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Eastern Diamondback Rattlesnake (Crotalus adamanteus) Ambush Site Selection in Coastal Saltwater Marshes

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EASTERN DIAMONDBACK RATTLESNAKE (*CROTALUS ADAMANTEUS*) AMBUSH SITE SELECTION IN COASTAL SALTWATER MARSHES

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Approved by
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APPROVAL OF THESIS

We, the faculty supervising the work of Emily Mausteller, affirm that the thesis, *Eastern Diamondback Rattlesnake (Crotalus adamanteus) Ambush Site Selection in Coastal Saltwater Marshes*, meets the high academic standards for original scholarship and creative work established by the Biological Sciences Program and the College of Science. This work also conforms to the editorial standards of our discipline and the Graduate College of Marshall University. With our signatures, we approve the manuscript for publication.

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Ethics Statement

Research was conducted in strict accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the National Institute of Health. I obtained protocol approval (703) from the Marshall University Institutional Animal Care and Use Committee. Isofluorane was used to anesthetize snakes during surgery in accordance with approved procedures. I also obtained South Carolina Department of Natural Resources permit (SC-20-2019).

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The eastern diamondback rattlesnake (*Crotalus adamanteus*; EDB) is a species of conservation concern associated with the imperiled longleaf pine-grassland ecosystem. The longleaf pine ecosystem is characterized by an open canopy and rich ground cover. Researchers have speculated that the vegetation structure of salt marshes may serve as a surrogate habitat for longleaf pine savannas. Although these marshes have little topography, they provide a heterogeneous landscape with patches of mud flats, sandy hard marsh along upper tidal areas, and salt marsh hummocks throughout. I used radio telemetry to monitor free-ranging EDBs on a South Carolina sea island. The goal of my analysis was to examine EDB habitat use within salt marsh habitats. My results indicate that EDBs use marsh edge and hummock habitat-patches when hunting in salt marshes. My study illustrates a potential interaction between EDB habitat use along coastal river ways and extreme tidal inundations that would result in a down-river dispersal pattern. Tidally-biased dispersal may misguide EDB conservation if high EDB densities along coastal islands mischaracterize critical habitat for the species.

INTRODUCTION

The longleaf pine-grassland ecosystem of the southeastern U.S. Coastal Plain once occupied over 30 million ha (Van Lear et al., 2005). However, disruption of historical fire regimes and anthropogenic change have resulted in a rapid decline of this ecosystem (Brockway and Lewis, 1997). Approximately four percent of native open-canopy pine savannas and woodlands remain today, resulting in drastic habitat loss for endemic species such as *Crotalus adamanteus*, the eastern diamondback rattlesnake (EDB) (Gibbons et al., 2000; Van Lear et al., 2005). The EDB is a remnant of the longleaf pine-grassland ecosystem and is of considerable importance for long-term ecosystem resilience of the declining southeast savanna community (Waldron et al., 2008). The longevity (>10 years) and habitat specificity of the eastern diamondback rattlesnake make this species ideal for prioritizing land conservation of the savannas and woodlands of the southeastern coastal plain (Waldron et al., 2008; Waldron et al., 2013).

The EDB is associated with areas of open-canopy savanna habitat dominated by pines and a dense herbaceous understory (Martin and Means, 2000; Fill et al., 2015). However, with improper management of these limited tracts of pine-grassland ecosystems, EDBs have lost vast areas of principal habitat. Consequently, long-term EDB monitoring sites are sporadic and limited. Habitats of similar structure, such as coastal tidewater regions, have been proposed as surrogates for EDBs (Fill et al., 2015). With the loss of principal habitat, EDBs may exploit habitats that meet similar structural and spatial requirements including foraging opportunities, hibernacula, and protection from predation. Salt marsh in coastal tidewater regions may provide similar trophic interactions and vegetation structure as longleaf pine savannas, thereby acting as a surrogate habitat.

Salt marshes along the southeastern coastal plain are areas of high primary productivity. Although these marshes are characteristically of low topography, they provide a heterogeneous landscape with patches of mud flats, sandy hard marsh along upper tidal areas, and salt marsh hummocks (hammocks) throughout. *Spartina (Sporobolus)* dominates patches of mud flats while sea ox-eye (*Borrichia frutescens*) dominates sandy hard marsh areas (Stuckey and Gould, 2000; Lichvar et al., 2016). Salt marsh hummocks are topographic features extending slightly above mean high tide and are characterized by salt-tolerant trees and shrubs. Hummocks likely provide the best EDB ambush locations because these habitat patches are rarely inundated by tidal surges and thus concentrate prey items (Bigler and Jenkins, 1975).

Selection of an appropriate foraging site by EDBs is necessary for survival and reproduction, especially for a sit-and-wait predator (Tsairi and Bouskila, 2004). A successful ambush site is frequently visited by prey, facilitates prey detection and capture, prevents detection of the snake by both prey and predators, and protects the snake from environmental extremes (Shine and Sun, 2002). However, foraging sites are often subject to trade-offs with other needs of the EDB. An ambush predator needs to select sites that provide maximal benefits while sustaining minimal costs (Tsairi and Bouskila, 2004). Hummocks may offer maximal benefits with necessary ambush cover and high prey encounter probability in the absence of native pine savannas.

A potential artifact of EDB salt marsh use is the apparent relationship between EDB densities and coastal areas along tidal river-ways. Extremely high EDB densities have been observed on some coastal islands, despite these islands being characterized by mature, closed-canopy maritime forests that do not provide typical EDB habitat (US FWS, 1999; Hill, 2002). High densities on coastal islands may result from EDB salt marsh use interacting with passive, tidally-biased dispersal (Yacelga et al., 2012). Specifically, EDB use of salt marsh hummocks for ambush site selection allows individuals to capitalize on areas of limited to no human interaction (Stohlgren et al., 2015) with concentrated prey populations (Bigler and Jenkins, 1975). In a coastal area, EDBs may position themselves along the marsh edge to access foraging opportunities in both inland and marsh habitats. During normal tidal cycles, these ambush locations are unaffected by tidal inundation. However, during king tides (perigean spring tide), marsh edge and hummocks can become inundated, thereby acting as a mechanism for EDB dispersal along a coastal gradient. Although able to navigate river-ways during slack tide, a period of little to no current lasting 15-45 minutes, EDBs are not likely to swim freely between marsh edge habitats and hummocks (Tucker et al., 1997; Carbajal-Márquez and Cedeño-Vázquez, 2017). However, if EDBs are simply using river-ways for habitat and prey base, there should be no directional bias along the coastal gradient. Rather, marsh edge and hummock inundation due to extreme high tides likely influences individual movements. Tidal outflow may create a downward gradient toward the ocean and away from historical EDB habitat, resulting in higher densities of EDBs on coastal islands over a period of several years. Thus, prior approaches to studying EDB surrogate habitat based on species density and abundance may hinder conservation efforts if the occurrence of EDBs in maritime forest is an artifact of salt marsh habitat use. There will be severe ramifications for EDB conservation if this density gradient is overlooked. More information is needed in order to understand the mechanism behind passive, tidally-biased dispersal of EDBs.

In this study, I examined coastal saltwater marshes as a potential surrogate habitat for EDBs. Specifically, I identified ambush site locations throughout a heterogeneous island landscape to examine differences in habitat use as a function of behavior. I determined habitat selection by comparing EDB habitat use relative to availability (Johnson, 1980). My objectives were to 1) evaluate the role of marsh as a potential surrogate habitat, 2) quantify EDB habitat use within a salt marsh landscape, and 3) examine salt marsh ambush site selection as a potential contributor of EDB dispersal. I hypothesized that salt marsh hummocks provide an unrivaled foraging opportunity for EDBs compared to other habitats at my study site. I predicted that EDBs would preferentially select marsh edge and hummocks over hard marsh. I also expected tidal flows within coastal rivers and periods of inundation on hummocks to be potential mechanisms for differential habitat use of salt marsh hummocks. The success of this study could improve understanding about interactions between EDBs and salt marshes and how to best guide conservation efforts and designations of critical habitat.

METHODS

Study Species

The EDB is endemic to the imperiled longleaf pine ecosystem of the southeastern Coastal Plain (Martin and Means, 2000; Timmerman and Martin, 2003). The species is dependent on the ecosystem's savanna structure and is considered a remnant of the historical southeastern pine-savanna landscape (Martin and Means, 2000; Waldron et al., 2006, 2008). The EDB occurs in the southeastern Atlantic and Gulf Coastal Plains from southeastern North Carolina through eastern Louisiana, including Florida (Martin and Means, 2000; Timmerman and Martin, 2003). The species faces population declines across its historic range and is a candidate species for protection under the Endangered Species Act (Martin and Means, 2000; US DOI, 2012). Habitat loss, negative human-wildlife interactions, and a lack of public policy regarding species protection have accelerated the EDB's decline (Martin and Means, 2000).

Study Area

I conducted this study on Marine Corps Recruit Depot (MCRD) Parris Island, a sea island in the southeastern coastal plain of South Carolina. I delineated the study area in ArcGIS 10.6 (ESRI, Redlands, CA) as the property boundary, encompassing approximately 3,257 hectares of mixed upland habitats and tidal marsh. The sea island is bordered almost entirely by tidal salt marsh. Approximately 1,325 hectares of Parris Island are dry, upland habitats while the remaining 1,932 hectares are tidal marsh and creeks (Burst, 2008). Habitat types on Parris Island consist of salt marsh, brackish marsh, salt flat, salt shrub thicket, oyster reef, mixed pine-hardwood forest, maritime forest (maritime live oak forest), midden (shell mounds), mud flat/borrow pit, and developed areas (Burst, 2008; Nelson, 1986). I developed a simplified marsh habitat classification in which these habitats were grouped into hard marsh, marsh edge, hummock, and inland communities. I considered salt marsh, brackish marsh, salt flat, and mud flat/borrow pit as hard marsh. I grouped salt shrub thicket, oyster reef, and midden into marsh edge. I identified hummocks using a DEM (Digital Elevation Model). All other habitats including mixed pine-hardwood forest, maritime forest, and developed areas, were considered inland habitat, which was excluded from my final analysis.

Salt marsh, brackish marsh, salt flat, and salt shrub thicket, although distinct communities, intergrade into each other due to the interaction of elevation and tides (Zedler, 1984). Salt marsh consists almost exclusively of smooth cordgrass (*Spartina alterniflora* (*Sporobolus alterniflorus*)) and is inundated by tides twice daily. The high productivity of this community provides the foundation for extensive marine food chains (Burst, 2008). Salt marsh grades into brackish marsh, mud flat, sand flat, and salt shrub thicket communities. Brackish marsh is less frequently inundated by tides than salt marsh and is thus more diverse, consisting of

Spartina patens, *Scirpus* sp., *Elocharis* sp., *Distichlis spicata*, and *Sporobolus virginicus*, among others (Nelson, 1986; Burst, 2008). Mud flats around Parris Island are non-vegetative communities due to their associations with old borrow operations (Burst, 2008). Salt flats are slightly higher in elevation than brackish marsh and mud flats and are often inundated only once per day. Specialized salt-tolerant vegetation such as *Salicornia virginica* and *Batis maritima* are characteristic of this community (Stuckey and Gould, 2000; Burst, 2008). Salt shrub thicket is a narrow, bushy habitat that serves as a transitional zone between lower tidal habitats and maritime forest and is characterized by *Baccharis* sp., *Iva frutescens*, *Borrichia frutescens*, *Morella cerifera*, *Sabal palmetto*, *Juncus roemerianus*, and *Spartina* sp. (Stuckey and Gould, 2000; Burst, 2008). Vegetation in this transitional zone regularly experiences wind shearing, thereby limiting vertical growth (Nelson, 1986).

Parris Island consists of scattered hummocks within the tidal salt marsh ranging from less than one acre to hundreds of acres. These areas are often diverse but vary depending on physical and environmental influences (Nelson, 1986; Whitaker et al., 2004). Hummocks with dune ridges and raised shell mounds may reach 5 m above sea-level (a.s.l.) while others, usually smaller hummocks, may have maximum elevations less than 0.3 m above sea-level (Whitaker et al., 2004). Hummock plant communities are most often variants of maritime forest and are dominated by *Quercus virginiana*, *Pinus elliottii*, *Sabal palmetto*, and *Baccharis* sp. (Nelson, 1986; Zomlefer et al., 2008). The faunal diversity associated with a given hummock may largely be determined by physical and botanical diversity, island size, location, topography, and extent of human impact (Whitaker et al., 2004). As hummock size increases, diversity of habitats, plant communities, and associated fauna generally increase as well (Whitaker et al., 2004). Hummocks of less than one acre are often uniformly low in elevation and may become inundated by salt water during extreme tidal events, thus exhibiting low floral diversity (Whitaker et al., 2004). Hummocks of at least one acre are most often dominated by variants of maritime forest (Whitaker et al., 2004).

Maritime forest on Parris Island ranges from low-diversity forests that border salt shrub thickets and marsh habitats to high-diversity upland forests with some elements of southern mixed hardwood forest (Burst, 2008). Maritime forests are most often dominated by broadleaved evergreen trees and shrubs, species capable of surviving periods of saltwater inundation, salt spray, increased salinity, limited freshwater, soil erosion, and wind damage (Bellis, 1995, Bertness et al., 2002). Species such as *Carya glabra, Pinus glabra, Liquidambar styraciflua, Vaccinium arboreum, Serenoa repens, Prunus serotina, Sabal minor,* and *Callicarpa americana* are characteristic of maritime forest (Nelson, 1986; Burst, 2008). Tree canopies are often stunted by salt spray and the herbaceous layer is sparse and low in diversity (Bellis, 1995). Much of the maritime forest habitat on Parris Island has been disturbed from logging, ditching, and development (Burst, 2008).

The remaining areas of Parris Island are either developed or are mixed pine-hardwood forest. Pine stands were planted in the late 1960s/early 1970s, but due to a lack of early management, they have succeeded to present-day mixed pine-hardwood forests. Today, the mixed pine-hardwood stands consist of predominantly *Pinus elliottii* with mixed *Pinus taeda*, *Quercus* sp. and *Liquidambar styraciflua* (Nelson, 1986; Burst, 2008). There are also various shrub species including *Ilex vomitoria*, *Morella cerifera*, and *Quercus nigra*, which dominate the understory of these stands (Nelson, 1986; Stuckey and Gould, 2000). The herb layer is sparse in areas with a dense shrub layer.

Habitat modifications, both natural and prescribed, have changed the landscape on Parris Island throughout this long-term mark-recapture study. Several major weather events, especially hurricane Matthew (2016) and tropical storm Irma (2017), resulted in downed trees, temporary flooding, and changes in shoreline. The Natural Resources staff of MCRD Parris Island executed several thinning and prescribed burning events before and after these natural occurrences. Prior to the long-term mark-recapture study, sporadic thinning and burning occurred. Mechanical thinning occurred in 2008 and 2011 followed by prescribed burns in 2009 and 2012. In 2013, Natural Resources staff mechanically thinned the same general areas, followed by prescribed burning in 2014 and 2015. Hurricane Matthew and tropical storm Irma initiated further natural habitat modifications. The damage from these storms influenced Natural Resources staff to thin and burn following Matthew and Irma in late 2017 and early 2018. Since this time, no mechanical thinning or prescribed burning has occurred on Parris Island.

Marsh Delineation

I classified habitats within the study area by combining aerial photographs with LiDAR (Light Detection and Ranging) data. I classified habitats into four categories: hard marsh, marsh edge, hummock, and inland (Table 1). I obtained 9-inch resolution imagery from the Beaufort County, SC GIS Department to hand-digitize marsh habitats on Parris Island using Raster Paint in ArcGIS (ESRI, Redlands, CA). I grouped salt marsh, brackish marsh, mud flat, and sand flat communities into my hard marsh classification. Hard marsh encompasses non-vegetated and monocultural cordgrass and rush intertidal zones that experience daily inundation. I considered salt shrub thickets, oyster reef, midden, and maritime forest that bordered the hard marsh as marsh edge. I used the buffer tool in ArcGIS to apply a 10 m buffer around the inland areas of Parris Island to classify marsh edge (Figure 1). Marsh edge exhibits transitional vegetation types that are tolerant to saltwater spray and infrequent inundation. Marsh edge is a gradually sloping ecotone of salt-tolerant shrubs and shrubby trees which may be stunted from salt exposure. I used a digital elevation model (DEM) to classify hard marsh and hummocks, where hummocks were considered as > 0.1 m a.s.l. Hummocks were characterized by small islands slightly above high tide with various types of maritime forest. Hummocks on Parris Island are dominated by terminal-stage succession *Quercus virginiana* forest on older hummocks and by secondary forest succession pine-oak habitat and scrub on smaller, fragmented islands. I considered inland habitat as any of the following areas on Parris Island: maritime forest other than that previously classified as hummock or marsh edge, mixed pine/hardwood forest, longleaf pine savanna restoration forest, freshwater ponds, grassy fields, manicured habitat and anthropogenic areas including training and residential. Inland was excluded from my final marsh habitat analysis. I systematically verified this classification throughout the study area by field visits to the various habitats.

Habitat type	Description
Hard marsh	Low-lying brackish/saltwater tidal wetland typically inundated twice daily; Dominated by non-diverse grasses and rushes.
Marsh edge	Transitional zone (10m) between upland maritime forest and brackish/saltwater tidal wetland; Only flooded during extreme tidal or weather events; Dominated by shrubs, herbaceous vegetation, and some trees.
Hummock	Elevated area (0.1m a.s.l.) within brackish/saltwater wetland rarely inundated by tides; Dominated by variants of maritime forest.
Inland	Other habitats at study site including upland maritime forest, pine/hardwood forest, anthropogenic and manicured areas.

Table 1. Habitat types for eastern diamondback rattlesnake ambush site selection analyses on MCRD Parris Island

Habitat types of Marine Corps Recruit Depot Parris Island were identified and characterized based on 2018 aerial imagery, LiDAR data, ground-truthing, and previous descriptions from land-use surveys.

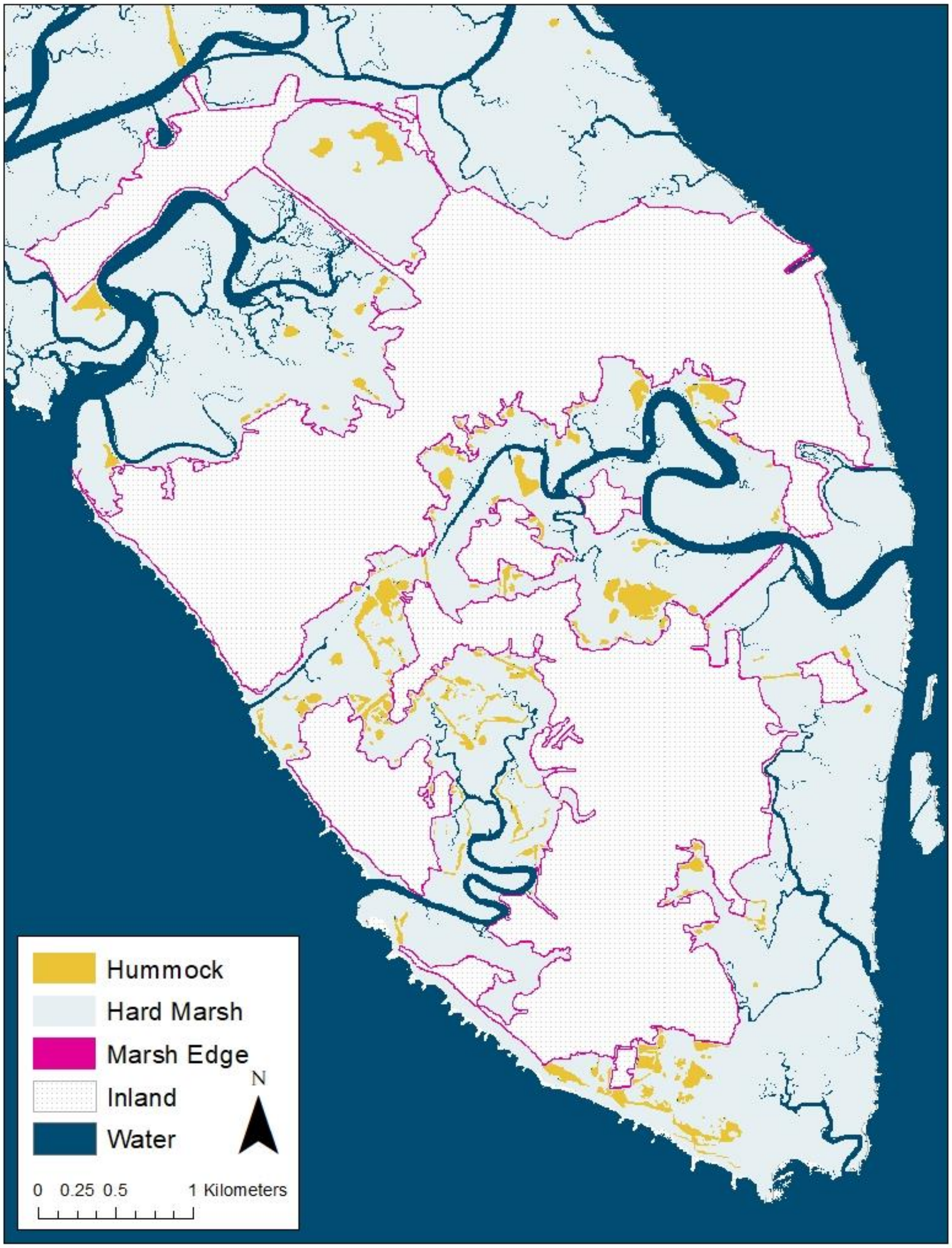

Figure 1. Marine Corps Recruit Depot Parris Island 2018 Habitat Classification

Classified habitats of Marine Corps Recruit Depot Parris Island in 2018. Tidal creeks and open water were not considered as EDB habitat in habitat analysis.

Data Collection

MCRD Parris Island has a healthy population of EDBs which have been observed in a variety of habitats ranging from marsh hummock to developed areas. Rattlesnake monitoring began in 2008 as a long-term mark-recapture study and has since incorporated radio-telemetry to obtain movement, behavioral, and survival data. I monitored 55 adult EDBs (females, $n = 31$; males, $n = 24$) between 2010 and 2020 using mark-recapture surveys and radio-telemetry. I captured rattlesnakes using visual surveys, coverboard sampling, incidentally on roads, wildlife response calls, and while conducting radio-telemetry surveys. I collected morphological data while safely restraining individuals according to methods described by Waldron et al. (2013). I used both external (Model R1640; Advanced Telemetry Systems, Isanti, MN, USA; 2g, 9-11 by 22mm; Pulse rate: 17ppm; Pulse width: 15ms; Battery life: 240 days) and internal (SI-2, Holohil Systems, Carp, ON, Canada; 11g, 40 by 110mm; Pulse rate: 35ppm; Pulse width: 24ms; Battery life: 18 months) radio-transmitters as needed. I attached external transmitters to the rattle of EDBs using the attachment method described by Jungen et al. (2019). Rattlesnakes were surgically implanted with radio transmitters as described by Waldron et al. (2008) with methods adopted from Reinert and Cundall (1982). I monitored individuals from 2 months up to approximately 3 years using a radio receiver (Telonics, Inc., TR-4, Mesa, AZ) and a directional antenna, and thus some individuals required multiple transmitter implantation and removal surgeries or external attachment and removals. I located radio-telemetered individuals two to three times weekly during the active period (mid-March to early November) and weekly or biweekly during the inactive period (November to early March), which included hibernation and emergence. I identified each EDB in the field and recorded location, behavior, and relevant environmental variables at the time of observation using a handheld Global Positioning System

(GPS; Trimble, Sunnyvale, CA) with real-time differential correction and an estimated spatial accuracy < 5 m. Individuals tracked for less than one month were omitted from the final analysis due to limited location and behavioral data.

Statistical Analysis

I evaluated EDB ambush site selection with use versus availability analysis where a "used" observation was defined as an individual in ambush posture. I generated 2 random points for each observed ambush location ($n = 671$; total random points $n = 1342$) within classified habitats but removed any points that fell in open water. I also removed individuals observed in ambush less than 5 times within the study area. The average distance between the paired and random locations was 3.2 km. I spatially assigned habitat variables to areas of known ambush sites and compared with randomly generated points across the landscape (use versus availability), allowing habitat selection to be modeled as ambush-site selection at Johnson's 4^{th} order of habitat selection (Johnson 1980).

I used binomial logistic regression (PROC GLIMMIX) in SAS (SAS Institute, Cary, NC) to compare used versus random locations (use versus availability) where ambush habitat was the predictor variable and use was the response variable. I ran each mixed-model as a logistic regression with the Laplace approximation (Raudenbush et al., 2000), including snake as a random factor to account for a lack of independence among observations from the same individual. I ran two logistic regression models to identify habitat use where hard marsh was the reference habitat and again where hummock was the reference habitat. I examined fit using Pearson's χ^2/df.

RESULTS

Ambush Site Selection

I monitored 55 adult EDBs (females, n = 31; males, n = 24) on MCRD Parris Island from July 2010 to June 2020. I identified ambush locations in hard marsh, marsh edge, and hummock habitats. I observed 106 ambush locations in hard marsh, 329 in marsh edge habitat, and 236 in hummock habitat. The average elevation for hard marsh was 0.58 m ± 0.36 m, for marsh edge was 1.71 m ± 0.71 m, and for hummock was 1.62 m ± 0.43 m. At the habitat-use scale, EDBs preferred marsh edge and hummock compared to hard marsh, and model fit was good (Pearson χ^2/df = 1.00, Table 2). Diamondback rattlesnakes also preferred marsh edge to hummocks and were least likely to use hard marsh, and model fit was good (Pearson χ^2/df = 1.00, Table 3). Odds ratios indicated that EDBs were 2.9 and 2.0 times more likely to use marsh edge and hummocks than hard marsh, respectively (Table 2). Rattlesnakes were also 1.5 times more likely to use marsh edge than hummocks and they were least likely to use hard marsh (Table 3).

Parameter	Estimate	SE	LCL	UCL	P > |t|	Odds
Intercept	-1.3816	0.1086	-1.5994	-1.1638	<0.0001	-
Marsh Edge	1.0728	0.1307	0.8166	1.3291	<0.0001	2.9
Hummock	0.6884	0.1348	0.4241	0.9527	<0.0001	2.0

Table 2. Habitat Use Parameter Estimates for Hard Marsh

Parameter estimates and 95% confidence intervals for EDB marsh habitat use at the home-range scale. Hard marsh was used as a reference habitat category. SE = standard error, LCL = 95% lower confidence limit, UCL = 95% upper confidence limit, Odds = odds of using hard marsh compared to other habitat classes.

Parameter	Estimate	SE	LCL	UCL	P > |t|	Odds
Intercept	-0.6931	0.0797	-0.8530	-0.5333	<0.0001	-
Hard Marsh	-0.6884	0.1348	-0.9527	-0.4241	<0.0001	0.5
Marsh Edge	0.3844	0.1078	0.1729	0.5959	0.0004	1.5

Table 3. Habitat Use Parameter Estimates for Hummocks

Parameter estimates and 95% confidence intervals for EDB marsh habitat use at the home-range scale. Hummock was used as a reference habitat category. SE = standard error, LCL = 95% lower confidence limit, UCL = 95% upper confidence limit, Odds = odds of using hummock compared to other habitat classes.

DISCUSSION

In this study, I observed differential EDB ambush site selection in salt marsh habitats as a behavioral interaction with topography. I expected that EDBs would prefer hummocks and marsh edge habitats due to EDB and prey item associations with longleaf pine savannas. Longleaf pine savannas provide a unique foraging opportunity in that primary productivity is brought to the ground level. Similarly, marsh edge and hummock habitats provide easy ground-level access to food resources for small mammal species. Hummocks likely serve to concentrate these species, creating an unrivaled foraging opportunity for predators (Bigler and Jenkins, 1975; Whitaker et al., 2004). Rattlesnakes were 2.0 times more likely to use hummocks than hard marsh (Table 2) but were 1.5 times more likely to use marsh edge than hummocks for ambush site selection (Table 3). Rattlesnakes were least likely to use hard marsh. My hypothesis that EDBs preferentially select for hummock and marsh edge ambush sites was supported. I expected to see a greater use of marsh edge and hummocks compared to hard marsh due to greater resource availability and similarities in habitat structure to native EDB pine savannas.

Salt marsh has previously been evaluated as a potential surrogate habitat for EDBs due to the structural similarities to longleaf pine savannas, but no significant associations between EDBs and tidal marshes were observed (Fill et al., 2015). Fill et al. examined EDB habitat selection at home range (HR) and within home range (WHR) scales in proposed surrogate habitats including forested areas, wildlife food plots, herbaceous wetlands, woody wetlands, and open water (2015). Fill et al. used canopy cover and ground cover likenesses to pine savannas to evaluate EDB habitat selection in proposed surrogate habitats (2015). Authors identified all habitats at a landscape scale based on National Land Cover Classification categories. Both herbaceous wetlands and woody wetlands categories encompassed marshy areas, brackish impoundments, and areas adjacent to marsh (Fill et al., 2015). This landscape scale analysis was unable to account for the spatial heterogeneity within these areas, especially along tidal gradients. At the HR scale, Fill et al. observed that EDBs exhibited significantly negative associations with all surrogate habitats, including tidal marsh (2015). At the WHR scale EDBs exhibited a negative association with forest but a positive association with ground cover. Fill et al.’s findings suggested that EDBs may use surrogate habitats of similar structure, including marsh, at smaller scales (Fill et al., 2015).

I expanded upon the work of Fill et al. by examining the salt marsh surrogate habitat at a finer scale. Specifically, I divided up the heterogeneous salt marsh landscape into homogeneous patches of hard marsh, hummocks, and marsh edge. Similar to Fill et al., I used the characteristic open canopy and diverse herbaceous understory of pine savannas to evaluate EDB salt marsh use within their home ranges (Johnson, 1980). I evaluated EDB patch use within the salt marsh landscape based on structural and resource similarities to pine savanna. By defining microhabitats within the salt marsh, I identified habitat use at the patch scale. Hard marsh does not offer the same resources or structure as marsh edge and hummocks; thus, these habitats should be considered as different patches within the salt marsh landscape.

I observed a greater use of hummocks than hard marsh habitat, suggesting preferential selection for ambush in these areas. Pine savanna vegetation structure is often similar to that of hummocks in which saltwater spray can limit the growth of tree and shrub species (Whitaker et al., 2004). Hummocks offer high productivity at the ground level, providing protective habitat and foraging opportunities for small mammals. Thus, hummocks likely serve to concentrate EDB prey items and create opportune ambush locations (Bigler and Jenkins, 1975). Hummocks also provide a respite from human encounter for both predator and prey, further facilitating resource production and consumption (Whitaker et al., 2004). I expected to see a greater use of hummocks than hard marsh due to these potential artifacts.

My results indicated EDB ambush site selection was greater on marsh edge than hummocks. Functionally, marsh edge could provide more benefits to EDBs than hummocks. Marsh edge, like hummocks, exhibits primary productivity at the ground-level with stunted overstory canopies due to salt spray (Stuckey and Gould, 2000; Pennings and Moore, 2001; Kunza and Pennings, 2008). As a transitional zone between hard marsh and inland habitats, marsh edge serves as a corridor for EDB movement (Kincaid and Cameron, 1985; Bowne et al., 1999; Micheli and Peterson, 1999). Diamondback rattlesnakes can move between upland shrubby patches for ambush (Platt, 1999, Waldron et al., 2008) or into the marsh toward hummocks using tides to avoid human encounters while maintaining similar foraging and ambush cover opportunities. Both hummocks and marsh edge exemplify characteristics of a surrogate habitat for EDBs in the absence of their native longleaf pine ecosystem.

Hard marsh did not provide the same refugia and foraging opportunities for ambush predators as compared to hummocks and marsh edge. Hard marsh exhibits high salinity and tidal inundation regularly, resulting in extreme environmental fluctuations (US FWS, 1999). Few species can adapt to hard marsh conditions, but some reptiles and mammals are transient inhabitants of salt marsh (Klauber, 1982; US FWS, 1999; Carbajal-Márquez and Cedeño-Vázquez, 2017). Small mammals and primary prey items including cotton rats (*Sigmodon hispidus*) and marsh rice rats (*Oryzomys palustris*) are often semi-aquatic, feeding opportunistically within all salt marsh habitats while nesting in marsh edge and hummocks (Golley et al., 1965; Bigler and Jenkins, 1975; Timmerman, 1995; Cook et al., 2001). Marsh rabbits (*Sylvilagus palustris*), EDB prey associated with marsh and bottomland habitats, also inhabit the transitional marsh zone, feeding on *Sporobolus* sp., *Spartina* sp., and *Borrichia frutescens* (Webster et al., 1985; Forys, 1999). Diamondback rattlesnakes can exploit marsh edge and hummocks for hunting opportunities created by these transient small mammal species. Due to tidal inundation and extreme environmental conditions, however, EDBs likely use hard marsh for migration only (Timmerman, 1995; Carbajal-Márquez and Cedeño-Vázquez, 2017).

Habitat selection is one of the most important drivers of organismal fitness and is essential for ambush predators (Wasko and Sasa, 2012; Avgar et al., 2013; Dickie et al., 2017). Critical EDB habitat resources such as hibernacula and prey items vary on spatial and temporal scales (Glaudas and Rodriguez-Robles, 2011). The EDB has a predictable temporal pattern of behaviors throughout the year, with defined foraging, reproduction, and hibernation seasons (Waldron et al., 2006; Heres et al., 2018). However, influences on spatial patterns are not as well known (Wasko and Sasa, 2012). At the landscape (macrohabitat) level of selection, an EDB will identify a home range and within this home range, select sites for foraging (microhabitat) (Johnson, 1980; Glaudas and Rodriguez-Robles, 2011). Presumably, ambush sites require careful selection of microhabitats to maximize foraging success. These ambush sites are indicative of habitat use at the patch scale where an EDB selects for an increased opportunity of successful prey capture while minimizing predation risk and maintaining appropriate thermal and hydric conditions (Eskew et al., 2009).

Marsh edge and hummocks provide opportunities for foraging as well as protection from predators and harsh conditions. As EDBs select these areas for ambush, extreme tidal fluxes create a mechanism for dispersal along a coastal gradient. King tides and other extreme tidal events may influence EDB movement during slack tides to migrate between mainland areas and coastal islands for new foraging opportunities. Similarly, these tidal influxes may push EDBs out of marsh edge or hummock ambush locations due to inundation. After a slack tide, tidal outflows provide a passive tidally-biased dispersal mechanism along a coastal gradient. This mechanism may likely be the cause of increased EDB densities along the southeastern U.S. coastline, especially on barrier and sea islands.

Constructively, various state and federal mandates, such as the U.S. Environmental Protection Agency's Coastal Zone Management Act of 1972 and the South Carolina Coastal Tidelands and Wetlands Act of 1977, provide beneficial protections of marsh habitat. However, coastal salt marshes face threats from sea-level rise due to global climate change. As a function of climate change and sea-level rise, the rate of high-tide flooding or sunny day flooding has increased (Wdowinski et al., 2016; Sukop et al., 2018). In turn, this could accelerate the passive tidal dispersal mechanism of EDBs along the southeastern coastal gradient. Furthermore, if salt marshes cannot increase in elevation at rates to match sea-level rise, salt marsh ecosystems are in danger of disappearing and with them, critical and surrogate habitats of native species (Crosby et al., 2016; FitzGerald and Hughes, 2019). Under the most optimistic climate change models, 60% of salt marshes will be unable to keep pace with sea-level rise by 2100 (Crosby et al., 2016). Without mitigation efforts, this potential loss could exceed 90%, resulting in substantial ecological, economic, and human health-related consequences (Crosby et al., 2016). Increased inundation frequency will negatively impact the demography of small and isolated wildlife populations as well as their community interactions (Thorne et al., 2012). Although salt marsh edge and hummocks may present an optimal surrogate habitat for EDBs along coastal areas, salt marshes are high-risk zones subject to the increased frequency of extreme weather and impacts of sea-level rise (IPCC, 2007). Ultimately, a combination of increased tidal inundation of surrogate salt marsh habitat and anthropogenic land-use change may result in an accelerated directional dispersal of EDBs along the southeastern coastal gradient.

Habitat loss, particularly of pine savannas, is a dominant factor in EDB decline (Martin and Means, 2000; Waldron et al., 2006; Waldron et al., 2008). As large tracts of southeast pine savanna are limited, endemic species face loss of native habitat. Eastern diamondback rattlesnakes are a species of conservation concern due to their habitat specificity for open-canopy pine-grassland ecosystems. Previous habitat management on MCRD Parris Island as well as extreme weather-influenced habitat changes have opened inland areas to reflect the open canopy and dense understory of longleaf pine savannas. These changes may, over several years, draw EDBs back to inland variants of pine savanna and mixed pine-hardwood forest. Further study of EDB ambush site selection in the presence of habitat management and extreme weather is necessary to quantify pine savanna restoration success when salt marsh is a viable surrogate habitat.

My classification approach supported marsh edge and hummocks as surrogate habitats for tidal-region EDB populations at the patch scale. Structural similarities, resource availability, concentration of prey, and limited human influences on marsh edge and hummocks characterize these salt marsh patches as viable surrogate habitats for EDBs in the absence of pine savanna. Examining the differential habitat use of salt marsh hummocks by EDBs allows us to better approach conservation efforts that may be misled by studies based on species abundance. My study is important for conservation efforts and designating critical habitat for EDBs, a species under review for federal protection (US DOI, 2012). These results demonstrate the utility of patch-scale analyses of surrogate habitat potential that may inform animal conservation and habitat management approaches.

My study adds to previous research that emphasizes the importance of pine savannas for maintaining EDB populations at large scales. However, in the absence of pine savannas, salt marsh edge and hummocks can provide surrogate habitat, offering both refugia and unrivaled foraging opportunities compared to other potential surrogates such as mixed pine-hardwood forest, woody wetlands, or grassland (Fill et al., 2015). Eastern diamondback rattlesnake conservation is fundamentally linked with management and restoration of remnant pine savanna landscapes (Waldron et al., 2008) but may also be linked to the management and preservation of salt marsh habitats. As we continue to lose what we think of as optimal habitat, the importance of surrogate habitat increases disproportionately. However, it is important to recognize the function of critical habitats versus surrogate habitats.

It is crucial to acknowledge the findings of this study when assessing EDB critical habitat. Eastern diamondback rattlesnake use of salt marsh is a function of a passive tidally-biased dispersal mechanism and thus must be considered when designating critical habitat for the declining species. In the coastal tidewater region of South Carolina, remnant longleaf pine plantations lie just upriver from sea and barrier islands within large tidal creeks. These islands are primarily composed of variants of maritime forest, a habitat structure with resources inferior to that of pine savannas. Maritime forest may act as a surrogate habitat in the absence of pine savanna, but it does not act to fill the critical habitat requirements of the endemic rattlesnake species. Use of maritime forest by EDBs is likely an artifact of involuntary tidally-biased migrations while foraging for marsh-based prey items in tidal riverways. Previous studies have examined EDB habitat use on coastal islands, but data are biased due to tidal outflow and the resulting movement of EDBs toward the ocean from inland habitats. If studies only consider the species' abundance and density as a measure of critical habitat, we risk mischaracterizing surrogate habitats for critical habitat. Specifically, if high EDB abundances and densities on coastal islands is an artifact of a passive tidally-biased dispersal mechanism, we run the risk of identifying maritime forest as critical habitat rather than pine savannas. Although EDBs have been observed to use coastal maritime forest habitats, maritime forest does not provide the necessary habitat, food resources, and hibernacula required by EDBs for survival, recruitment, and thriving. Rather, efforts to conserve remaining tracts of longleaf pine savannas are crucial to the persistence of the eastern diamondback rattlesnake.

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APPENDIX A

LETTER FROM IRB

MARSHALL UNIVERSITY.
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Office of Research Integrity

April 24, 2019

Emily Mausteller
5183 Cotton Hill Road
Tillman, SC 29943

Dear Ms. Mausteller:

This letter is in response to the submitted thesis abstract entitled *"Rattlesnake Ambush Site Selection in Coastal South Carolina Salt Water Marshes."* After assessing the abstract it has been deemed not to be human subject research and therefore exempt from oversight of the Marshall University Institutional Review Board (IRB). The Institutional Animal Care and Use Committee (IACUC) has reviewed and approved the study under protocol #703. The applicable human and animal federal regulations have set forth the criteria utilized in making this determination. If there are any changes to the abstract you provided then you would need to resubmit that information to the Office of Research Integrity for review and a determination.

I appreciate your willingness to submit the abstract for determination. Please feel free to contact the Office of Research Integrity if you have any questions regarding future protocols that may require IRB review.

Sincerely,

Bruce F. Day, ThD, CIP
Director

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