account for variation due to individual hatchling differences. An Akaike's Information Criteria (AIC) score was determined for the full model

including all variables and the interactions between those variables. This AIC score was compared to the AIC scores for each subset model, created by starting at the full model and removing factors in a stepwise fashion. The model with the lowest AIC score was determined to be the best fit model for each performance. Likelihood ratio tests (LRTs) were performed using the *nlme* package `anova()` function compare the model of best fit to a null model excluding the effects of season of emergence for each performance to determine the significance of season (Pinheiro et al. 2013). The best fit LMM was run for each performance to determine the magnitude of each explanatory variable. Alpha level for all tests was set a priori at $\alpha = 0.05$.

Results

ICC values indicate that endurance and speed were repeatable at each temperature during each emergence season (Table 7). Fall and spring righting behaviors were repeatable at each temperature except 20°C, where all three fall measurements of righting and spring time to right were not repeatable among trials. Overall, righting behaviors were less repeatable with lower ICC values than that of endurance and speed tests for each temperature for each emergent season. Generally, ICC values increased with temperature (Table 7).

Table 7

Intraclass Correlation Coefficients for Each Performance, Temperature, and Season

| <i>Performance</i> | Fall | | | Spring | | |
|-------------------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | <i>20°C</i> | <i>26°C</i> | <i>32°C</i> | <i>20°C</i> | <i>26°C</i> | <i>32°C</i> |
| Latency Time | 0.11 | 0.39* | 0.40* | 0.42* | 0.38* | 0.52* |
| Righting Time | 0.0009 | 0.18* | 0.31* | 0.42* | 0.12 | 0.52* |
| Total Righting Time | 0.10 | 0.39* | 0.41* | 0.42* | 0.39* | 0.52* |
| Terrestrial Burst Speed | 0.51* | 0.63* | 0.66* | 0.80* | 0.79* | 0.78* |
| Aquatic Burst Speed | 0.47* | 0.52* | 0.66* | 0.74* | 0.67* | 0.77* |
| Terrestrial Endurance | 0.77* | 0.93* | 0.87* | 0.90* | 0.92* | 0.93* |
| Aquatic Endurance | 0.46* | 0.66* | 0.83* | 0.93* | 0.83* | 0.91* |

Note: Intraclass correlation coefficients (ICCs) were calculated for each performance, at each temperature, for fall and spring emergent hatchlings. ICC values range between zero and one with higher values indicating a higher repeatability. *specifies significantly repeatable value with $P < 0.05$.

Spearman rank repeatability also suggests that aquatic endurance, terrestrial endurance, and aquatic burst speed were repeatable at all temperatures for both spring and fall emergent hatchlings (Table 8; Table 9). Terrestrial burst speed was repeatable except for in fall emergent hatchling trials at 20°C, where only two out of the three pairs of trials were correlated. Righting behavior repeatability does not seem to follow a seasonal or temperature trend. There was no case in which the three measured righting behaviors were correlated in all three pairs of trials. Latency time and total righting time had the same number or a greater number of correlated pairs of trials than time to right at every temperature and for each emergence season (Table 8; Table 9).

Table 8

Spearman Rank Repeatability for Each Performance and Temperature in the Fall

| <i>Performance</i> | 20°C | | | | 26°C | | | | 32°C | | | |
|--------------------|--------------|--------------|--------------|-------------------|--------------|--------------|--------------|-------------------|--------------|--------------|--------------|-------------------|
| | <i>T1-T2</i> | <i>T2-T3</i> | <i>T1-T3</i> | <i>Sig. Trial</i> | <i>T1-T2</i> | <i>T2-T3</i> | <i>T1-T3</i> | <i>Sig. Trial</i> | <i>T1-T2</i> | <i>T2-T3</i> | <i>T1-T3</i> | <i>Sig. Trial</i> |
| L | 0.232 | 0.639* | 0.121 | 1/3 | 0.592* | 0.730* | 0.378 | 2/3 | 0.453* | 0.535* | 0.285 | 2/3 |
| R | 0.353 | >0.001 | >0.001 | 0/3 | 0.194 | 0.372 | 0.032 | 0/3 | 0.393 | 0.385 | 0.429* | 1/3 |
| TR | 0.227 | 0.611* | 0.113 | 1/3 | 0.591* | 0.731* | 0.376 | 2/3 | 0.460* | 0.545* | 0.289 | 2/3 |
| TBS | 0.662* | 0.515* | 0.363 | 2/3 | 0.553* | 0.566* | 0.781* | 3/3 | 0.626* | 0.711* | 0.649* | 3/3 |
| ABS | 0.447* | 0.455* | 0.529* | 3/3 | 0.506* | 0.593* | 0.471* | 3/3 | 0.742* | 0.578* | 0.673* | 3/3 |
| TE | 0.817* | 0.865* | 0.627* | 3/3 | 0.961* | 0.959* | 0.917* | 3/3 | 0.950* | 0.856* | 0.831* | 3/3 |
| AE | 0.465* | - | - | 1/1 | 0.688* | - | - | 1/1 | 0.841* | - | - | 1/1 |

Note: L = latency time, R = righting time, TR = total righting time, TBS = terrestrial burst speed, ABS = aquatic burst speed, TE = terrestrial endurance, and AE = aquatic endurance. Three tests were done for each performance for each pair of Trial 1 (T1), Trial 2 (T2), and Trial 3 (T3). The number of significant correlations between trials is shown for each performance. Aquatic endurance only had two trials and therefore only has one correlative test. *specifies a significant correlation with $\alpha = 0.05$ adjusted with Bonferroni correction: $\alpha = 0.0167$.

Table 9

Spearman Rank Repeatability for Each Performance and Temperature in the Spring

| <i>Performance</i> | 20°C | | | | 26°C | | | | 32°C | | | |
|--------------------|--------------|--------------|--------------|-------------------|--------------|--------------|--------------|-------------------|--------------|--------------|--------------|-------------------|
| | <i>T1-T2</i> | <i>T2-T3</i> | <i>T1-T3</i> | <i>Sig. Trial</i> | <i>T1-T2</i> | <i>T2-T3</i> | <i>T1-T3</i> | <i>Sig. Trial</i> | <i>T1-T2</i> | <i>T2-T3</i> | <i>T1-T3</i> | <i>Sig. Trial</i> |
| L | 0.431* | 0.635* | 0.458* | 3/3 | 0.709* | 0.334 | 0.26 | 1/3 | 0.357 | 0.766* | 0.483* | 2/3 |
| R | 0.795* | 0.305 | 0.37 | 1/3 | 0.446* | 0.23 | 0.138 | 1/3 | 0.587* | 0.313 | 0.733* | 2/3 |
| TR | 0.431* | 0.636* | 0.463* | 3/3 | 0.709* | 0.337 | 0.268 | 1/3 | 0.356 | 0.766* | 0.484* | 2/3 |
| TBS | 0.798* | 0.868* | 0.774* | 3/3 | 0.737* | 0.837* | 0.820* | 3/3 | 0.838* | 0.789* | 0.753* | 3/3 |
| ABS | 0.715* | 0.817* | 0.687* | 3/3 | 0.685* | 0.785* | 0.559* | 3/3 | 0.755* | 0.807* | 0.737* | 3/3 |
| TE | 0.869* | 0.938* | 0.943* | 3/3 | 0.923* | 0.949* | 0.910* | 3/3 | 0.927* | 0.935* | 0.954* | 3/3 |
| AE | 0.934* | - | - | 1/1 | 0.827* | - | - | 1/1 | 0.914* | - | - | 1/1 |

Note: L = latency time, R = righting time, TR = total righting time, TBS = terrestrial burst speed, ABS = aquatic burst speed, TE = terrestrial endurance, and AE = aquatic endurance. Three tests were done for each performance for each pair of Trial 1 (T1), Trial 2 (T2), and Trial 3 (T3). The number of significant correlations between trials is shown for each performance. Aquatic endurance only had two trials and therefore only has one correlative test. *specifies a significant correlation with $\alpha = 0.05$ adjusted with Bonferroni correction: $\alpha = 0.0167$.

Season, temperature, and the interaction between season and temperature had an effect on hatchling performance for all tests of endurance and speed (repeated measures ANCOVAs, season: $P < 0.01$ for each; temperature: $P < 0.001$ for each; Table 10). Body size had an effect on terrestrial endurance and speed ($P < 0.01$ for each; Table 10), but not on aquatic performance ($P > 0.05$ for each; Table 10). The MANCOVA indicated that season, temperature, and body size had an effect on overall righting behavior, but the season*temperature interaction did not ($P < 0.001$ for season and size; $P < 0.05$ for temperature; Table 11). When analyzed separately, season and size affected latency time ($P < 0.001$ for each; Table 11), while temperature affected time to right ($P < 0.05$; Table 11). These data were non-normally distributed (Shapiro-Wilk test, *stats* package `shapiro.test()` function) and did not exhibit homogeneity in variance (Lavene's test, *car* package, `laveneTest()` function), violating assumptions of repeated measures ANCOVAs and MANCOVAs. Transformations did not improve the fit of the data, therefore linear mixed models were used to better test for a seasonal difference in hatchling performance.

Table 10

Repeated Measures ANCOVA Table Showing F and P Values for Each Performance

| <i>Performance</i> | <i>Season</i> | <i>Temperature</i> | <i>Size</i> | <i>Season*</i> <i>Temperature</i> | <i>d.f.</i> |
|----------------------------|---------------|--------------------|-------------|--------------------------------------|-------------|
| Terrestrial Burst Speed | 8.331* | 143.471** | 7.674* | 8.354* | 1, 506 |
| Aquatic Burst Speed | 107.516** | 196.179** | 0.186 | 8.883* | 1, 506 |
| Terrestrial Endurance | 113.170** | 402.460** | 54.450** | 172.410** | 1, 314 |
| Aquatic Endurance | 13.050** | 162.448** | 1.704 | 30.573** | 1, 195 |

Note: * $P < 0.01$ and ** $P < 0.001$

Table 11

MANCOVA Table Showing F and P Values for Each Performance

| <i>Performance</i> | <i>Season</i> | <i>Temperature</i> | <i>Size</i> | <i>Season*</i> <i>Temperature</i> | <i>d.f.</i> |
|----------------------|------------------------|------------------------|------------------------|--------------------------------------|-------------|
| Overall | 10.447*** | 3.550* | 16.626*** | 0.773 | 2, 186 |
| Righting Behavior | (Pillai's = 0.1010) | (Pillai's = 0.0368) | (Pillai's = 0.1517) | (Pillai's = 0.0082) | |
| Latency | 20.013*** | 2.787 | 30.556*** | 0.166 | 1, 187 |
| Time to Right | 1.133 | 4.244* | 2.596 | 1.373 | 1, 187 |

Note: Performance for each individual was averaged over three trials. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Pillai's Test values are shown for overall righting behavior.

For endurance, burst speed, latency time, and total time to right, the best fit linear mixed model included season as a variable. The best fit model was selected by choosing the model with the lowest AIC value. Aside from time to right, each model including season was favored over each null model lacking emergent season as an independent variable (LRT, aquatic and terrestrial speed and endurance, latency time, and total time to right $P < 0.005$; Table 12; Table 13) indicating that season of emergence significantly affects performance ability of *M. terrapin* hatchlings. Season did not have an effect on time to right (LRT, $P < 0.2819$; Table 12; Table 13). Righting behavior had a longer latency time and total righting time for spring emergent individuals (Table 14; Figures 4 and 5). Terrestrial and aquatic burst speed increased with temperature and was faster in the spring than in the fall (Table 14). Similarly, terrestrial and aquatic endurance was longer at higher temperatures and in the spring (Table 14). Though there is a seasonal effect for each performance but time to right, season of emergence did not always have significance as the explanatory variable within the linear mixed model (Table 15).

Table 12

AIC Values of Linear Mixed Models for Each Performance

| <i>Model</i> | <i>Latency</i> | <i>Righting</i> | <i>TR AIC</i> | <i>TBS AIC</i> | <i>ABS AIC</i> | <i>TE AIC</i> | <i>AE AIC</i> |
|--------------|----------------|-----------------|---------------|----------------|----------------|---------------|---------------|
| | <i>AIC</i> | <i>AIC</i> | | | | | |
| P~S*T*size | 8143.06* | 4706.99 | 8144.17* | 3129.09* | 3340.74* | 5855.85* | 4172.76 |
| P~S*T+size | 8152.19 | 4703.59 | 8153.65 | 3140.43 | 3341.15 | 5878.86 | 4172.12 |
| P~S*size+T | 8144.85 | 4704.70 | 8146.49 | 3150.29 | 3346.12 | 6039.28 | 4198.84 |
| P~S+T*size | 8145.68 | 4703.31 | 8146.86 | 3137.48 | 3351.22 | 6016.78 | 4199.86 |
| P~S+T+size | 8150.52 | 4702.98* | 8152.07 | 3148.30 | 3349.27 | 6043.37 | 4198.54 |
| P~S*T | 8164.01 | 4704.45 | 8165.78 | 3139.77 | 3341.26 | 5897.61 | 4170.75* |
| P~S+T | 8162.02 | 4703.61 | 8163.81 | 3147.67 | 3349.19 | 6083.74 | 4201.40 |
| P~S*size | 8145.67 | 4706.68 | 8147.68 | 3292.91 | 3527.25 | 6213.84 | 4300.00 |
| P~S+size | 8152.36 | 4704.86 | 8154.32 | 3290.95 | 3529.90 | 6226.11 | 4298.07 |
| P~S | 8166.03 | 4705.89 | 8168.36 | 3290.06 | 3528.79 | 6279.50 | 4312.31 |
| P~T*size | 8152.89 | 4702.62 | 8153.92 | 3140.91 | 3392.27 | 6073.06 | 4224.36 |
| P~T+size | 8158.17 | 4702.12** | 8159.56 | 3151.73 | 3390.32 | 6096.36 | 4222.47 |
| P~T | 8167.72 | 4702.75 | 8169.35 | 3151.29 | 3390.15 | 6114.77 | 4223.17 |

Note: P = performance, S = season, and T = temperature. The best fit seasonal model was compared to a null model lacking the effects of season of emergence using a likelihood ratio test. Seasonal models are located above the dotted line and null models without season are below the dotted line. TR = total righting time, TBS = terrestrial burst speed, ABS = aquatic burst speed, TE = terrestrial endurance, and AE = aquatic endurance. *specifies seasonal model of best fit as indicated by the lowest AIC value. Aside from righting, each performance's model of best fit including season is significantly better than the corresponding null model (LRT, $P < 0.001$; Table 13). **specifies model of best fit not including season. Though the non-seasonal model for righting has the lowest AIC value, it is not significantly different from the seasonal model of best fit (LRT, $P = 0.285$; Table 13).

Table 13

Linear Mixed Model of Best Fit and Likelihood Ratio Test Results for Each Performance

| | <i>Latency</i> | <i>Righting</i> | <i>TR</i> | <i>TBS</i> | <i>ABS</i> | <i>TE</i> | <i>AE</i> |
|---------|----------------|-----------------|--------------|--------------|--------------|---------------|--------------|
| Season | $T=0.340$ | $T=-1.062$ | $T=2.390$ | $T=-1.594$ | $T=0.085$ | $T=2.245$ | $T=-3.248$ |
| | $P=0.735$ | $P=0.292$ | $P=0.772$ | $P=0.116$ | $P=0.933$ | $P=0.031^*$ | $P=0.002^*$ |
| Temp | $T=-2.254$ | $T=-1.967$ | $T=-2.335$ | $T=1.481$ | $T=1.251$ | $T=-1.312$ | $T=5.196$ |
| | $P=0.025^*$ | $P=0.050^*$ | $P=0.020^*$ | $P=0.140$ | $P=0.212$ | $P=0.191$ | $P=0.000^*$ |
| Size | $T=-2.188$ | $T=-1.618$ | $T=-2.274$ | $T=1.389$ | $T=-0.0308$ | $T=-0.596$ | - |
| | $P=0.029^*$ | $P=0.106$ | $P=0.023^*$ | $P=0.166$ | $P=0.758$ | $P=0.551$ | - |
| Season: | $T=0.733$ | - | $T=0.777$ | $T=1.867$ | $T=-1.034$ | $T=-2.016$ | $T=5.906$ |
| Temp | $P=0.464$ | - | $P=0.437$ | $P=0.062$ | $P=0.302$ | $P=0.045^*$ | $P=0.000^*$ |
| Season: | $T=-0.325$ | - | $T=-0.280$ | $T=1.524$ | $T=-0.025$ | $T=-2.016$ | - |
| Size | $P=0.745$ | - | $P=0.780$ | $P=0.133$ | $P=0.981$ | $P=0.003^*$ | - |
| Temp: | $T=2.179$ | - | $T=2.255$ | $T=-1.178$ | $T=-0.896$ | $T=1.651$ | - |
| Size | $P=0.030^*$ | - | $P=0.025^*$ | $P=0.239$ | $P=0.371$ | $P=0.100$ | - |
| Season: | $T=-0.692$ | - | $T=-0.733$ | $T=-1.714$ | $T=1.180$ | $T=3.295$ | - |
| T:Size | $P=0.490$ | - | $P=0.464$ | $P=0.087$ | $P=0.239$ | $P=0.001^*$ | - |
| LMM | | | | | | | |
| d.f. | 63, 505 | 63, 509 | 63, 505 | 62, 506 | 63, 505 | 39, 313 | 38, 198 |
| | $x^2=17.830$ | $x^2=1.143$ | $x^2=17.748$ | $x^2=19.829$ | $x^2=59.530$ | $x^2=225.207$ | $x^2=53.721$ |
| LRT | $P=0.001^*$ | $P=0.285$ | $P=0.001^*$ | $P<0.001^*$ | $P<0.001^*$ | $P<0.001^*$ | $P<0.001^*$ |
| | d.f.=6 | d.f.=4 | d.f.=6 | d.f.=6 | d.f.=6 | d.f.=6 | d.f.=4 |

Note: T -values, P -values, and degrees of freedom (d.f.) for the best fit linear mixed model (LMM) for each performance are shown above the solid line. Chi squared values (x^2), P -values, and degrees of freedom for each likelihood ratio test (LRT) comparing the best fit model to a null model excluding season are shown below the solid line.

Table 14

Mean Performance for Spring and Fall Emergent Hatchlings at Each Temperature

| | <i>Latency</i> | <i>Righting</i> | <i>TR Time</i> | <i>TBS</i> | <i>ABS</i> | <i>TE</i> | <i>AE</i> |
|--------|-------------------|-------------------|----------------|-----------------|-----------------|--------------|--------------|
| | <i>Time (sec)</i> | <i>Time (sec)</i> | <i>(sec)</i> | <i>(cm/sec)</i> | <i>(cm/sec)</i> | <i>(sec)</i> | <i>(sec)</i> |
| Fall | 130 | 6.50 | 136.95 | 5.29 | 7.31 | 500 | 1336 |
| 20°C | (SE±43.62) | (SE±3.53) | (SE±43.68) | (SE±0.26) | (SE±0.36) | (SE±26) | (SE±95) |
| Fall | 46.57 | 1.32 | 47.89 | 7.67 | 8.65 | 1026 | 2524 |
| 26°C | (SE±12.11) | (SE±0.09) | (SE±12.11) | (SE±0.45) | (SE±0.46) | (SE±101) | (SE±235) |
| Fall | 62.33 | 1.93 | 64.25 | 8.50 | 11.90 | 1091 | 2772 |
| 32°C | (SE±9.63) | (SE±0.24) | (SE±9.69) | (SE±0.48) | (SE±0.62) | (SE±83) | (SE±288) |
| Spring | 257 | 2.80 | 260.65 | 6.62 | 12.78 | 1433 | 1986 |
| 20°C | (SE±39.21) | (SE±0.30) | (SE±39.30) | (SE±0.33) | (SE±0.44) | (SE±135) | (SE±136) |
| Spring | 216.91 | 1.79 | 218.69 | 9.85 | 18.58 | 2785 | 4963 |
| 26°C | (SE±34.82) | (SE±0.27) | (SE±34.88) | (SE±0.59) | (SE±0.58) | (SE±202) | (SE±320) |
| Spring | 194.87 | 1.35 | 196.22 | 11.89 | 19.83 | 5064 | 5730 |
| 32°C | (SE±37.94) | (SE±0.12) | (SE±37.96) | (SE±0.66) | (SE±0.74) | (SE±253) | (SE±304) |

Note: Mean values with standard error compared between spring and fall emergent hatchling *M. terrapin* for each performance at each testing temperature. TR is total righting time measured in seconds, TBS is terrestrial burst speed measured in centimeters per second, ABS is aquatic burst speed measured in centimeters per second, TE is terrestrial endurance in seconds, and AE is aquatic endurance in seconds.

Table 15

Results of the Best Fit Linear Mixed Model for Each Performance

| <i>Variable</i> | <i>Latency</i> | <i>Righting</i> | <i>TR</i> | <i>TBS</i> | <i>ABS</i> | <i>TE</i> | <i>AE</i> |
|------------------|----------------|-----------------|----------------|----------------|----------------|----------------|----------------|
| | <i>P-value</i> | <i>P-value</i> | <i>P-value</i> | <i>P-value</i> | <i>P-value</i> | <i>P-value</i> | <i>P-value</i> |
| Season | 0.7352 | 0.2923 | 0.7718 | 0.1159 | 0.9329 | 0.0305* | 0.0024* |
| Temp | 0.0246* | 0.0497* | 0.0199* | 0.1394 | 0.2116 | 0.1906 | 0.0000* |
| Size | 0.0291* | 0.1064 | 0.0234* | 0.1655 | 0.7584 | 0.5513 | - |
| Season:Temp | 0.4640 | - | 0.4374 | 0.0624 | 0.3017 | 0.0446* | 0.0000* |
| Season:Size | 0.7452 | - | 0.7795 | 0.1327 | 0.9805 | 0.0033* | - |
| Temp:Size | 0.0298* | - | 0.0246* | 0.2393 | 0.3709 | 0.0998 | - |
| Season:Temp:Size | 0.4896 | - | 0.4638 | 0.0872 | 0.2386 | 0.0011* | - |

Note: The *P*-values of the best fit linear mixed model for each performance including season as a variable. TR is total righting time, TBS is terrestrial burst speed, ABS is aquatic burst speed, TE is terrestrial endurance, and AE is aquatic endurance. A dash indicates that the metric was not used in the model. *specifies a significant *P*-value with $\alpha = 0.05$.

The full linear mixed model including season of emergence, testing temperature, and body size as the independent variables was the best fit model for both latency time and total time to right (Table 12). A model including season of emergence as the independent variable with testing temperature and body size as covariates was the best fit seasonal model for time to right (Table 12). Temperature explained most of the variation for all righting behavior trials, along with size and the temperature*size interaction for latency and total righting times (Table 15). Larger *M. terrapin* as well as fall emergent individuals righted themselves more quickly, with righting behavior generally occurring more quickly with increasing temperature (Figures 4 and 5).

The full linear mixed model including season of emergence, temperature, and size was the best fit for both terrestrial and aquatic burst speed (Table 12). For terrestrial endurance the full model was also the best fit model (Table 12). Additionally, a model including season of emergence and temperature as independent variables was the model of best fit for aquatic endurance (Table 12). Variation within aquatic and terrestrial endurance models were both explained by season of emergence (LMM, $P < 0.05$; Table 13). Temperature and season*temperature were significant explanatory variables for aquatic endurance trials (Table 15). Hatchlings which emerged in the spring or were larger could move faster and longer with increasing temperatures (Figures 6-9).

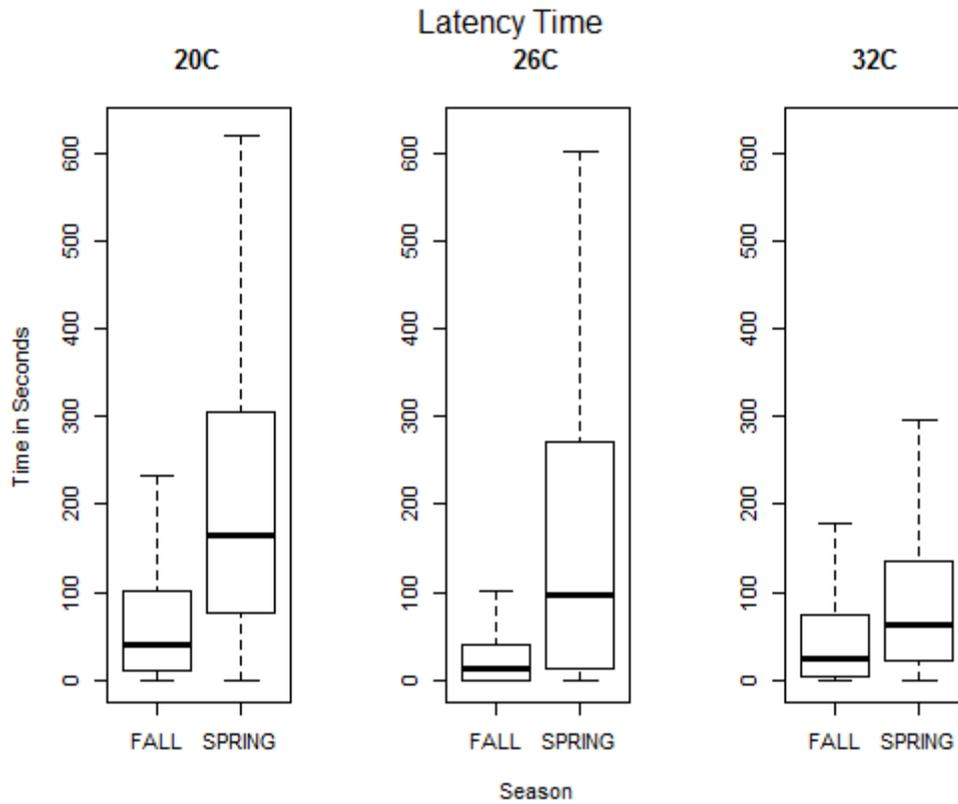


Figure 4. Box plots comparing latency time for fall and spring emergent hatchlings at 20, 26, and 32°C. Outliers were removed to allow for a better visual comparison of data.

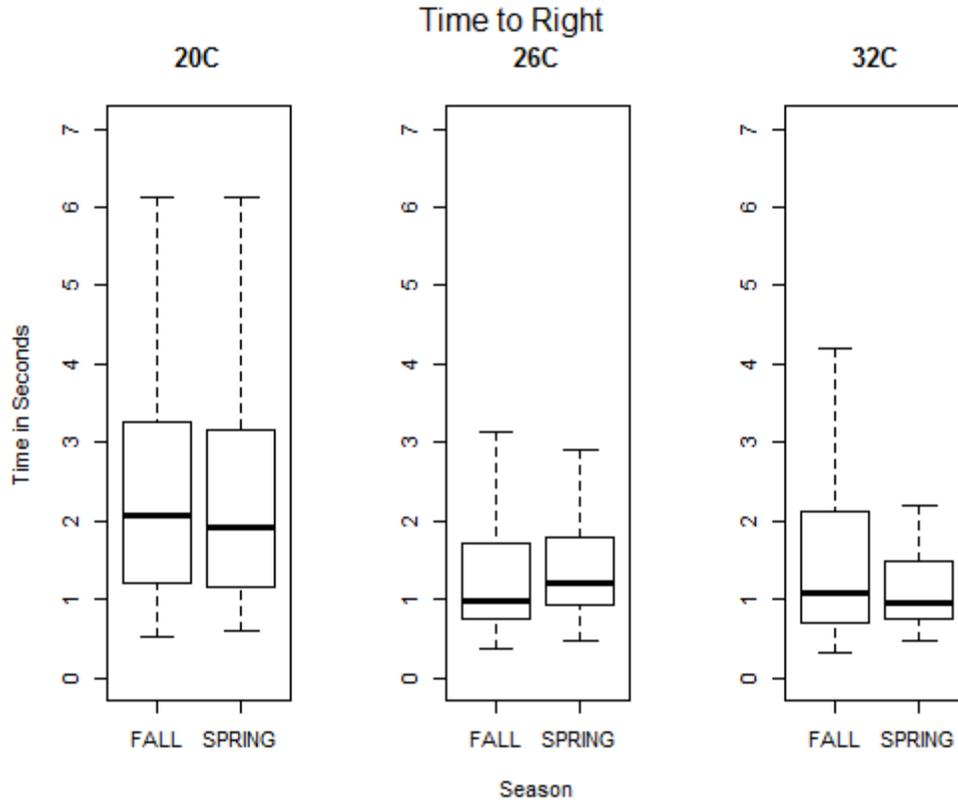


Figure 5. Box plots comparing time to right for fall and spring emergent hatchlings at 20, 26, and 32°C. Outliers were removed to allow for a better visual comparison of data.

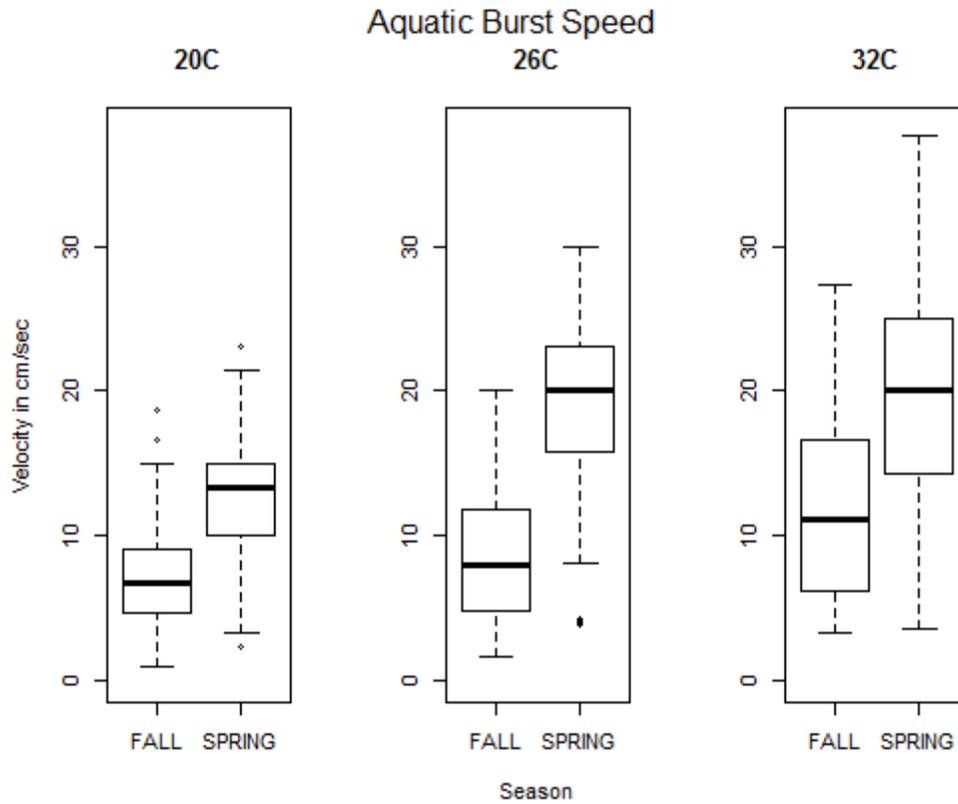


Figure 6. Box plots comparing aquatic burst speed for fall and spring emergent hatchlings at 20, 26, and 32°C.

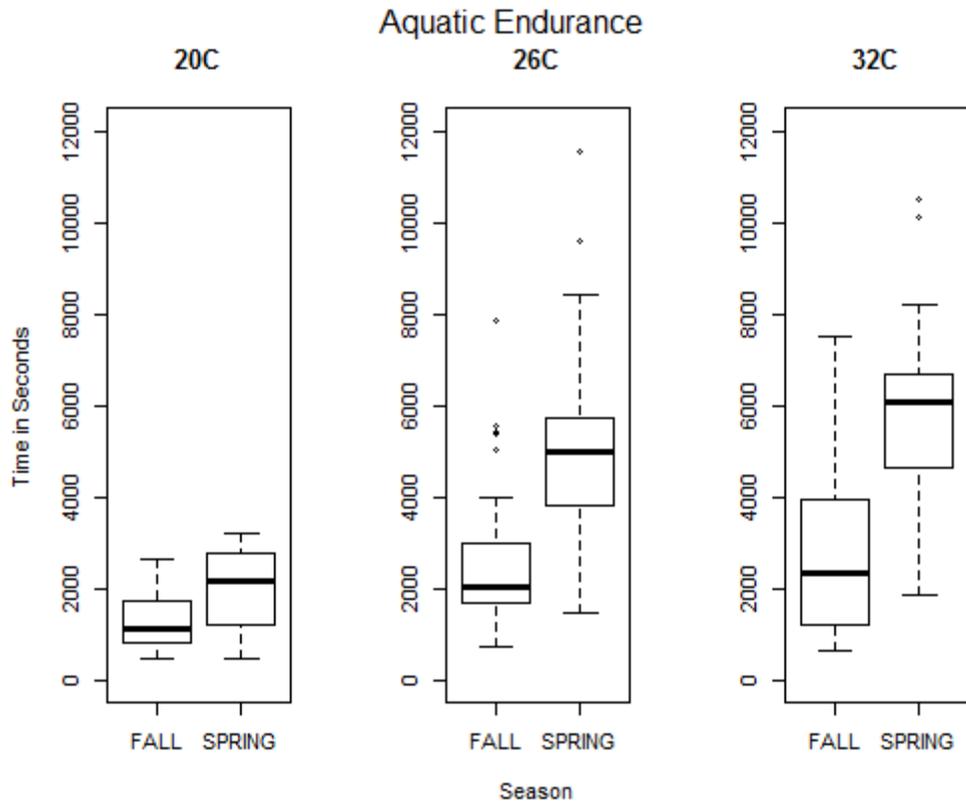


Figure 7. Box plots comparing aquatic endurance for fall and spring emergent hatchlings at 20, 26, and 32°C.

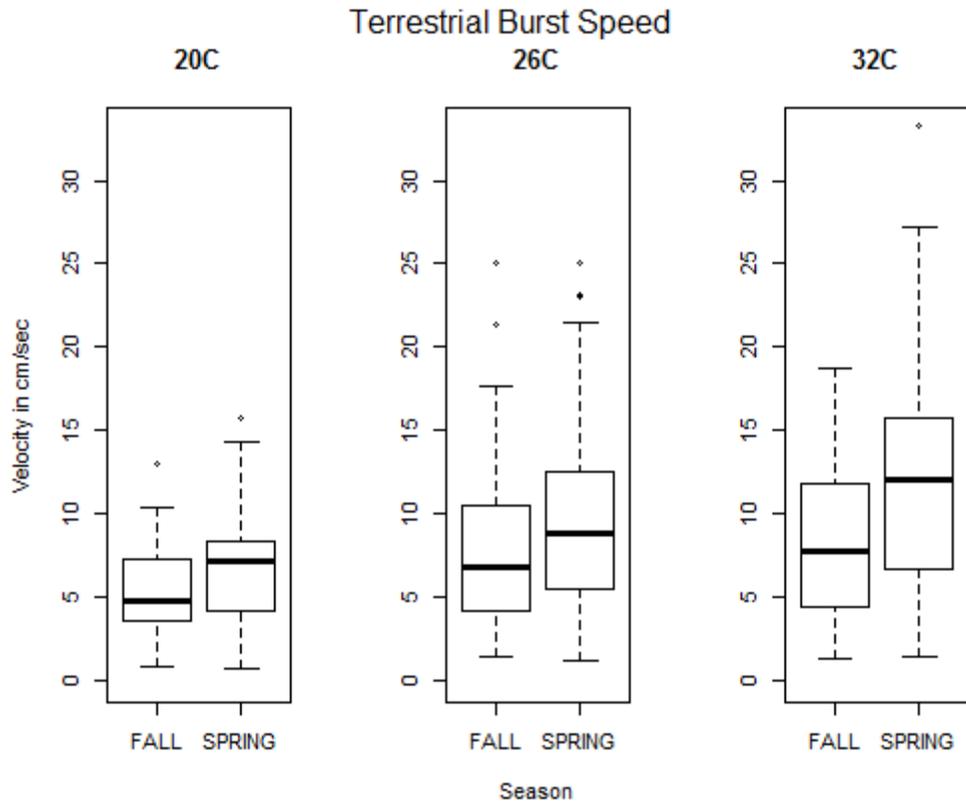


Figure 8. Box plots comparing terrestrial burst speed for fall and spring emergent hatchlings at 20, 26, and 32°C.

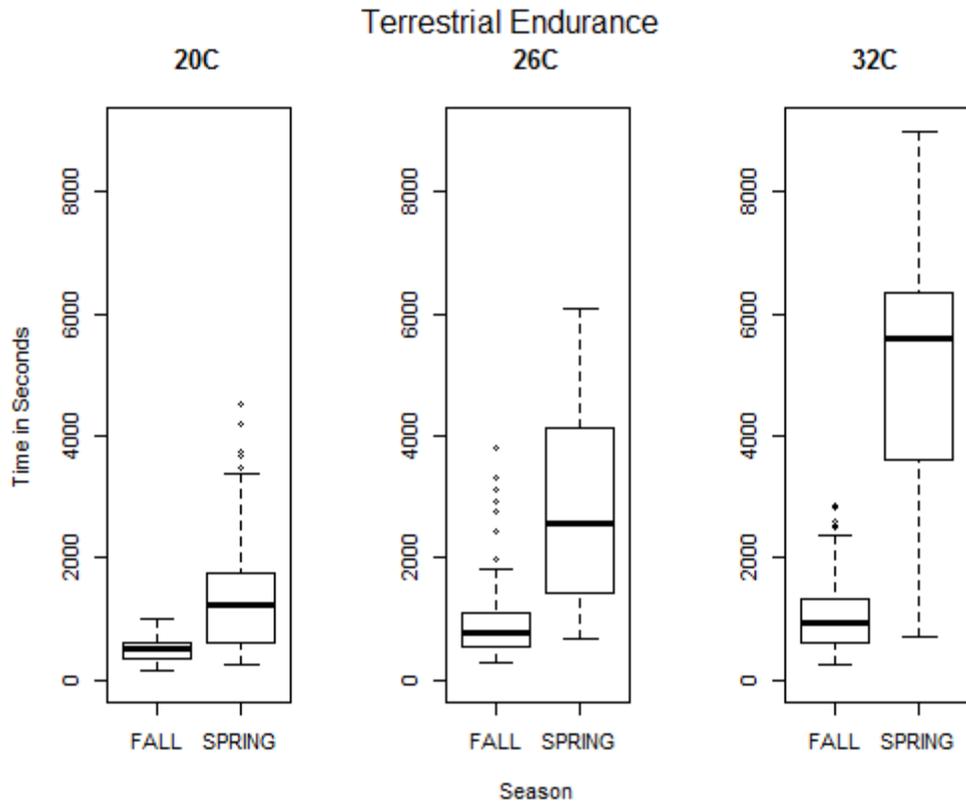


Figure 9. Box plots comparing terrestrial endurance for fall and spring emergent hatchlings at 20, 26, and 32°C.

Discussion

Tests of endurance and speed were repeatable across testing temperatures for both seasons of emergence (Table 7; Table 8; Table 9) and therefore, were appropriate tests of performance as a fitness proxy (Davey et al. 2014). ICC and Spearman rank repeatability tests indicated that latency time and total righting time are more repeatable than time to right, though no measure of righting behavior was as well supported as the speed and endurance tests as a measure of fitness (Table 7; Table 8; Table 9). For hatchling terrapins, righting behavior seems to be sporadic, with individuals varying the time they take to respond and the amount of time they spend in motion to physically right themselves. Instead of righting behavior being relative to the fitness of an individual, perhaps it is a plastic behavior for which the timing can change based on each situation encountered by the individual. Though righting behavior is a common measure of fitness in turtles (Elnitsky and Claussen 2006; Delmas et al. 2007; Domokos and Varkonyi 2008), these data suggest that it may not be applicable to all species, supporting the individual variability observed in Davy et al., 2014.

I found differences in performance of hatchling terrapins as a function of temperature and emergence season. Interestingly, spring emergent hatchlings had higher performance metrics than fall emergent hatchlings. Though fall emergence is the more common strategy for Poplar Island *M. terrapin*, spring emergent hatchlings had a higher survivorship (Chapter 1). After testing locomotor performance of Poplar Island individuals from the 2014 nesting season, spring emergent *M. terrapin* hatchlings were found to have higher endurance and faster burst speeds than fall emergent hatchlings in

both aquatic (Figures 6 and 7) and terrestrial trials (Figures 8 and 9). This association implies that hatchling locomotor performances, such as speed and endurance upon emergence, may be an important factor allowing for higher survivorship in better performing individuals. Overall righting behavior also differed between season of hatchling emergence. When each righting behavior performance was analyzed separately, the MANCOVA indicated that time to right did not differ by season. This was supported by the LRT performed on the best fit LMM indicating that season did not have a significant effect on time to right. Due to the violated assumptions of the MANCOVA test and the LMM's ability to better handle the non-normally distributed data, the LRT results have stronger support than the MANCOVA results. As suggested by the LRTs, righting behavior did not follow the same trend as other performances and was faster in the fall than in the spring.

Though trials started within days of emergence for both spring and fall individuals, the spring emergent hatchlings were older than the fall emergent hatchlings during testing. Both fall and spring emergent *M. terrapin* hatch in the fall. Spring emergent individuals overwinter within their natal nest while fall individuals emerge and hibernate terrestrially elsewhere (Costanzo et al. 2008; Chapter 1). This allows spring emerging hatchlings to have a longer development period between hatching and emergence. Height and mass are smaller in spring emergent hatchlings, suggesting that the residual yolk is absorbed while overwintering (Chapter 1). This extended development period results in a chance to fully incorporate yolk nutrients and a longer maturation period for body tissues involved in the neuromuscular mechanics of

locomotion. With this, age is confounded by emergence season but is likely an important factor in the seasonal variation seen in performance upon emergence.

Greater performance ability could allow for better predator avoidance and increased foraging success. Hatchling turtles do not have means to actively defend themselves from predators and thus avoidance through crypsis or escape are the best strategies for survival (Steyermark and Spotila 2001). On Poplar Island, greater spring hatchling performance in endurance and speed corresponds with a higher period of survival (Chapter 1). These differences in performance could contribute to the higher fitness in spring emergent hatchlings. In this case rapid escape, potentially toward an area to hide, may be the beneficial strategy for *M. terrapin* hatchlings upon emergence in a salt marsh habitat.

Within my data, latency time and time to right often show similar statistical results. This is due to total time to right being the combination of time to right and latency time. Time to right was often only a fraction of a second in duration. Mean righting times are below seven seconds across all testing temperatures, making up a very small portion of total righting time where means are tens to hundreds of seconds, depending on temperature (Table 15). A shorter latency time may be beneficial for an individual as decreasing latency time also decreases total righting time. This limits exposure to predators and increases the chance of escape (Elnitsky and Claussen 2006; Delmas et al. 2007). The ability to right quickly can also limit risks such as dehydration (Delmas et al. 2007). If this is the case for *M. terrapin*, as suggested by Burger (1976), fall emergent hatchlings would have the righting behavior fitness advantage over spring

emergent hatchlings (Table 14). However, a longer latency time could also benefit an individual by making them less conspicuous to a predator by limiting movement until danger has passed (Steyermark and Spotila 2001). If preventing attention from predators by limiting movement is a beneficial strategy for *M. terrapin*, spring emergent hatchlings would have a fitness advantage.

This suggests that within the Poplar Island population, there may be a divergence in hatchling *M. terrapin* righting behavior strategy corresponding to selective pressures in the emergent environment. Baker et al. (2013) found that emergence strategies often correspond to favorable conditions for the hatchlings, such as lowered risk of predation or advantageous temperatures for emerging ectotherms. For righting behavior in this facultative population, favorable conditions may be different depending on season of emergence. Disruptive selection occurs when extreme values of a trait are favored over intermediate values, resulting in bimodal phenotypes within a population. Though many studies have suggested that environmental cues play a role in emergence timing within the known emergence season for each species (Graham 2009; Baker et al. 2013; Gibbons 2013; Lovich et al. 2014), it is currently unknown whether an individual's emergent season within a facultative population is due to an environmental signal, the genes inherited by each individual (Gibbons 2013), or due to gene-environment interaction. On Poplar Island, there is a weak relationship between environmental cues and emergence timing (Graham 2009). Future genetic studies are necessary to determine the heritability of season of emergence and whether disruptive selection may be occurring in *M. terrapin* righting behavior strategies.

On Poplar Island, fall and spring emerging hatchlings face different predation regimes. Fall emergence occurs between August and early November during which fledgling cormorants and other young predatory birds have begun foraging. Fall emergence is the more common strategy in the Poplar Island population but results in slower hatchlings with less stamina. In the spring, emergence in April to early May partially overlaps with the arrival of predatory birds (Chapter 1). Though there are proportionally fewer spring emergent hatchlings, they can move faster and longer, even in the colder temperatures present during the spring (Table 14; Figures 6-9). Though fall hatchlings are lacking in speed and endurance, faster total righting time could benefit these slower individuals by giving them a chance to reach cover from the abundance of predators in their emergent environment. A longer latency time in the spring may allow individuals to remain unnoticed until they are sure it is safe to initiate movement and escape quickly to cover (Table 14). With a lower number of predators in the spring, this could be a beneficial strategy.

Gibbons and Nelson (1978) suggest natural selection may select for delayed emergence where there is high fall emergent mortality and those who wait to emerge in the spring have a higher probability of survival. Baker et al. (2013) also found that emergence strategies often correspond to favorable emergent conditions for the hatchlings. The data from this study suggest that selection in a facultative emergence system may put differing selective pressures on each emergent group. These different selective pressures over time could lead to differing favorable conditions between emergent groups, potentially as a result of disruptive selection. If emergent hatchlings are

selected for within their seasonal environment, this seasonally diverse selective pull could allow for the persistence of a facultative emergent strategy.

Throughout the linear mixed models, temperature explained much of the variation in the data (Table 15). As ectothermic animals, *M. terrapin* at higher temperatures were able to operate faster and longer. The mean performance values for speed and endurance show that at colder temperatures, spring emergent individuals can perform at the same level as fall individuals (Table 14). Because spring emergent hatchlings are facing cooler environmental temperatures than most fall emergent hatchlings, this ability may allow them to survive comparably at a similar level in the cooler, early spring and excel in survival once temperatures increase throughout the season. With a general increase in overwintering *M. terrapin* hatchlings at higher latitudes, this could also allow spring individuals to have a longer active period annually where the preferred temperatures are available for a shorter time than in the southern latitudes. This could benefit spring emergent *M. terrapin* by allowing them to be sufficiently active at lower temperatures, affording them a longer foraging period or enhanced predator avoidance.

As noted, this study is limited to a single nesting season in a single population. There is variation in emergent strategy throughout the terrapin's large distribution with populations in northern latitudes overwintering in larger proportions than the southern populations. Variation could also exist within emergent strategy and should be investigated in other populations. Additionally, it is possible that performance abilities could vary between nesting seasons on Poplar Island, though the association between the 2014 performance and survivorship from 2008 to 2014 suggests that this could be a

reoccurring trend. Investigation into the relationship between survivorship and performance of other turtle species displaying facultative emergence is necessary to determine whether this is a common trend throughout temperate regions.

In conclusion, fall and spring emergent hatchlings differ in performance capabilities. Spring emergent hatchlings are faster and have a higher endurance terrestrially and aquatically. Righting behavior strategies may vary between fall and spring emergent hatchlings, with fall emergent hatchlings displaying a shorter latency time and spring emergent hatchlings waiting longer before righting themselves. On Poplar Island, spring emergent hatchlings have a higher survivorship. The greater aptitude for performance displayed in spring emergent hatchlings corresponds to a higher fitness, allowing for better survival. The difference in seasonal selective pressures and corresponding fitness seen here could allow for the persistence of facultative emergence as a strategy in temperate turtle species.

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